

HABITAT ASSOCIATIONS OF CALIFORNIA SPOTTED OWLS IN THE CENTRAL SIERRA NEVADA

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Abstract: Habitat requirements of spotted owls (*Strix occidentalis*) are controversial, particularly with respect to private lands. Therefore, we studied the distribution and roosting and nesting habitat of California spotted owls (*S. o. occidentalis*) throughout a 355-km² study area in the central Sierra Nevada, Eldorado and Placer counties, California, from May to August 1986 and 1987. Fewer ($P \leq 0.001$) owls were detected on private land than expected from its relative land area. Slope; total canopy closure; number of possible nest trees; maximum shrub height; basal areas of old-growth, medium, pole, and live trees; percent ground cover by litter; and small and large dead or dying woody vegetation were different ($P \leq 0.05$) between public and private land. Habitat types of mixed-conifer, large-tree successional stage, with $\geq 70\%$ total canopy closure were most abundant (38.1%) on public land; whereas mixed-conifer, pole-medium successional stage, with $\geq 70\%$ total canopy closure habitat types dominated private land (44.1%). Roost sites occurred in habitats with relatively greater total canopy closure, and basal areas of snags, medium, and old-growth trees than the abundance of habitat (Johnson 1980). Nests of owls occurred in habitats with relatively greater basal areas of live trees, snags, medium, mature, and old-growth trees; and total canopy closure than found in the abundance of habitat. Twenty-six of 29 observed roosts (89.7%) and all 11 owl nests were on public land. Our results provide forest managers with a direction towards appropriate silvicultural and logging practices for the conservation of California spotted owl roost and nest habitats. These include adequate representation of all tree size classes, especially mature and old-growth, combined with essential habitat elements (e.g., nest trees).

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The northern spotted owl (*S. o. caurina*) is strongly associated with old-growth and mature forests in the Pacific Northwest (Forsman et al. 1984, Carey 1985, Solis and Gutiérrez 1990), and is a threatened species because of the impact logging of old-growth forests has had on their populations (U.S.D.I. 1990). Habitat requirements of the California spotted owl in the Sierra Nevada are assumed to be similar to those of northern spotted owls (Laymon 1988). However, California spotted owls also use mid-successional forests to some degree for foraging (Call 1990). Because the habitat requirements of spotted owls are controversial, particularly with respect to private lands (L. L. Irwin, S. Self, and L. Smith, Timber Association of Calif., Sacramento, unpubl. rep.), we studied habitat associations of the California spotted owl in the central Sierra Nevada. Our study objectives were to assess the spatial distribution of California spotted owls on 1 contiguous study area that contained both public (U.S. Dep. of Agric., For. Serv., hereafter referred to as FS) and private land; estimate habitat structure of forests that

occurred within these 2 land ownerships; and compare habitat structure of known owl roost and nest sites with the abundance of habitat (the quantity of that habitat throughout the environment defined independently of the owl [Johnson 1980]).

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STUDY AREA

Our study area was located in the central Sierra Nevada, California, about 50 km northeast of Sacramento, within the boundaries of the Eldorado and Tahoe National Forests, Eldorado and Placer counties (Fig. 1). It encompassed 355 km² and ranged in elevation from 366 to 2,257 m. Public land comprised about 60% of the study area; whereas the remaining 40% was private land (Fig. 1). The area was selected because of a history of spotted owl occupation, previous spotted owl research (Laymon 1985, 1988), and easy access by road.

The major vegetation type of the study area was Sierran Montane Forest (Küchler 1977). Ponderosa pine (*Pinus ponderosa*) dominated xeric sites at elevations from 600 to 1,500 m (Küchler 1977). White fir (*Abies concolor*) was dominant at mesic sites from 1,000 to 1,500 m. Red fir (*A. magnifica*) was dominant above 1,500 m (Rundel et al. 1977). Forests below 1,500 m were generally more diverse floristically and structurally. For example, Pacific dogwood (*Cornus nuttallii*), Douglas-fir (*Pseudotsuga menziesii*), canyon live oak (*Quercus crysolepis*), California black oak (*Q. kelloggii*), and incense cedar (*Calocedrus decurrens*) were common associate species in these forests.

Mean annual precipitation in the study area was 130 cm. Annual temperatures ranged from 2 to 35 C at low elevations and -1 to 32 C at higher elevations (Elford 1974).

METHODS

Spotted Owl Surveys

We surveyed the entire study area between 1 April and 30 August 1986 and 1987 by eliciting responses to imitated spotted owl calls. All areas were surveyed regardless of habitat type, land ownership, or land-use practice. Nocturnal surveys (Forsman 1983) were conducted between dusk and 2400 hours PST. These surveys were used to establish owl presence in an area. Diurnal surveys were then used to locate roosting and nesting owls (Franklin et al. 1990).

During 1986-87, we completed 625 separate spotted owl surveys (624 survey hr). Of these surveys, 153 were diurnal. We also conducted 548 random, diurnal surveys in 1987 (i.e., call surveys were conducted at each randomly sam-

pled vegetation plot, see below) requiring 91 additional survey hours.

We used only diurnal detections for analyses because we were certain of owl locations by direct observation. Nocturnal surveys can attract owls to areas they otherwise might not occupy and bias inferences regarding owl habitat use (J. P. Ward, Humboldt State Univ., Arcata, Calif., pers. commun.).

Spotted owl locations were plotted onto U.S. Geological Survey (GS) topographic maps (1:24,000 scale) and FS Capability Area Maps (Eldorado Natl. For., Placerville, Calif., unpubl. data). The Capability Area Maps represented timber stand classification polygons ≥ 4 ha (U.S. For. Serv., Eldorado Natl. For., Placerville, Calif., unpubl. data). Only public lands were classified by the FS. Timber stand classifications of owl locations on private land were not available.

We used Chi-square analysis (Zar 1984:40-43) to test the frequency difference of owl detections between public and private land. Expected frequencies were proportional to the relative area of public and private land within the study area.

Vegetation Sampling

During 1987, we compared habitat structure among public and private land, and spotted owl roost and nest sites. We used the variable plot-radius method (Mueller-Dombois and Ellenberg 1974:100-105, Dilworth 1981:259-328) with a basal area prism of factor 20 to determine the trees to measure within sample plots. All other habitat measurements were taken within 0.04-ha circular plots (Solis and Gutiérrez 1990). We classified tree size by diameter at breast height (dbh): trees ≥ 90 cm were classified as old-growth; trees 52.5-89.9 cm as mature; trees 27.5-52.4 cm as medium; those 12.5-27.4 cm as pole; and trees 10.0-12.4 cm as saplings. We classified possible nest trees as: any broken top tree with a diameter of ≥ 53 cm at the break with bayonet limbs (i.e., lateral limbs that assume a vertical growth pattern following terminal leader break) or some cover from adjacent trees, any tree tallied with a cavity ≥ 48 cm at the long axis, or any tree tallied with an existing raptor nest.

We used stratified random sampling (Cochran 1977:89) to select public and private land sample plots. The number of plots was proportional to the relative land area of public and private land within the study area. No random

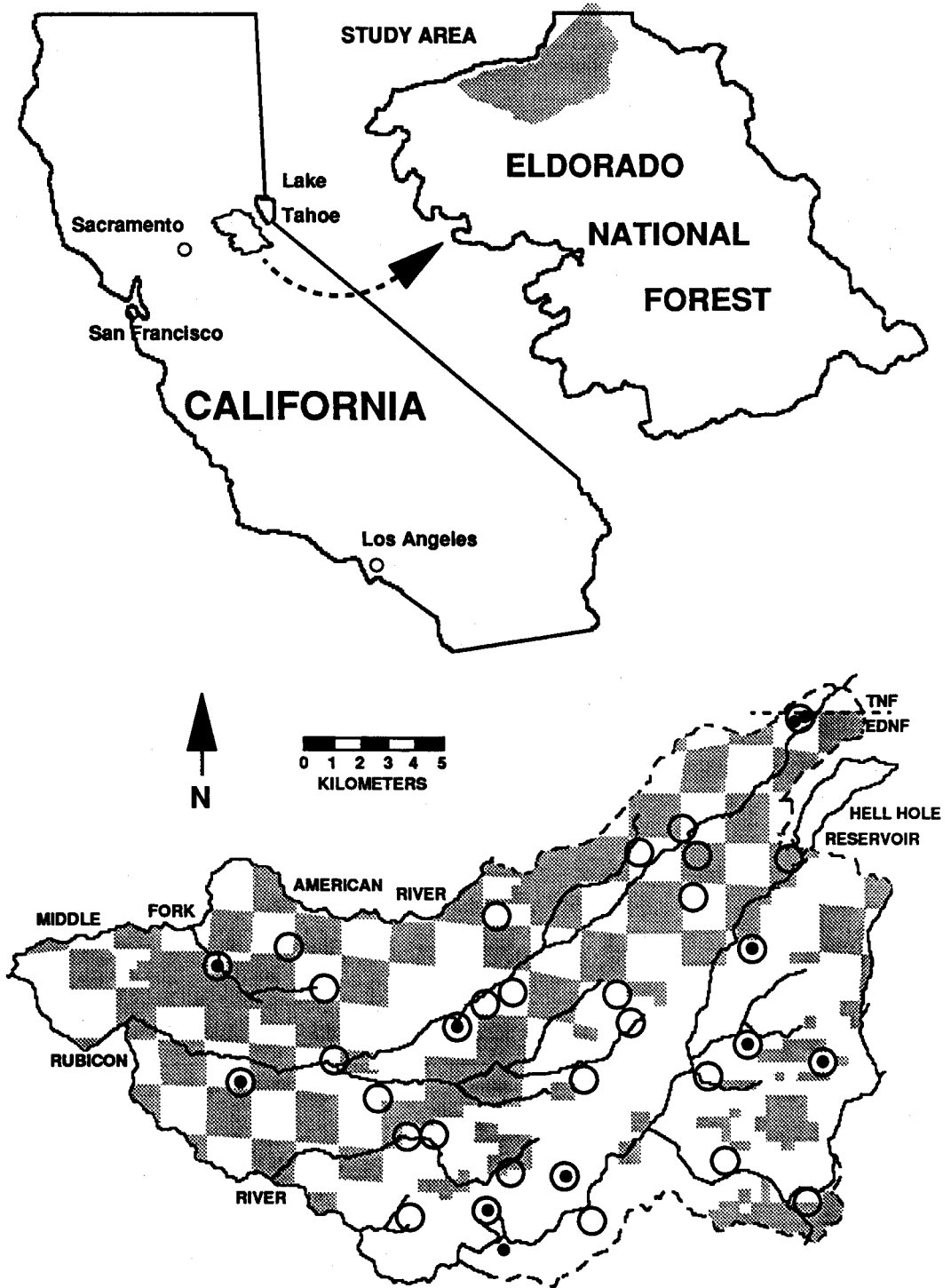


Fig. 1. Location of the study area within the Eldorado (EDNF) and Tahoe (TNF) National Forests, Eldorado and Placer counties, California. Also shown are the locations and distribution of private lands (shaded) as of 1987, and the locations of California spotted owl territories (circles) and nest sites (dots) during 1986-87.

plots ≤ 100 m of a property boundary or ≤ 50 m of a road were sampled.

We also sampled habitat characteristics at all roost and nest locations. Roost plots were centered directly below an owl's observed roost position (Solis and Gutiérrez 1990), and nest trees served as the center of nest site sample plots.

We estimated sample size for random plots using the greatest variance of a habitat variable measured from the first 50 plots (Snedecor and Cochran 1980:441). Enough samples were taken to estimate all vegetation variables within at least 10% of the mean at a 95% confidence level.

Because private land was not typed by timber stand classification on the Capability Area Maps, we classified all plots sampled to 1 of 9 different habitat types. Our habitat types matched the classifications of those on the Capability Area Maps. Habitat types were based on forest cover type, successional stage, and canopy cover class of the sample plot (Eyre 1980, Verner 1980, Verner and Boss 1980:5). Forest cover types were either Sierra Nevada mixed-conifer or oak (Eyre 1980). The mixed-conifer cover type was divided into 4 successional stages defined by the most frequent size class of trees that occurred in the plot: (1) grass-forb stage, defined by the absence of shrubs and trees; (2) shrub-sapling stage; (3) pole-medium stage; and (4) large-tree stage, predominantly mature or old-growth trees. Successional stages 3 and 4 were described further by 3 canopy cover classes: $\leq 39\%$, 40–69%, and $\geq 70\%$. We compared the habitat type of roost and nest sample plots on public lands with the timber stand classification from the Capability Area Maps to assess their accuracy in predicting spotted owl roosting and nesting habitat. We used Chi-square analysis (Zar 1984:62–78) to test the relative frequencies of habitat types between public and private land.

Northern spotted owls often were found near streams or on the lower portions of slopes (Solis and Gutiérrez 1990, Blakesley et al. 1992). Because the land ownership pattern within our study area was a "checkerboard," streams flowed through all ownerships. We evaluated this by randomly selecting 167 of the plots within the study area (100 public land, 67 private land; a 60:40 ratio) and measured the distance to the nearest stream.

Habitat Structure Analyses

We transformed habitat variables by $\log_{10}$ transformations when group variances were

proportional to the means, and used square-root transformations for discrete variables (Sokal and Rohlf 1981:419–423). We used arcsin transformations for percentage variables (Zar 1984:239) to meet the statistical assumptions of normality and homogeneity of variances.

To examine specific habitat structural differences between public and private lands, we used *t*-tests when sample variances were equal and Mann-Whitney tests when sample variances were not equal (Zar 1984:122–144). Further, to examine specific habitat structure differences among public land, private land, and owl roost and nest sites, we used Kruskal-Wallis (KW) 1-way analysis of variance (ANOVA) tests (Hull and Nie 1981:237–238) with protected non-parametric multiple comparisons of means (Zar 1984:199–201). Because ANOVA is very sensitive to unequal sample sizes (Day and Quinn 1989), we selected random subsets of 11 plots each (equal to the number of nest site samples) from the public land, private land, and roost sample plots. We repeated these analyses 20 times using different random subsets. We inferred differences among public land, private land, and roost and nest sites based on the number of significant multiple comparison differences. We used circular statistics (Batschelet 1981, Zar 1984:442–444) to test whether mean slope aspects among public land, private land, and owl roost and nest sites were oriented uniformly.

We used discriminant analysis (Klecka 1975, Huberty 1984) to derive a structural gradient that maximized the difference between habitat structure of public and private land. For highly correlated ($r \geq 0.65$) variables, we omitted one from the pair, retaining the variable that had the greatest among-group variation or was ecologically interpretable (Whitmore 1981, Solis and Gutiérrez 1990). We interpreted the discriminant function by the standardized coefficients and correlations of variables to the discriminant function (Stevens 1986:235–236).

To predict if habitat characteristics of owl roost and nest sites were associated more closely with public or private land we used the classification equation derived from the discriminant analysis. Roost and nest plots were entered into the discriminant model as unknown groups and classified as public or private land based on the discriminant function. We used Box's *M*-Test to examine heterogeneity between group covariance matrices, and if significant, we used

Table 1. Habitat characteristics of public- ($n = 328$) and private-land ($n = 220$) plots sampled in Eldorado and Placer counties, California, 1987.

Variables	Public		Private		Statistics ^a	
	$\bar{x}^b$	SE	$\bar{x}^b$	SE	t	Z
Elevation (m)	1,441.2	14.4	1,481.1	16.1		ns
Slope (%)	32.3	1.1	27.4	1.3	3.08**	
Canopy strata (n)	2.1	<0.1	2.1	<0.1	ns	
Canopy closure (%)	79.2	1.4	74.4	1.7	2.63**	
Possible nest trees (n)	0.2	<0.1	0.1	<0.1		2.08*
Decadence ^c	1.6	<0.1	1.5	0.1		ns
Max. shrub ht (m)	5.1	0.1	4.6	0.1	2.30*	
Min. shrub ht (m)	0.3	<0.1	0.3	<0.1		ns
Tree basal areas (m ² /ha)						
Old-growth ^d	9.8	0.8	4.7	0.5		3.35**
Mature ^d	12.0	0.7	10.7	0.7	ns	
Medium ^d	14.2	0.7	16.9	1.0	2.20*	
Pole ^d	10.2	0.6	9.2	0.8	2.13*	
Sapling ^d	0.9	0.1	0.6	0.1		ns
Live	42.7	1.4	38.2	1.6		2.30*
Conifers	34.1	1.4	31.9	1.5		ns
Hardwoods	8.7	0.7	6.1	0.7	ns	
Snags	4.3	0.3	3.7	0.4	ns	
Ground cover (%)						
Trees <10.0 cm dbh	14.4	0.8	12.4	0.9	ns	
Shrubs	14.2	1.1	14.5	1.3	ns	
Herbaceous	3.9	0.5	5.0	0.7	ns	
Litter	86.9	0.9	81.4	1.4		3.59**
Small dead or dying woody debris (large end 12.5–30.0 cm)	9.0	0.4	11.2	0.8		2.77**
Large dead or dying woody debris (large end >30.0 cm)	2.9	0.3	3.9	0.5		2.04*

^a t -test, 546 df; Mann-Whitney test, Z scores corrected for ties; * = $P \leq 0.05$, ** = $P \leq 0.01$, ns = not significant.^b Mean of plot means.^c Decadence estimated as the mean condition of all trees and snags measured. Condition of trees was based on the numerical classification of Thomas (1979:80).^d Trees measured at all sample plots were classified based on dbh: old-growth = ≥ 90.0 cm; mature = 52.5–89.9 cm; medium = 27.5–52.4 cm; pole = 12.5–27.4 cm; and sapling = 10.0–12.4 cm.

the individual group covariance matrices for classification analyses (Klecka 1975, 1980; Huberty 1984). Further, we tested classification rates to determine if they were significantly different from chance (Huberty 1984, Titus et al. 1984).

Habitat Heterogeneity

We used Landsat Thematic Mapper images to estimate if the interspersions of habitats (Baxter and Wolfe 1972) was the same among public land, private land, and owl nest sites. We transcribed 50 randomly located transect lines (30 north-south, 20 east-west) on GS topographic base maps (scale = 1:63,580) throughout the study area. We measured the length of all transect segments that occurred on public and private land and estimated ground distance. Additionally, 2 1-km (scale-equivalent length) transect lines were transcribed onto the base maps at each nest location. One transect was

oriented north-south, the other east-west, with their mid-points at the nest location. We used a Bausch and Lomb Stereo Zoom Transfer Scope to superimpose each Landsat image on the base maps. We interpreted vegetation changes from the Landsat images based on recognition and identification of image characteristics (i.e., tone, texture, color; Lo 1986:35). We calculated habitat interspersions indices as the number of habitat changes along a segment divided by the scale-equivalent length of that segment. These indices were calculated for each transect segment and each nest-site transect line for the 1986 and 1987 Landsat images. This provided standardized indices (habitat change/km) that were comparable among public land, private land, and nest sites. We used the Mann-Whitney tests to examine differences between sample means (Zar 1984:139–143).

Table 2. Distribution of habitat types among public land, private land, and California spotted owl roost and nest sites sampled in Eldorado and Placer counties, California, 1987.

Plot type	Number of plots (%) by habitat type ^a								
	M4C	M4B	M4A	M3C	M3B	M3A	M2	M1	OAK
Public	125 (38.1)	16 (4.9)	13 (4.0)	108 (32.9)	20 (6.1)	10 (3.0)	3 (0.9)	10 (3.0)	23 (7.0)
Private	48 (21.8)	24 (10.9)	6 (2.7)	97 (44.1)	24 (10.9)	8 (3.6)	5 (2.3)	2 (0.9)	6 (2.7)
Roosts	19 (65.5)			10 (34.5)					
Nests	8 (72.7)	1 (9.1)		2 (18.2)					

^a Classifications of plot habitat types were based on Eyre (1980), Verner (1980), and Verner and Boss (1980:5). Forest cover types, M = mixed-conifer forest, OAK = oak forest; successional stages, 4 = large-tree, dbh ≥ 52.5 cm, 3 = pole-medium, dbh of 12.5–52.4 cm, 2 = shrub-sapling, dbh ≤ 12.4 cm, 1 = grass-forb, no trees; canopy cover classes, A $\leq 39\%$, B = 40–69%, C $\geq 70\%$.

RESULTS

Spotted Owl Surveys

We tallied 240 separate spotted owl detections during all surveys, of which 106 were diurnal. Ninety-five (89.6%) of the diurnal survey owl detections were on public land. Fewer owls were detected on private land than expected for all surveys combined ($\chi^2 = 43.69$, 1 df, $P < 0.001$) and for diurnal surveys only ($\chi^2 = 32.86$, 1 df, $P < 0.001$). The distribution of spotted owls within the study area coincident with public land prompted the major private landowner in the area to conduct independent surveys of their land, and they found no owl nests during 1990 (M. Garcia, Fruit Growers Supply Co., Hilt, Calif., pers. commun.).

Vegetation Sampling

Habitat Characteristics of Public and Private Land.—Percent slope; percent total canopy closure; number of possible nest trees; maximum shrub height; basal areas of old-growth, medium, pole, and total live trees; percent of ground cover by litter, and small (diameter < 30 cm) and large (diameter > 30 cm) dead or dying woody vegetation were different ($P \leq 0.05$) between public and private land (Table 1). Additionally, the frequency of habitat types between public and private land differed ($\chi^2 = 111.42$, 8 df, $P < 0.01$). Mixed-conifer, large-tree successional stage forests, with $\geq 70\%$ total canopy closure were most abundant (38.1%) on public land. In contrast, mixed-conifer, pole-medium successional stage forests, with $\geq 70\%$ total canopy closure were most abundant (44.1%) on private land (Table 2).

Mean aspect of plots on public (mean angle,

$a = 217^\circ$; angular deviation, $s = 77^\circ$) and private land ($a = 253^\circ$, $s = 79^\circ$) differed ($F = 6.69$; 1, 546 df; $P < 0.01$). Mean aspect of plots on public land were different from a uniform distribution ($Z = 2.99$, $P < 0.05$), whereas mean aspect of plots on private were not ($Z = 2.99$, $P > 0.05$). There was no difference in the distance to the nearest stream between public and private land ($t = 1.00$, 165 df, $P = 0.32$).

Habitat Characteristics of Roost and Nest Sites.—Spotted owl roost sites occurred in habitats with relatively greater total canopy closure, and basal areas of snags, medium, and old-growth trees than the abundance of habitat (Table 3). Mean aspect for roost sites ($a = 16^\circ$, $s = 66^\circ$) was northward ($Z = 2.97$, $P < 0.05$). Nineteen of the 29 observed roost sites occurred in mixed-conifer, large-tree successional stage forests, with $\geq 70\%$ total canopy closure; whereas the remaining 10 roost sites were within mixed-conifer, pole-medium successional stage forests, with $\geq 70\%$ total canopy closure (Table 2). However, all roost sample plots contained at least 1 mature or old-growth tree.

Nests of California spotted owls occurred in habitats with relatively greater basal areas of live trees, snags, medium, mature, and old-growth trees; and total canopy closure than the abundance of habitat (Table 3). Mean aspect of nest sites was not different from a uniform distribution ($Z = 0.15$, $P > 0.05$). Eight of the 11 observed nest sites were in mixed-conifer, large-tree successional stage forests, with $\geq 70\%$ total canopy closure, 1 was in mixed-conifer, pole-medium successional stage forest, with 40–69% total canopy closure, and 2 were in mixed-conifer, pole-medium successional stage forest, with $\geq 70\%$ total canopy closure (Table 2). How-

Table 3. Habitat characteristics of California spotted owl roost ($n = 29$) and nest sites ($n = 11$) sampled in Eldorado and Placer counties, California, 1987.

Variables	Roosts		Nests	
	$\bar{x}^a$	SE	$\bar{x}^a$	SE
Elevation (m)	1,390.3	37.6	1,493.5	83.7
Slope (%)	30.7	3.3	26.1	3.7
Canopy strata (n)	2.8	0.1	2.4	0.1
Canopy closure (%)	95.5	0.7	89.3	4.3
Possible nest trees (n)	0.5	0.1	1.3	0.2
Decadence ^b	1.7	0.1	1.9	0.1
Max. shrub ht (m)	6.0	0.4	4.1	0.6
Min. shrub ht (m)	0.4	0.1	0.3	0.0
Tree basal areas (m ² /ha)				
Old-growth ^c	21.8	3.5	25.5	4.5
Mature ^c	19.0	2.4	20.9	3.6
Medium ^c	20.7	2.5	18.8	3.9
Pole ^c	14.6	1.9	3.3	1.5
Sapling ^c	1.1	0.4	1.3	0.6
Live	67.4	4.6	57.6	6.8
Conifers	61.6	5.0	53.8	7.1
Hardwoods	5.9	1.1	3.7	1.5
Snags	10.0	1.6	12.1	1.7
Ground cover (%)				
Trees <10.0 cm dbh	19.1	4.3	10.9	5.3
Shrubs	1.2	0.5	3.5	1.4
Herbaceous	2.1	0.8	5.2	2.2
Litter	90.9	1.1	87.5	3.5
Small dead or dying woody debris (large end 12.5–30.0 cm)	10.1	1.3	12.1	2.1
Large dead or dying woody debris (large end >30.0 cm)	2.6	0.9	2.7	0.7

^a Mean of plot means.^b Decadence estimated as the mean condition of all trees and snags measured. Condition of trees was based on the numerical classification of Thomas (1979:80).^c Trees measured at all sample plots were classified based on dbh: old-growth = ≥ 90.0 cm; mature = 52.5–89.9 cm; medium = 27.5–52.4 cm; pole = 12.5–27.4 cm; and sapling = 10.0–12.4 cm.

ever, all nest sample plots contained at least 1 old-growth tree.

Twenty-six of the 29 roosts (89.7%) and all 11 nests were on public land. Only 13 of 26 (50%) roost and 6 of 11 (54.5%) nest sites were the same timber stand classification on the Capability Area Maps as our observed habitat types. Further, the probability of all 11 nests and 26 of 29 roosts occurring on public land (given a land ownership distribution of 60:40) was 0.04 and 0.004, respectively, indicating that chance alone could not explain roost and nest distributions.

Habitat Structure Analysis.—Number of possible nest trees, basal area of old-growth trees, mean height of old-growth trees, number of possible nests in old-growth trees, and basal area of the snags were different ($P < 0.05$) among public land, private land, and roost and nest sites for all 20 K-W ANOVA repetitions (Appendix 1). Roost and nest sites differed ($P < 0.01$) from

public and private lands, primarily among the old-growth tree related variables (Appendix 1). Nest sites differed ($P < 0.01$) from roost sites only among the pole tree related variables (Appendix 1).

Public-land (group centroid = 0.29) and private-land (group centroid = -0.44) plots were separated (Wilks' Lambda = 0.89, $P < 0.001$) along the discriminant function. Five habitat characteristics discriminated between public and private lands. Four were greater on public land: slope, total canopy closure, old-growth tree basal area, and ground cover by litter. Ground cover by small (<30 cm diameter) dead or dying woody vegetation was greater on private land (Appendix 2).

Sixty-nine percent of the public- and private-land plots were classified correctly, a greater ($Z = 7.16$, $P < 0.01$) percentage than expected by chance. Eighty-two percent of the public-land plots were classified correctly, exceeding ($Z =$

Table 4. Habitat-interspersion indices (index/km) of public and private land, and California spotted owl nest sites in Eldorado and Placer counties, California derived from 1986 and 1987 Landsat images.^a

Sample	1986			1987		1986 and 1987 (combined)		
	<i>n</i> ^b	$\bar{x}$ ^c	SE	$\bar{x}$ ^c	SE	<i>n</i> ^b	$\bar{x}$ ^c	SE
Public	204	4.84	0.14	5.02	0.16	408	4.93	0.11
Private	176	5.16	0.15	4.96	0.19	352	5.06	0.12
Public and private	380	4.99	0.10	4.99	0.12	760	4.99	0.08
Nest sites ^d	26	3.73	0.25	3.96	0.25	52	3.85	0.17

^a Nest site samples for 1987 include 2 nest sites from 1988.

^b Number of transect segments for each sample.

^c Mean habitat interspersion index/km.

^d For the 1986 ($Z = 4.81$), 1987 ($Z = 2.92$), and combined image data ($Z = 4.81$), nest sites had lower ($P \leq 0.01$) indices than public and private land combined.

8.07, $P < 0.01$) the a priori probability of 60% based on relative sample size. Correct classification rate of private-land plots was 50%, also exceeding ($Z = 2.98$, $P < 0.01$) the a priori probability of 40%. A total of 93.1% of roost and 100% of nest sites was classified as public land based on the discriminant function.

Habitat Heterogeneity

Random transect lines included 204 public- and 176 private-land segments (Table 4). Public-land segments totaled 347 km (64%) and private-land segments totaled 192 km (36%), which were about proportional to their relative land area within the study area. Public and private land habitat-interspersion indices did not differ ($P > 0.05$) on either the 1986 or 1987 Landsat images (Table 4). For the combined image data, areas around nest sites had lower indices ($Z = 4.81$; $U = 11,890$; $W = 13,268$; $P < 0.01$) than public and private land combined.

DISCUSSION

Laymon (1988) reported that private lands within and around our study area were heavily logged, typically by "high-grading" for larger trees of certain species, and by "sanitation" logging which also removes dead or dying trees. As a result, younger forests (20–90 yr old) dominated private lands, and more mature forests were most abundant on public land. Our results strongly support Laymon's (1988) observations. Although the forest structure of private land overlapped that of private lands (Appendix 2), the distribution was skewed towards younger forests on private land. Further, habitat structure describing spotted owl roost and nest sites occurred more frequently on public than private land. This also was supported by the significant differences that resulted from the series

of K-W ANOVAs among public land, private land, and owl roost and nest sites (Appendix 1) and the significant differences among habitat types (Table 2). Therefore, we believe that the habitat differences between public and private land were associated with the presence of California spotted owls, and their roost and nest sites.

Habitat characteristics of California spotted owl roost sites were similar to those reported for northern spotted owls (Barrows and Barrows 1978, Forsman et al. 1984, Solis and Gutiérrez 1990), and were within the habitat variable ranges reported by Laymon (1988). However, California spotted owl roost sites had greater total canopy closure ($t = 2.73$, 77 df, $P \leq 0.05$), and less ($P \leq 0.05$) percent ground cover by small trees ($t = 4.18$) and shrubs ($t = 3.30$) than comparable estimates of northern spotted owl roost sites (Solis and Gutiérrez 1990). California spotted owl roost sites occurred more frequently on north-facing slopes, similar to the findings of Solis and Gutiérrez (1990) for northern spotted owls.

Although we found spotted owl roost and nest sites within mixed-conifer, pole-medium successional stage habitat types, residual old-growth trees occurred in such stands. Forsman et al. (1977) also noted the use by northern spotted owls of younger-aged forests that contained residual old-growth trees. Further, habitat attributes at roost and nest sites were similar to old-growth habitats described by others (Franklin et al. 1981, Forsman et al. 1984, Mannan and Meslow 1984). Apparently, old-growth-like forest structure (i.e., not forest or tree ages per se) also was important to California spotted owls.

Our findings that more potential spotted owl nest trees occurred within nest sites than those in the abundance of habitat, supports the work

of Forsman et al. (1984) who reported that the abundance of suitable nest sites influenced northern spotted owls to use old-growth forests for nesting. They also noted that suitable nest sites were uncommon or absent in younger forests. Further, selection of nest sites by California spotted owls may be influenced by the presence of larger, contiguous habitat patches. During our study, habitat-interspersion indices were not different between public and private land (Table 4), indicating that forests on both land ownerships were fragmented. However, habitat-interspersion indices at nest sites were lower than on the remaining public or private land, indicating that nest sites were less fragmented.

The habitats we classified by ground observation at spotted owl roost and nest sites that occurred on public land were not reflected accurately by the FS Capability Area Maps. Tree size of forest stands was the primary discrepancy between our classifications and the timber stand classifications. We think the observed inconsistency resulted from the scale at which the forest stand types were described and the methods used to estimate tree size. The timber stand classification polygons were typed from aerial photographs to a minimum stand size of 4 ha, and tree-crown diameters were used to estimate tree size (Eldorado Natl. For., Placerville, Calif., unpubl. data). Thus, timber stand classification polygons described a larger area than our ground observations. We classified habitat at individual points within a stand and tree sizes were measured directly. Thus, our habitat types described smaller areas that were more site specific. We suggest that small-scale, coarse-grained habitat analyses, such as the FS Capability Area Maps, generally are not suitable for assessing spotted owl roost and nest habitat.

Spotted owls seem to use distinct pockets of habitat that differ in forest structure and type from the surrounding habitat (see also Call 1990). Our results supported Laymon and Reid's (1986) observations on the effect of grid-cell size on predicting owl habitat in the central Sierra Nevada. They noted that the spotted owls used pockets of habitat that ranged from 2 to 7 ha for foraging and that these areas were masked if habitat suitability was assessed on small-scale, 16-ha grids. They concluded that if spotted owl habitat was evaluated at a larger, more fine-grained scale, suitable spotted owl habitat became more evident and that small-scale, coarse-grained evaluation of habitat (i.e., 16 ha) was not adequate because of high stand heterogeneity.

RESEARCH AND MANAGEMENT IMPLICATIONS

The mixed-conifer forests of the Sierra Nevada are among the most heavily harvested forest types (Verner 1980). The complex history of different logging practices and forest use there complicate inferences on the effects of logging on California spotted owl populations. Modern forest-management practices have altered the species composition and structure of the mixed-conifer forests. The most important change has been the substantial reduction of mature and old-growth forest habitats (Verner 1980). Therefore, based on the present distribution and habitat use of California spotted owls, we think that conservative management of suitable and potential spotted owl habitat is imperative to reduce the past and present adverse effects of logging practices on the California spotted owl.

The management strategies used by industrial timber land owners and the FS served as an ad hoc test of the effects of habitat change on California spotted owls in our study area. We also think that forest management practices (i.e., sanitation and high-grade logging) resulted in less roosting and nesting use of private lands in our area. Silvicultural practices that promote structural diversity (e.g., representation of all tree size classes, especially mature and old-growth) in combination with key habitat elements (e.g., nest trees) should be developed and tested. We think our results provide forest managers with a direction for appropriate silvicultural and logging practices for the conservation of California spotted owls on both public and private lands.

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APPENDIX 1. Number of differences ($P \leq 0.05$) of 20 repetitions for Kruskal-Wallis (KW) ANOVAs, and Protected Multiple Comparisons of Means ($P \leq 0.01$) for habitat features among public land (PUB), private land (PVT), and California spotted owl roost (RST) and nest (NST) sites sampled in Eldorado and Placer counties, California, 1987.

Variable	KW ^a	Protected multiple comparisons of means					
		NST vs. RST	NST vs. PUB	NST vs. PVT	RST vs. PUB	RST vs. PVT	PUB vs. PVT
Elevation (m)	1						1
Slope (%)	2				1		
Canopy closure (%)	12					5	
Canopy strata (<i>n</i>)	12				1	2	
Possible nest trees (<i>n</i>)	20		14	16			
Decadence ^b	14		3	3			
Max. shrub ht (m)	4					1	
Old-growth trees ^c							
Basal area (m ² /ha)	20		6	17	2	3	
Mean dbh (cm)	19		9	13	2	2	
Mean ht (m)	20		10	10	3	4	
Mean condition ^b	16		3	4	2	2	
Possible nests	20						
Mature trees ^c							
Basal area (m ² /ha)	12			1	1	1	
Mean dbh (cm)	15		2	6			
Mean ht (m)	11		1	1	4	2	
Mean condition ^b	13		1	3			
Possible nests	2						
Medium trees ^c							
Basal area (m ² /ha)	1						
Mean dbh (cm)	2						
Mean ht (m)	12					1	
Mean condition ^b	3						
Pole trees ^c							
Basal area (m ² /ha)	15	4					
Mean dbh (cm)	11	1					
Mean ht (m)	13	1			1	1	
Mean condition ^b	8	1				2	
Basal areas (m ² /ha)							
Live trees	13				1	6	
Conifer trees	18				3	5	
Hardwood trees	1						
Snags	20		9	11		2	
Ground cover (%)							
Shrubs	14					2	
Herbaceous	1						
Litter	2						
Small dead or dying woody debris (large end 12.5–30.0 cm)	2						
Large dead or dying woody debris (large end >30.0 cm)	1						1

^a Only variables that had ≥ 1 significant KW ANOVA difference are reported.

^b Decadence estimated as the mean condition of all trees and snags measured. Condition of trees was based on the numerical classification of Thomas (1979:80).

^c Trees measured at all sample plots were classified based on dbh: old-growth = ≥ 90.0 cm; mature = 52.5–89.9 cm; medium = 27.5–52.4 cm; pole = 12.5–27.4 cm; and sapling = 10.0–12.4 cm.

APPENDIX 2. Standardized discriminant function coefficients and pooled within-groups correlations between the discriminant functions and the variables entered into the direct discriminant analysis between public- and private-land plots sampled in Eldorado and Placer counties, California, 1987.

Variables	Standardized discriminant function coeff. ^a	Pooled within-groups correlations
Elevation (m)	-0.0180	-0.2359
Slope (%)	0.2647	0.3666
Canopy strata (n)	0.0944	0.0556
Canopy closure (%)	0.3277	0.3131
Possible nest trees (n)	0.2745	0.2459
Max. shrub ht (m)	0.0807	0.2740
Min. shrub ht (m)	-0.0397	-0.0473
Old-growth trees ^b		
Basal area (m ² /ha)	0.4678	0.4026
Possible nests (n)	-0.2180	0.0866
Mature trees ^b		
Basal area (m ² /ha)	0.2502	0.0735
Possible nests (n)	0.0108	0.1314
Medium trees ^b		
Basal area (m ² /ha)	-0.2501	-0.2617
Possible nests (n)	-0.1730	-0.1335
Tree basal areas (m ² /ha)		
Pole ^b	0.4275	0.2540
Sapling ^b	0.1854	0.2093
Conifers	-0.7212	-0.0948
Hardwoods	-0.2831	0.2278
Snags	0.1069	0.1407
Ground cover (%)		
Trees <10.0 cm dbh	-0.0708	0.1593
Shrubs	0.0116	-0.0586
Herbaceous	-0.2341	-0.1864
Litter	0.3342	0.4271
Small dead or dying woody debris (large end 12.5–30.0 cm)	-0.1992	-0.3607
Large dead or dying woody debris (large end >30.0 cm)	-0.0383	-0.2350

^a Absolute values of the coefficients represent the relative contribution of a variable in combination with all other variables to the discriminant function. Signs of the coefficients are arbitrary, however they reflect the direction of the function value from zero.

^b Trees measured at all sample plots were classified based on dbh: old-growth = ≥ 90.0 cm; mature = 52.5–89.9 cm; medium = 27.5–52.4 cm; pole = 12.5–27.4 cm; and sapling = 10.0–12.4 cm.

SITE OCCUPANCY, APPARENT SURVIVAL, AND REPRODUCTION OF CALIFORNIA SPOTTED OWLS IN RELATION TO FOREST STAND CHARACTERISTICS

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Abstract: The California spotted owl (*Strix occidentalis occidentalis*) has been at the center of political and administrative debate due to its association with commercially valuable forest. Several studies have compared the forest cover types used by California spotted owls with the cover types that are generally available, establishing the association between spotted owls and old/large tree components of forests at the landscape scale. We sought a deeper understanding of spotted owl habitat associations in areas in which owls had already selected territories. We mapped and classified vegetation within circular plots (radius 2.4 km) around 67 spotted owl sites in northeastern California, USA. We evaluated the relationships between habitat composition within the different owl sites and variation in (1) nest success (1990–2000) and (2) site occupancy, apparent survival probability, and reproductive output (1993–1998). All analyses included data representing 2 spatial scales: core area (814 ha) and nest area (203 ha). Site occupancy was positively associated with the amount of the nest area dominated by large trees with high canopy cover within the nest area. It was negatively associated with the amount of nonhabitat (nonforested areas and forest cover types not used for nesting or foraging) and with medium-sized trees with high canopy cover. Site occupancy also decreased with time and elevation. Apparent survival probability varied annually and was positively related to the area of each habitat class multiplied by the quotient proportion used/proportion available for each type, at both the nest and core scales. Reproductive output was negatively related to elevation and nonhabitat within the nest area. Nest success was positively associated with the presence of large remnant trees within the nest stand.

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Key words: California spotted owl, demography, forest cover types, habitat associations, nest success, reproduction, site occupancy, *Strix occidentalis occidentalis*, survival.

Administrative policy and political debate has centered on the California spotted owl due to its association with commercially valuable coniferous forest (U.S. Forest Service 1998, 2001, 2004; HFQLG 1998). The U.S. Forest Service sought to balance the demand for timber production in the Sierra Nevada with 2 other priorities: maintenance of habitat for spotted owls and forest carnivores, and reduction of the risk of catastrophic wildfire (U.S. Forest Service 2001, 2004). Despite years of effort devoted to preparing Sierra Nevada Forest Plan Amendments, debate continues regarding the forest conditions required by California spotted owls for survival and reproduction.

The California spotted owl inhabits coniferous and hardwood forests of the southern Cascades, western Sierra Nevada, and central and southern coastal mountains of California (Verner et al. 1992). Its association with old and large trees at the landscape scale is well established: several studies have shown that, throughout the Sierra Nevada, owls select forest stands that are domi-

nated by large trees (>61-cm diameter at breast height [dbh]) and have moderate to high levels of canopy cover ($\geq 40\%$), for foraging (Call et al. 1992, Zabel et al. 1992), nesting, and roosting (Bias and Gutiérrez 1992, Gutiérrez et al. 1992, LaHaye et al. 1997, Moen and Gutiérrez 1997). In addition, owls used forest stands dominated by intermediate-sized trees (30–61-cm dbh) less than the availability of these stands in the landscape. At finer spatial scales, stands used by owls for roosting contained trees >100 cm dbh more frequently than did randomly selected stands (Moen and Gutiérrez 1997).

The studies cited above were important for discriminating the cover types used by owls from cover types generally available across the forest landscape. We sought a deeper understanding of spotted owl habitat associations by modeling spotted owl demographic response variables (site occupancy, apparent survival, reproductive output, and nest success) as a function of forest composition, predicated on owls having selected territories within the landscape. To evaluate these relationships, we used empirical data from

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a long term study of spotted owl demography (Blakesley et al. 2001, Franklin et al. 2004) in conjunction with vegetation maps and ground measurements taken in the immediate vicinity of spotted owl nests.

Our objectives were to determine (1) whether variability in site occupancy, apparent survival probability, or reproduction were related to attributes of forest cover and stand structure in territories of California spotted owls; (2) whether such relationships were stronger at the scale of home-range core areas or at the scale of smaller nest areas; (3) which characterization(s) of high-quality habitat best explained variation in site occupancy, apparent survival probability, and reproduction; and (4) whether forest cover type, nest tree characteristics, and/or local nest stand measures were related to nesting success.

STUDY AREA

Our study area encompassed 2,200 km² of the Lassen National Forest (LNF) and adjacent forested land in northeastern California, USA (40°00'–40°50'N, 120°30'–121°40'W). We studied 1 owl pair in Lassen Volcanic National Park, and several owls on private land managed primarily for timber production. Most forested stands on the study area were classified as white fir-mixed conifer, and were composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), Jeffrey pine (*P. jeffreyi*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), and red fir (*A. magnifica*). The study area is located at the southern end of the Cascade Geographic Province. However, it has been included in the Sierra Nevada Province for spotted owl management purposes (e.g., U.S. Forest Service 2001a), and it is near the northern limit of the distribution of the California spotted owl. Elevations on the study area ranged from 1,200 to 2,100 m.

Timber harvest in the Sierra Nevada has primarily been accomplished through selective thinning. Clearcut areas are uncommon in Sierra Nevada coniferous forests, in contrast to most forests in the range of the northern spotted owl. Forest cover is relatively continuous and there are few high-contrast edges at the landscape scale (Sierra Nevada Ecosystem Project 1996). Therefore, we did not attempt to quantify the spatial distribution of habitat, as was accomplished for 2 studies of northern spotted owl demography in relation to habitat (Franklin et al. 2000, Olson et al. 2004).

METHODS

Owl Data

We collected data on owls during an 11-year demographic study (Blakesley et al. 2001, Franklin et al. 2004), following a standardized field protocol similar to that used in studies of northern spotted owls (Franklin et al. 1996). The protocol was approved by the Colorado State University Animal Care and Use Committee. We located owls during night and daytime surveys and captured, banded, and resighted them to estimate apparent survival probability. Neither home range nor territory boundaries were known. However, because owls were individually identifiable with colored leg bands, we established the locations of owl sites by repeated observations of individuals and owl pairs at nest and roost locations (Hunsaker et al. 2002). We recorded occupancy data for each site in each year and categorized sites as pair, single, or unoccupied after 4 complete surveys of circular plots (2.4-km radius). We determined reproduction for as many sites as possible using standardized field procedures (Blakesley et al. 2001). We defined reproductive output as the number of offspring fledged at a site in a given year (0, 1, 2+), and we recorded zero for sites confirmed to be vacant or occupied by single males.

Vegetation Mapping

Vegetation was mapped within circular plots (2.4-km radius) centered on 67 spotted owl sites in and adjacent to the Almanor Ranger District of the Lassen National Forest. The area mapped contained approximately the western two-thirds of the owl territories in the study area. Homogeneous vegetation polygons were delineated and characterized using color aerial photographs, 2 sets of digital orthophoto quads (1993 and 1998) and timber sale information (Jo Ann Fites-Kaufmann, U.S. Forest Service, personal communication). Separate maps were created for each year from 1993 to 1998. The dominant tree size class, percent canopy cover and large tree density were estimated and assigned to 3–6 categories per variable for each polygon. We followed the standard size class and canopy cover categories used by the U.S. Forest Service for timber mapping (e.g., Verner et al. 1992) in order to make our results compatible with Forest Service methods, policies and land use planning. Size class categories were: zero (no trees), 1 (seedlings; <15-cm diameter at breast height [dbh]), 2 (small trees; 15–29-cm dbh), 3 (medium trees; 30–61-cm dbh), and 4 (large trees; >61-cm dbh). Canopy cover cat-

egories were zero (<10%), S (sparse; 10–25%), P (poor; 25–40%), N (normal; 40–70%), and G (good; >70%). Large tree density categories (number of trees >76-cm dbh per ha) were: zero (<1.2), 1 (1.2–4.9), 2 (4.9–14.8) and 3 (>14.8). Thus, a forest stand dominated by trees from 30 to 61-cm dbh with 50% canopy cover and 2 large trees per ha would be coded as 3N1.

We based our analyses on mapped vegetation polygons within circular plots with radii 0.8 and 1.6 km for 67 spotted owl sites. We selected 1 center for each site, defined by nest trees whenever possible ($n = 48$), and by areas of repeated roosting otherwise ($n = 19$). Specifically, selection of site centers followed this hierarchical process: we identified the Universal Transverse Mercator (UTM) coordinates of (1) the most frequently used nest; (2) if there was a tie, the most recently used nest; (3) if no nest was known, the most recent location of young juvenile owls; (4) if no juvenile location was known, the most recent pair roost location; and (5) if no pair was known, the most recent owl roost location. The coordinates of all nest trees were located with a Global Positioning System. Coordinates of roost locations were estimated in the field using 1:24,000 topographical maps and altimeters. We selected the larger plot size (814 ha; radius 1.6 km) based on the estimated size of spotted owl breeding season core areas in the LNF (Bingham and Noon 1996). Core areas were empirically estimated regions within the home range that received concentrated use. These core areas overlapped for several adjacent owl pairs, so we used approximately half the minimum distance between nest sites of adjacent pairs to define the radius of the smaller plot (0.8 km; area 203 ha), to represent the area assumed to be used exclusively by 1 pair, hereafter referred to as the nest area.

Combinations of the 3 vegetation measures resulted in 36 different polygon classifications within the core areas ($\bar{x} = 17/\text{site}$, range = 9–26). To reduce the number of explanatory variables in modeling site occupancy, apparent survival probability and reproductive output, we created habitat classes by grouping cover types based on current knowledge of spotted owl ecology (Table 1). We defined the category SELECT as cover types used by California spotted owls for nesting in greater proportions than were available in the landscape (Verner et al. 1992). We defined OTHER as cover types used for nesting by spotted owls proportionately less than available in the landscape (Verner et al. 1992). We created additional categories of SELECT and OTHER as areas with canopy cover >70% (CCG), presence of remnant trees (REM), or both (CCGREM; see Table 1). We calculated the variable NESTUSE by weighting all of the cover types used for nesting by the quotient proportion used/proportion available for each type (based on Verner et al. 1992). The final habitat class variable was NON, which represented the amount of nonforested land as well as forested stands not used by California spotted owls for nesting (dominated by small trees and/or low canopy cover; Verner et al. 1992).

We hypothesized that habitat classes selected by owls for nesting (SELECT, SELCCG, SELREM, SELCCGREM, NESTUSE) would be positively associated with spotted owl reproductive output and apparent survival probability. These competing variables may be considered alternative models of high-quality spotted owl habitat, and we designed our model sets to elucidate which characteristics of forest stands (dominant tree size, canopy cover, presence of large remnant trees) were most important for explaining variation in spotted owl demographic rates. We expected NON to be negatively

Table 1. Habitat classes used for modeling site occupancy, probability of apparent survival, and reproductive output of California spotted owls in northeastern California, USA.

Habitat class	Definition	Cover types
SELECT	Large trees with normal to good canopy cover	4N0 4N1 4N2 4G0 4G1 4G2 4G3
SELCCG	Canopy cover good	4G0 4G1 4G2 4G3
SELREM	Remnant trees present	4N1 4N2 4G1 4G2 4G3
SELCCGREM	Canopy cover good and remnant trees present	4G1 4G2 4G3
OTHER	Large trees with poor canopy cover; medium trees with poor to good canopy cover; small trees with good canopy cover	2G0 2G1 3P0 3P1 3P3 3N0 3N1 3N2 3G0 3G1 3G2 4P0 4P1 4P2
OTHCCG	Canopy cover good	2G0 2G1 3G0 3G1 3G2
OTHREM	Remnant trees present	2G1 3P1 3P3 3N1 3N2 3G1 3G2 4P1 4P2
OTHCCGREM	Canopy cover good and remnant trees present	2G1 3G1 3G2
NESTUSE	Medium and large cover types used for nesting, weighted by proportion used/proportion available.	$0.65*(2G) + 0.29*(3P) + 1.19*(3N + 3G) + 0.48*(4P) + 2.26*(4N + 4G)$
NON	Nonforested area or small trees	All size zero and 1; 2S 2P 2N 3S 4S

associated with spotted owl reproductive output and apparent survival probability.

We had no a priori basis for predicting the effects of habitat classes that were used by owls for nesting but not selected at the landscape scale (OTHER, OTHCCG, OTHREM, or OTHCCGREM) on either reproductive output or apparent survival probability. However, we hypothesized that selected habitat classes with canopy cover >70% and/or large remnant trees present (SELCCG, SELREM, or SELCCGREM) could exhibit stronger positive relationships with owl life history traits when combined with nonselected habitat classes having canopy cover >70% and/or large remnant trees present (SELCCG + OTHCCG, SELREM + OTHREM, or SELCCGREM + OTHCCGREM, respectively).

Nest Stand Measurements

We measured physiographic and vegetation characteristics immediately surrounding owl nest trees at 132 nests in 64 owl territories throughout the area of the demographic study. We established sampling strip plots 10 m in width, beginning 5 m from the nest tree and extending 30 m in each of the 4 cardinal directions. We measured dbh and height of all trees ≥ 40 cm dbh, all snags ≥ 12 cm dbh, and all logs ≥ 25 cm diameter within the entire plots. We measured dbh and height of trees <40 cm dbh in the central third of each plot and estimated canopy cover 10 m and 25 m from the nest tree in each of the 4 cardinal directions using a spherical densiometer. In addition, we recorded nest type (top cavity, side cavity, platform); species, dbh, and height of the nest tree; nest height; tree condition (live tree or snag); slope; aspect; and elevation. We used the vegetation polygon layer in a Geographic Information System (GIS) to determine the habitat class of stands containing owl nests.

Data Analysis

Site Occupancy.—We modeled site occupancy, O , as a function of habitat class in logistic regression with an ordered multinomial response: no owls (zero), single owl (1), owl pair (2), $n = 273$, using PROC LOGISTIC in the program SAS (SAS Institute 2000). As we had noticed a decline in site occupancy over time on the study area, we modeled year as a linear trend (T) as well as a categorical variable (t), and a constant (no year effect). In addition to the a priori models, we ran single habitat class covariate models containing SELCCG, SELREM and SELCCGREM, and a set of post hoc models that added the variable NON to the original models. We ran the habitat class models at 2

spatial scales (core and nest) in combinations with and without elevation, with and without T, and with and without NON, yielding 214 models.

We used Akaike's Information Criterion, corrected for small sample size (AIC_c), for model selection. Akaike weights, w_i , estimate the relative predictive strength of each model and may be viewed as the weight of evidence for model i (Burnham and Anderson 2002:75–77). Evidence ratios, w_i/w_k , express the relative likelihood of model i vs. model k (Anderson and Burnham 2002). Because the same variable may appear in several competing models, we estimated the relative importance of each variable by calculating the cumulative Akaike weights, $w_+(j)$, where $w_+(j)$ is the sum of w_i across all models in the set in which variable j occurred (Burnham and Anderson 2002:77–79).

For logistic regression, the maximum of $R^2 < 1$. Therefore, we measured the proportion of variance explained by a model using $\bar{R}^2$, the maximum-rescaled R^2 , where $\bar{R}^2 = R^2/\max(R^2)$ (Nagelkerke 1991).

Apparent Survival.—We used a subset of the owl capture history data from the demographic study, which contained records of adult and subadult owls found at the 67 sites for which vegetation mapping was completed. For owls that moved between sites, we split capture histories so that the relevant portion of each history was associated with the corresponding vegetation data ($n = 231$ capture histories from 203 individual owls at 67 sites). For owls that moved from 1 site to another, we did not record “loss on capture” at the initial site. Consequently, our estimate of apparent survival probability, $\hat{\phi}$, was negatively biased. The purpose of our analysis, however, was to determine which habitat classes were positively or negatively associated with persistence at a site and not to estimate apparent survival probabilities per se. Thus, an owl's dispersal from a given site reflected negatively on the habitat class composition of that site.

We used the program RELEASE (Burnham et al. 1987:77) to evaluate goodness-of-fit of the data set to open population mark–recapture models. We used maximum likelihood methods, based on an a priori set of product-multinomial models (Lebreton et al. 1992) to estimate apparent survival probabilities. We modeled the effects of vegetation covariates on apparent survival probabilities using a linear model framework with logit link functions. We used program MARK (White and Burnham 1999) to obtain maximum likelihood estimates and AIC_c for model selection.

We initially modeled time and sex effects without habitat class covariates to determine the underlying structure of subsequent models. Only 1 set of habitat class covariates may be included per individual capture history; i.e., we could not incorporate changes in habitat over time in our analysis. Therefore, we used mean amounts of habitat classes at a site as the vector of habitat class covariates for all owls at that site. The candidate set of a priori models of apparent survival included time and sex effects and the habitat classes described above.

We estimated variance components using MARK (White and Burnham 1999) to assess how much process variance existed in the capture history data (Franklin et al. 2000). We ranked each owl site according to its overall reproductive output, and then grouped the sites into 7 ranked categories ($n = 8\text{--}11$ sites/group, 63 sites total) and estimated the apparent survival probability for owls in each group. This is similar to evaluating temporal variation, using "site quality" groups rather than year. The justification for these groupings was that a previous analysis indicated that fecundity and apparent survival probability were positively related on the Lassen study area (Blakesley 2003).

Reproduction.—We modeled reproduction, R , as a function of habitat classes using binomial logistic regression (no juveniles produced, including no breeding attempt and breeding failure [zero], 1–3 juveniles produced [1]), using PROC LOGISTIC in SAS (SAS Institute 2000). We used records for adult females only because subadult female spotted owls have much lower fecundity than do adult females (Blakesley et al. 2001). We used AIC_c for model selection and estimated $\bar{R}^2$ for the best model. We included year in all models because of the high annual variability in reproduction in the population (Blakesley et al. 2001). After running all a priori models with year and habitat class covariates, we re-ran the models including elevation. In all cases, models with elevation had lower AIC_c than models without elevation. Therefore, we eliminated all models without elevation.

Nest Success.—A large sample of nest tree and nest stand measurements was available from throughout the study area, with corresponding nest success data from 1990 to 2000 ($n = 174$ reproductive outcomes). Habitat class data were available for most of these records ($n = 122$ reproductive outcomes; 89 successes, 33 failures). Although other analyses were restricted to 1993–1998 because of limited availability of annual vegetation maps, we included all years in our analysis because nest stands were rarely affected by timber harvest

between 1990–1993 and 1998–2000 (J. Blakesley, Colorado State University, personal observation). Nest stands that were harvested after the nest was used and before the area was mapped ($n = 2$) were eliminated from the data set.

We used logistic regression with PROC LOGISTIC in SAS (SAS Institute 2000) to model nest success, S , as a function of nest tree and nest stand characteristics, habitat class of the nest stand, and year, and we used $QAIC_c$ for model selection (AIC_c corrected for overdispersion [lack of independence] in the data). We also created 3 variables for our analysis by breaking the cover type codes down into the variables SizeClass, CoverClass, and Remnant (binary). We hypothesized that nest success would be affected by the interaction between dominant size class and remnant trees within the nest stand, with remnants being more important in size class 3 than in size class 4 stands.

RESULTS

Landscape Composition

Seventy percent of the total mapped area, 78% of the owl core areas and 83% of nest areas were composed of forested stands dominated by trees ≥ 30 cm dbh (size class 3 or larger) with $\geq 40\%$ canopy cover (codes N and G). The values of NESTUSE, SELECT, SELCCG, SELREM, SELCCGREM, and OTHCCG (3G0, 3G1, and 3G2) all increased as the scale of analysis around site centers decreased. In contrast, the percent composition of OTHER decreased with decreasing area around site centers (despite OTHCCG being higher). The following cover types each comprised $<1\%$ of the total mapped area: 3P1, 3P2, 3P3, 4P0, 4P1, 4P2, 3N2, 3G2, 4G3.

Variation in all cover types and habitat classes among sites was 14–126% greater within nest areas than within core areas. There was generally more variation among sites in the original cover types than in the aggregated habitat classes. For example, within nest areas, the coefficient of variation (CV) for cover types 4G0, 4G1, and 4G2–3 were 2.26, 1.47, and 1.75, respectively, whereas the CV for habitat class SELCCG (comprised of 4G0, 4G1, 4G2–3) was 0.88. Several habitat classes were strongly correlated with each other (Blakesley 2003); notably SELECT and OTHER ($r = 0.90$), NESTUSE and SELECT ($r = 0.88$), and NESTUSE and OTHER ($r = -0.62$).

Fifty-six percent of spotted owl nesting occurred in stands dominated by large trees (cover types 4G0, 4G1, 4G2, 4G3), even though these stands

comprised only 16% of the mapped area (Fig. 1). No nests occurred in stands dominated by small trees (size classes 0, 1, 2), nor were any nests in stands dominated by medium or large trees with poor canopy cover (cover types 3S, 3P, 4S, 4P). Stands dominated by medium trees with normal canopy cover (cover types 3N0, 3N1, 3N2) comprised 24% of the mapped area, yet contained only 9% of all nesting attempts. Stands dominated by medium sized trees with good canopy cover and large remnant trees

<1.2/ha (cover type 3G0) were used for nesting in proportion to availability within the mapped area (12%), whereas similar stands with remnant trees ≥ 1.2 /ha (cover types 3G1 and 3G2) comprised 6% of the area and contained 14% of nesting attempts.

Only 4 of 92 nest trees (representing 5 of 138 nesting attempts) were <76 cm dbh, the size of remnant trees identified in air photos. However, 20 nest trees (representing 30 nesting attempts) were within stands classified as having <1.2 remnant trees/ha (cover types 3N0 and 3G0). Therefore, many of the large nest trees occurred at densities <1.2/ha within their respective forest stands.

Timber harvest occurred within 18 nest areas and 37 core areas from 1993 to 1997. Within sites subject to timber harvest, total harvest ranged from <1–60% of nest areas ($\bar{x}$ = 10%) and <1–48% of core areas ($\bar{x}$ = 4%).

Site Occupancy

All competitive models of site occupancy ($\Delta AIC_c < 5$) included a declining trend in occupancy over time (T); in the best model (lowest AIC_c), $\beta(T) = -0.33$, SE (β) = 0.10. When nest and core area models were considered together, the combined Akaike weight of core area models was <1% (Table 2). The best model revealed that the amount of nest area dominated by large trees and canopy cover >70% was positively associated with site occupancy ($\beta[\text{SELCCG}] = 0.0044$, SE (β) = 0.0019), whereas the amount of nest area dominated by medium-sized trees with canopy cover

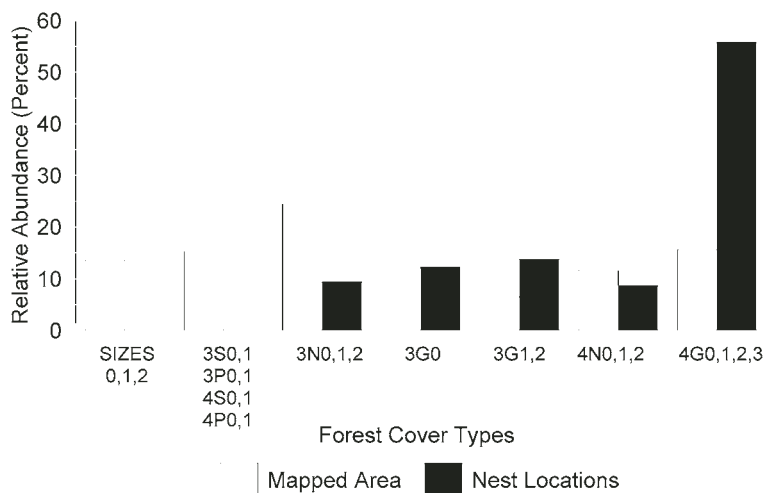


Fig. 1. Relative abundance (percent) of different cover types within circular plots (radius 2.4 km) around 67 California spotted owl site centers in northeastern California, USA, and relative abundance (percent) of nesting attempts ($n = 138$) within cover types. Cover type codes are described in text.

>70% and the amount of area unforested or dominated by small trees were negatively associated with site occupancy ($\beta[\text{OTHCCG}] = -0.0038$, SE (β) = 0.0015; $\beta[\text{NON}] = -0.0094$, SE (β) = 0.0044). Adjusted R^2 of the highest ranked model = 0.18. Cumulative Akaike weights of all site occupancy models (Table 3) indicated that elevation was also an important explanatory variable and was negatively related to site occupancy (in the best model that included elevation, $\beta[\text{ELEV}] = -0.00044$, SE (β) = 0.00033).

Apparent Survival

Results from program RELEASE indicated that the capture history data fit the assumptions of open population mark-recapture models. The structure of the data before adding covariates included an effect of year on apparent survival probability and an effect of sex on recapture probability (model $\phi[t] p[g]$). The 4 top-ranked models indicated that apparent survival increased with greater amounts of habitat classes selected by the owls at the landscape scale and in stands dominated by large trees with normal to good canopy cover containing large remnant trees (best model: $\beta[\text{NESTUSE}] = 0.242$, SE (β) = 0.141; best model containing SELREM: $\beta[\text{SELREM}] = 0.242$, SE (β) = 0.141; Tables 3, 4). Although the remaining models with 1 habitat class covariate all explained more variation in apparent survival probability than did the model $\{\phi(t) p(g)\}$, (i.e. they had lower deviance than the base model), the increase in number of parameters resulted in

Table 2. Models of site occupancy (O) including habitat class covariates for California spotted owls in northeastern California, USA, 1993–1998 ($n = 273$). Models are ordered by AIC_c . Habitat classes are defined in Table 1.

Model ^a	log(L)	K	AIC_c	ΔAIC_c	w_i
O (T + SELCCG + OTHCCG + NON)	–160.98	6	334.28	0.00	0.19
O (T + Elev + SELCCG + OTHCCG + NON)	–160.13	7	334.68	0.40	0.16
O (T + Elev + SELCCGREG + OTHCCGREG + NON)	–160.57	7	335.56	1.29	0.10
O (T + Elev + SELCCGREG + OTHCCGREG)	–161.74	6	335.79	1.52	0.09
O (T + SELCCG + OTHCCG)	–163.30	5	336.82	2.55	0.05
O (T + Elev + SELCCG + OTHCCG)	–162.44	6	337.19	2.91	0.05

^a Models shown had Akaike weights (w_i) > 0.05 and were all for habitat classes within nest areas.

higher AIC_c values, and therefore we did not consider these models to be parsimonious.

The CV of process variation = 0.049, which suggests there was not much process variation to be explained by any variable. Reproductive rank for female owls (higher number = lower reproductive output) was related to apparent survival: $\beta = -0.488$, SE (β) = 0.157.

Reproduction

Successful nests in 1993–1998 produced 1 or 2 fledglings with 1 exception: 1 nest produced 3 fledglings in 1998. Subadult (1- and 2-year-old) female spotted owls had lower reproductive rates than did adult females (Blakesley et al. 2001) and exhibited higher rates of breeding dispersal (Blakesley 2006). Because our sample size of subadult owls was small, we excluded subadults from analyses. Not all territories were sampled every year ($n = 258$ records from 63 mapped sites, 1993–1998).

Reproductive output varied by year, was lower at higher-elevation sites, and decreased as the amount of nest area that was unforested or dominated by small trees increased (best model: $\beta[\text{ELEV}] = -0.00078$, SE [β] = 0.00035; $\beta[\text{NON}] =$

-0.0080 , SE [β] = 0.0053; Tables 3, 5). Although many other models with habitat class covariates explained some variation in reproduction, they were less parsimonious than the second best model, which only contained year and elevation covariates.

Nest Stand Composition

Spotted owl nests occurred primarily in cavities of large live pines and firs (Table 6). Mean canopy cover in the immediate vicinity of the nest was virtually always >80%. Nest tree dbh ranged from 38–219 cm; however, 90% of nest trees were ≥ 76 cm dbh. The number of hardwood stems was highly variable because very few sites contained a measurable hardwood understory. Among the continuous nest site variables measured, the only strong correlation (>0.50) was between the 2 canopy cover measures (Blakesley 2003).

Nest Success

Nest success was higher when large remnant trees were present in the nest stand (best model: $\beta[\text{REMNANT } 0] = -0.826$, SE [β] = 0.247), and higher in size class 3 than size class 4 stands ($\beta[\text{SIZE CLASS } 3] = 0.636$, SE [β] = 0.266; Table 7).

Table 3. Cumulative Akaike weights (w_+) of covariates in models of site occupancy, apparent survival probability, and reproductive output for California spotted owls in northeastern California, USA, 1993–1998 ($n = 273$). Habitat classes are defined in Table 1.

Covariate ^a	Site occupancy		Apparent survival		Reproductive output	
	w_+	sign of $\hat{\beta}$	w_+	sign of $\hat{\beta}$	w_+	sign of $\hat{\beta}$
SELECT	0.10	Positive	0.11	Positive	0.28	Positive
SELCCG	0.55	Positive	0.10	Positive	–	–
SELREM	–	–	0.17	Positive	0.13	Positive
SELCCGREG	0.31	Positive	0.12	Positive	–	–
OTHER	–	–	0.06	Negative	–	–
OTHCCG	0.50	Negative	–	–	–	–
OTHCCGREG	0.32	Negative	–	–	–	–
NESTUSE	–	–	0.24	Positive	0.23	Positive
NON	0.67	Negative	0.08	Negative	0.47	Negative
Elevation	0.58	Negative	0.04	Negative	0.46	Negative
Year	–	–	1.00	–	–	–
T (time trend)	0.99	Negative	–	–	–	–

^a Covariates with Akaike weights (w_+) < 0.05 are not shown.

Table 4. Models of apparent survival probability (ϕ) including habitat class covariates for California spotted owls in northeastern California, USA, 1993–1999 ($n = 136$). All models included effects of sex on probability of recapture. Models are ordered by AIC_c . Habitat classes are defined in Table 1.

Model ^a	Area	log(L)	<i>K</i>	AIC_c	ΔAIC_c	w_i
ϕ (Year + NESTUSE)	Nest	−196.22	9	411.00	0.00	0.13
ϕ (Year + NESTUSE)	Core	−196.46	9	411.48	0.48	0.10
ϕ (Year + SELREM)	Nest	−196.68	9	411.93	0.93	0.08
ϕ (Year + SELREM)	Core	−196.68	9	411.93	0.93	0.08
ϕ (Year)		−197.75	8	411.95	0.95	0.08
ϕ (Year + SELCCGREGM)	Core	−197.03	9	412.63	1.62	0.06
ϕ (Year + SELCCGREGM)	Nest	−197.03	9	412.63	1.63	0.06
ϕ (Year + SELCCG)	Core	−197.06	9	412.69	1.69	0.06
ϕ (Year + SELECT)	Core	−197.07	9	412.71	1.71	0.06
ϕ (Year + SELECT)	Nest	−197.15	9	412.88	1.88	0.05
ϕ (Year + SELCCG)	Nest	−197.24	9	413.06	2.06	0.05
ϕ (Year + NON)	Nest	−197.29	9	413.15	2.15	0.05

^a Models shown had Akaike weights (w_i) > 0.05.

Table 5. Models of annual reproductive output (*R*) of California spotted owls in northeastern California, USA, 1993–1998 ($n = 258$). Models are ordered by AIC_c . Adjusted R^2 of the highest ranked model = 0.25. Models shown had Akaike weights (w_i) > 0.05.

Model ^a	Area	log(L)	<i>K</i>	AIC_c	ΔAIC_c	w_i
<i>R</i> (Year + Elev + NON)	Nest	−114.55	8	245.67	0.00	0.11
<i>R</i> (Year + Elev)		−115.74	7	245.93	0.26	0.09
<i>R</i> (Year + Elev + NESTUSE)	Nest	−115.27	8	247.13	1.46	0.05
<i>R</i> (Year + Elev + SELREM)	Nest	−115.39	8	247.37	1.70	0.05

^a Habitat classes are defined in Table 1.

Table 6. Nest tree and nest stand structural variables around California spotted owl nest trees in northeastern California, USA, 1990–2000.

Code	Definition	Unique nests ($n = 132$)		Nest uses ($n = 174$) ^a	
		Mean	CV	Mean	CV
DBH	Nest tree diameter at breast height (cm)	117	0.29	118	0.28
Slope	Percent slope above and below nest tree	25	0.55	27	0.48
Elev	Nest tree elevation (m)	1,714	0.09	1,701	0.08
SmallCon	Number of conifer stems/ha 13–40 cm dbh	140	0.92	156	0.92
SmallHw	Number of hardwood stems/ha 13–40 cm dbh	13	3.51	16	3.18
Cancov10	Percent canopy cover 10 meters from nest tree	82	0.14	83	0.13
Cancov25	Percent canopy cover 25 meters from nest tree	81	0.16	81	0.16
LogVol	Log volume (m ³ /ha) of logs >25 cm diameter	25	0.74	26	0.69
LiveBasal	Basal area (m ² /ha)/acre of trees >61 cm dbh	5.4	0.55	5.4	0.59
SnagBasal	Basal area (m ² /ha)/acre of snags >61 cm dbh	1.2	1.00	1.4	0.95
Summary					
TreeCond	Nest tree condition: live (L), snag (S)	L = 97, S = 35		L = 134, S = 40	
NestType	Nest type: platform (P), top cavity (T), side cavity (S)	P = 21, T = 45, S = 66		P = 22, T = 65, S = 87	
Species	Nest tree species: fir (F), pine (P), other (O)	F = 63, P = 54, O = 15		F = 79, P = 83, O = 12	
Aspect	Aspect of slope at nest tree: N, E, S, W	N = 45, E = 35, S = 22, W = 30		N = 59, E = 35, S = 31, W = 49	

^a Many nests were used by owls in more than 1 year, yielding a greater sample size than the number of unique nests.

Table 7. Models of nest success (*S*) including habitat class, nest tree, and nest stand structural covariates for California spotted owls in northeastern California, USA, 1990–2000 ($n = 122$). Models are ordered by $QAIC_c$. Adjusted R^2 of the highest ranked model = 0.16. Models shown had Akaike weights (w_i) > 0.05. Variables are defined in Table 6.

Model	log(L)	<i>K</i>	AIC_c	ΔAIC_c	w_i
<i>S</i> (Remnant + SizeClass)	−64.29	4	112.46	0.00	0.60
<i>S</i> (Remnant + SizeClass + Remnant * SizeClass)	−64.26	5	114.58	2.12	0.21
<i>S</i> (Remnant)	−67.49	3	115.50	3.04	0.07
<i>S</i> (CoverType)	−63.23	7	122.00	4.55	0.06

DISCUSSION

Although owls were found nesting and roosting in a variety of forest stand types, site occupancy and apparent survival increased with increasing amounts of habitat classes known to be selected by the owl at the landscape scale. Reproductive output decreased as the amount of nonhabitat within the nest area increased. Nest success was higher where remnant trees were present and higher in stands dominated by medium-sized trees than by large trees. The relationships of habitat class variables to demographic response variables consistently occurred as hypothesized, except that fewer owls occupied areas dominated by medium sized trees with high canopy cover than we expected. The composition of habitat in the nest area (203 ha) was a much better predictor of site occupancy than was the composition of habitat in the core area (814 ha), but relationships between habitat variables and apparent survival and reproductive output were similar at both spatial scales. Our models also revealed a decline in site occupancy over time and showed yearly variation in apparent survival probability. Site occupancy, reproductive output, and, to a lesser extent, apparent survival declined with increasing elevation.

The relatively low variability in habitat classes among nest and core areas within the study area limited the power of forest composition data to explain variation in demographic data. In addition, some variation among sites was lost when the original polygon classifications (cover types) were aggregated into habitat classes. Furthermore, the strong correlations between habitat classes limited the predictive power of models containing more than 1 habitat class variable.

Our use of broad categories of canopy cover and dominant tree size class may have limited our ability to draw stronger inferences from the data. "Normal" canopy cover in our study was defined as 40–70%, masking our ability to evaluate differences in response variables within this range of canopy cover. Similarly, stands dominated by all trees >61 cm dbh were classified as size class 4. This is roughly half the mean size of trees used for nesting (117-cm dbh); a larger size class category may be more strongly associated with spotted owl site occupancy, survival or reproduction. Furthermore, in 16 cases (within 3N0 and 3G0), remnant classification failed to account for the nest tree; we recommend mapping remnant trees at densities lower than 1.2/ha in size class 3 stands.

Some of the observed variation in reproduction among territories may have been due to individual

differences in ability to produce eggs or care for young. Because spotted owls are long lived and have strong site fidelity (Blakesley 2006), our data set is insufficient to separate the effects of site quality and individual owl quality on reproduction and survival. In magpies (*Pica pica*), individuals change territories and/or mates between years frequently enough for researchers to compare the effects of territory quality and bird quality on breeding success (Goodburn 1991). In one study, female quality accounted for 60% of the variance in magpie clutch size and male quality accounted for 70% of annual nesting success (Goodburn 1991).

The positive association we found between habitat classes affecting survival and fecundity contrasts with the trade-off found for northern spotted owls in northwestern California, in which the amount of interior mature and old-growth forest was positively associated with survival and negatively associated with reproductive output (Franklin et al. 2000). Both survival and reproductive output were positively associated with the length of edge between mature/old-growth forest and other vegetation types, including younger forest (Franklin et al. 2000). As a partial explanation of this pattern, Franklin et al. (2000) noted that dusky-footed woodrats (*Neotoma fuscipes*) are the primary prey of northern spotted owls in northwestern California (Ward et al. 1998) and are found in highest densities in sapling/brushy pole timber stands <25-years-old (Sakai and Noon 1993). Ecotones between mature/old forest and early seral forest may provide areas where woodrats are abundant and accessible to spotted owls (Franklin et al. 2000).

Olson et al. (2004) found that a mixture of older forest with younger forest and nonforested areas appeared to benefit northern spotted owl survival in the Oregon Coast Range. Habitat explained a negligible amount of variation in northern spotted owl reproduction in the Oregon Coast Range (Olson et al. 2004), where woodrats and flying squirrels (*Glaucomys sabrinus*) each comprised 37–39% of spotted owl prey (Forsman et al. 2004).

Previous research found that the primary prey of California spotted owls on the Lassen study area was northern flying squirrels (61% of the diet; Verner et al. 1992). Flying squirrel densities in the Lassen study area were highest in old forest stands, lowest in shelterwood logged stands, and intermediate in young forest stands (Waters and Zabel 1995). Although the interspersed of young and old forest stands appeared to benefit spotted owl reproduction in northwestern California where dusky-footed woodrats dominated the owls'

diet, the presence of young forest stands did not appear to benefit spotted owl reproduction in this study, where flying squirrels dominated the diet.

The decline in site occupancy over time that we identified corroborates evidence from other analyses of these spotted owl demographic data, in which the spotted owl population declined during the study period (Blakesley et al. 2001, Franklin et al. 2004).

MANAGEMENT IMPLICATIONS

Site occupancy and apparent survival of California spotted owls were enhanced in habitats with features known to be selected by the owl at the landscape scale. Land managers in the Sierra Nevada region should retain forest stands dominated by large trees with canopy cover >70% and minimize the amount of area unsuitable to spotted owls within 200 ha surrounding spotted owl site centers to promote site occupancy and increase spotted owl reproductive output. Our results suggest that within owl core areas (814 ha), increases in the availability of habitat used by spotted owls for nesting, roosting and foraging will increase owl survival. Large remnant trees >76 cm dbh should be retained in all forest stand types that are used by spotted owls for nesting or managed as potential future spotted owl nesting habitat.

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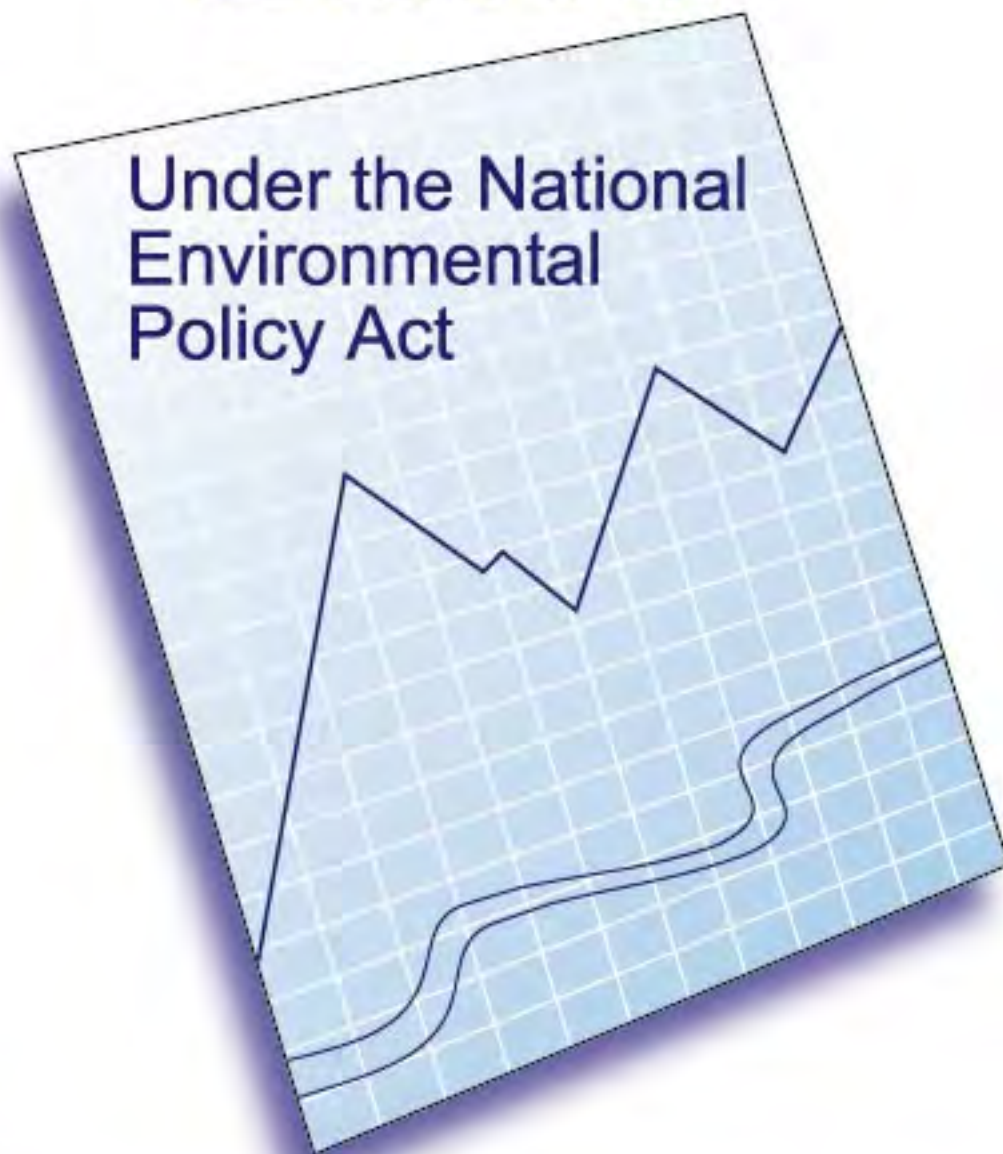
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Considering Cumulative Effects



Council on Environmental Quality
Executive Office of the President

Considering Cumulative Effects Under the National Environmental Policy Act

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Considering Cumulative Effects Under the National Environmental Policy Act

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PREFACE

This handbook presents the results of research and consultations by the Council on Environmental Quality (CEQ) concerning the consideration of cumulative effects in analyses prepared under the National Environmental Policy Act (NEPA). It introduces the NEPA practitioner and other interested parties to the complex issue of cumulative effects, outlines general principles, presents useful steps, and provides information on methods of cumulative effects analysis and data sources. The handbook does not establish new requirements for such analyses. It is not and should not be viewed as formal CEQ guidance on this matter, nor are the recommendations in the handbook intended to be legally binding.

EXECUTIVE SUMMARY

The Council on Environmental Quality's (CEQ) regulations (40 CFR §§ 1500 - 1508) implementing the procedural provisions of the National Environmental Policy Act (NEPA) of 1969, as amended (42 U.S.C. §§ 4321 *et seq.*), define cumulative effects as

the impact on the environment which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions regardless of what agency (Federal or non-Federal) or person undertakes such other actions (40 CFR § 1508.7).

Although the regulations touch on every aspect of environmental impact analysis, very little has been said about cumulative effects. As a result, federal agencies have independently developed procedures and methods to analyze the cumulative effects of their actions on environmental resources, with mixed results.

The CEQ's "Considering Cumulative Effects Under the National Environmental Policy Act" provides a framework for advancing environmental impact analysis by addressing cumulative effects in either an environmental assessment (EA) or an environmental impact statement (EIS). The handbook presents practical methods for addressing coincident effects (adverse or beneficial) on specific resources, ecosystems, and human communities of all related activities, not just the proposed project or alternatives that initiate the assessment process.

In their environmental analyses, federal agencies routinely address the direct and (to a lesser extent) indirect effects of the proposed

action on the environment. Analyzing cumulative effects is more challenging, primarily because of the difficulty of defining the geographic (spatial) and time (temporal) boundaries. For example, if the boundaries are defined too broadly, the analysis becomes unwieldy; if they are defined too narrowly, significant issues may be missed, and decision makers will be incompletely informed about the consequences of their actions.

The process of analyzing cumulative effects can be thought of as enhancing the traditional components of an environmental impact assessment: (1) scoping, (2) describing the affected environment, and (3) determining the environmental consequences. Generally it is also critical to incorporate cumulative effects analysis into the development of alternatives for an EA or EIS. Only by reevaluating and modifying alternatives in light of the projected cumulative effects can adverse consequences be effectively avoided or minimized. Considering cumulative effects is also essential to developing appropriate mitigation and monitoring its effectiveness.

In many ways, scoping is the key to analyzing cumulative effects; it provides the best opportunity for identifying important cumulative effects issues, setting appropriate boundaries for analysis, and identifying relevant past, present, and future actions. Scoping allows the NEPA practitioner to "count what counts." By evaluating resource impact zones and the life cycle of effects rather than projects, the analyst can properly bound the cumulative effects analysis. Scoping can also facilitate the interagency cooperation needed to identify agency plans and other

actions whose effects might overlap those of the proposed action.

When the analyst describes the affected environment, he or she is setting the environmental baseline and thresholds of environmental change that are important for analyzing cumulative effects. Recently developed indicators of ecological integrity (e.g., index of biotic integrity for fish) and landscape condition (e.g., fragmentation of habitat patches) can be used as benchmarks of accumulated change over time. In addition, remote sensing and geographic information system (GIS) technologies provide improved means to analyze historical change in indicators of the condition of resources, ecosystems, and human communities, as well as the relevant stress factors. Many dispersed local information sources and emerging regional data collection programs are now available to describe the cumulative effects of a proposed action.

Determining the cumulative environmental consequences of an action requires delineating the cause-and-effect relationships between the multiple actions and the resources, ecosystems, and human communities of concern. Analysts must tease from the complex networks of possible interactions those that substantially affect the resources. Then, they must describe the response of the resource to this environmental change using modeling, trends analysis, and scenario building when uncertainties are great. The significance of cumulative effects depend on how they compare with the environmental baseline and relevant resource thresholds (such as regulatory standards). Most often, the historical context surrounding the resource is critical to developing these baselines and thresholds and to supporting both imminent and future decision-making.

Undoubtedly, the consequences of human activities will vary from those that were predicted and mitigated. This will be even more problematic because of cumulative effects; therefore, monitoring the accuracy of predictions and

the success of mitigation measures is critical. Adaptive management provides the opportunity to combine monitoring and decision making in a way that will better ensure protection of the environment and attainment of societal goals.

Successfully analyzing cumulative effects ultimately depends on the careful application of individual methods, techniques, and tools to the environmental impact assessment at hand. There is a close relationship between impact assessment and environmental planning, and many of the methods developed for each are applicable to cumulative effects analysis. The unique requirements of cumulative effects analysis (i.e., the focus on resource sustainability and the expanded geographic and time boundaries) must be addressed by developing an appropriate conceptual model. To do this, a suite of primary methods can be used: questionnaires, interviews, and panels; checklists; matrices; networks and system diagrams; modeling; trends analysis; and overlay mapping and GIS. As with project-specific effects, tables and matrices can be used to evaluate cumulative effects (and have been modified specifically to do so). Special methods are also available to address the unique aspects of cumulative effects, including carrying capacity analysis, ecosystem analysis, economic impact analysis, and social impact analysis.

This handbook was developed by reviewing the literature and interviewing practitioners of environmental impact assessment. Most agencies that have recently developed their own guidelines for analyzing cumulative effects recognize cumulative effects analysis as an integral part of the NEPA process, not a separate effort. This handbook is not formal guidance nor is it exhaustive or definitive; it should assist practitioners in developing their own study-specific approaches. CEQ expects that the handbook (and similar agency guidelines) will be updated periodically to reflect additional experience and new methods, thereby, constantly improving the state of cumulative effects analysis.

new methods, thereby, constantly improving the state of cumulative effects analysis.

The handbook begins with an introduction to the cumulative effects problem and its relevance to the NEPA process. The introduction defines eight general principles of cumulative effects analysis and lays out ten specific steps that the NEPA practitioner can use to analyze cumulative effects. The next three chapters parallel the environmental impact assessment process and discuss analyzing cumulative effects while (1) scoping, (2) describing the affected environment, and (3) determining environmental consequences. Each component in the NEPA process is the logical place to complete necessary steps in cumulative effects analysis, but practitioners should remember that analyzing for cumulative effects is an iterative process. Specifically, the results of cumulative effects analysis can and should contribute to refining alternatives and

designing mitigation. Table E-1 illustrates how the principles of cumulative effects analysis can be the focus of each component of the NEPA process. Chapter 5 discusses the methods, techniques, and tools needed to develop a study-specific methodology and actually implement cumulative effects analysis. Appendix A provides summaries of 11 of these methods.

Cumulative effects analysis is an emerging discipline in which the NEPA practitioner can be overwhelmed by the details of the scoping and analytical phases. The continuing challenge of cumulative effects analysis is to focus on important cumulative issues, recognizing that a better decision, rather than a perfect cumulative effects analysis, is the goal of NEPA and environmental impact assessment professionals.

Table E-1. Incorporating principles of cumulative effects analysis (CEA) into the components of environmental impact assessment (EIA)

EIA Components	CEA Principles
Scoping	• Include past, present, and future actions. • Include all federal, nonfederal, and private actions. • Focus on each affected resource, ecosystem, and human community. • Focus on truly meaningful effects.
Describing the Affected Environment	• Focus on each affected resource, ecosystem, and human community. • Use natural boundaries.
Determining the Environmental Consequences	• Address additive, countervailing, and synergistic effects. • Look beyond the life of the action. • Address the sustainability of resources, ecosystems, and human communities.

1

INTRODUCTION TO CUMULATIVE EFFECTS ANALYSIS

Evidence is increasing that the most devastating environmental effects may result not from the direct effects of a particular action, but from the combination of individually minor effects of multiple actions over time.

Some authorities contend that most environmental effects can be seen as cumulative because almost all systems have already been modified, even degraded, by humans. According to the report of the National Performance Review (1994), the heavily modified condition of the San Francisco Bay estuary is a result of activities regulated by a wide variety of government agencies. The report notes that one mile of the delta of the San Francisco Bay may be affected by the decisions of more than 400 agencies (federal, state, and local). William Odum (1982) succinctly described environmental degradation from cumulative effects as "the tyranny of small decisions."

The Council on Environmental Quality's (CEQ) regulations for implementing the National Environmental Policy Act (NEPA) define cumulative effects as

the impact on the environment which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions regardless of what agency (Federal or non-federal) or person undertakes such other actions (40 CFR § 1508.7).

The fact that the human environment continues to change in unintended and unwanted ways in spite of improved federal decisionmaking resulting from the implementation of NEPA is largely attributable to this incremental (cumulative) impact. Although past environmental impact analyses have focused primarily on project-specific impacts, NEPA provides the context and carries the mandate to analyze the cumulative effects of federal actions.

NEPA and CEQ's regulations define the cumulative problem in the context of the action, alternatives, and effects. By definition, cumulative effects must be evaluated along with the direct effects and indirect effects (those that occur later in time or farther removed in distance) of each alternative. The range of alternatives considered must include the no-action alternative as a baseline against which to evaluate cumulative effects. The range of actions that must be considered includes not only the project proposal but all connected and similar actions that could contribute to cumulative effects. Specifically, NEPA requires that all related actions be addressed in the same analysis. For example, the expansion of an airport runway that will increase the number of passengers traveling must address not only the effects of the runway itself, but also the expansion of the terminal and the extension of roadways to provide access to the expanded terminal. If there are similar actions planned

in the area that will also add traffic or require roadway extensions (even though they are nonfederal), they must be addressed in the same analysis.

The selection of actions to include in the cumulative effects analysis, like any environmental impact assessment, depends on whether they affect the human environment. Throughout this handbook discussion of the environment will focus on resources (entities such as air quality or a trout fishery), ecosystems (local or landscape-level units where nature and humans interact), and human communities (sociocultural settings that affect the quality of life). The term resources will sometimes be used to refer to all three entities. Table 1-1 lists some of the common cumulative

effects situations faced by federal agencies (see Chapter 3 for a list of common cumulative effects issues affecting various resources, ecosystems, and human communities).

PURPOSE OF CUMULATIVE EFFECTS ANALYSIS

Congressional testimony on behalf of the passage of NEPA stated that

...as a result of the failure to formulate a comprehensive national environmental policy... environmental problems are only dealt with when they reach crisis proportions..... Important decisions concerning the use and shape of man's environment continue to be made in small but steady increments which perpetuate requirements.

Table 1-1. Examples of cumulative effects situations faced by federal agencies including both multiple agency actions and other actions affecting the same resource

Federal Agency	Cumulative Effects Situations
Army Corps of Engineers	■ incremental loss of wetlands under the national permit to dredge and fill and from land subsidence
Bureau of Land Management	■ degradation of rangeland from multiple grazing allotments and the invasion of exotic weeds
Department of Defense	■ population declines in nesting birds from multiple training missions and commercial tree harvests within the same land unit
Department of Energy	■ increased regional acidic deposition from emissions trading policies and changing climate patterns
Federal Energy Regulatory Commission	■ blocking of fish passage by multiple hydropower dams and Corps of Engineers reservoirs in the same river basin
Federal Highway Administration	■ cumulative commercial and residential development and highway construction associated with suburban sprawl
Forest Service	■ increased soil erosion and stream sedimentation from multiple timber permits and private logging operations in the same watershed
General Services Administration	■ change in neighborhood sociocultural character resulting from ongoing local development including new federal office construction
National Park Service	■ degraded recreational experience from overcrowding and reduced visibility

Interim guidelines issued in 1970 stated that the effects of many federal decisions about a project or complex of projects can be "individually limited but cumulatively considerable" (35 *Federal Register* 7391, May 12, 1970).

The passage of time has only increased the conviction that cumulative effects analysis is essential to effectively managing the consequences of human activities on the environment. The purpose of cumulative effects analysis, therefore, is to ensure that federal decisions consider the full range of consequences of actions. Without incorporating cumulative effects into environmental planning and management, it will be impossible to move towards sustainable development, i.e., development that meets the needs of the present without compromising the ability of future generations to meet their own needs (World Commission on Environment and Development 1987; President's Council on Sustainable Development 1996). To a large extent, the goal of cumulative effects analysis, like that of NEPA itself, is to inject environmental considerations into the planning process as early as needed to improve decisions. If cumulative effects become apparent as agency programs are being planned or as larger strategies and policies are developed then potential cumulative effects should be analyzed at that time.

Cumulative effects analysis necessarily involves assumptions and uncertainties, but useful information can be put on the decision-making table now. Decisions must be supported by the best analysis based on the best data we have or are able to collect. Important research and monitoring programs can be identified that will improve analyses in the future, but their absence should not be used as a reason for not analyzing cumulative effects to the extent possible now. Where substantial uncertainties remain or multiple resource objectives exist, adaptive management provisions for flexible project implementation can be incorporated into the selected alternative.

Sustainable America

President Clinton's Council on Sustainable Development was charged with recommending a national action strategy for sustainable development at a time when Americans are confronted with new challenges that have global ramifications. The Council adopted the Brundtland Commission's definition of sustainable development and articulated the following vision:

Our vision is of a life-sustaining Earth. We are committed to the achievement of a dignified, peaceful, and equitable existence. A sustainable United States will have a growing economy that provides equitable opportunities for satisfying livelihoods and a safe, healthy, high quality of life for current and future generations. Our nation will protect its environment, its natural resource base, and the functions and viability of natural systems on which all life depends.

The Council concluded that in order to meet the needs of the present while ensuring that future generations have the same opportunities, the United States must change by moving from conflict to collaboration and adopting stewardship and individual responsibility as tenets by which to live. This vision is similar to the first environmental policy listed in NEPA—that each generation should fulfill its responsibilities as trustee of the environment for succeeding generations. Analyzing for cumulative effects on the full range of resources, ecosystems, and human communities under NEPA provides a mechanism for addressing sustainable development.

AGENCY EXPERIENCE WITH CUMULATIVE EFFECTS ANALYSIS

Federal agencies make hundreds, perhaps thousands, of small decisions annually. Sometimes a single agency makes decisions on

similar projects; other times project decisions by many different authorities are interrelated. The Federal Energy Regulatory Commission must make licensing decisions on many individual hydropower facilities within the same river basin (Figure 1-1). The Federal Highway Administration and state transportation agencies frequently make decisions on highway projects that may not have significant direct environmental effects, but that may induce indirect and cumulative effects by permitting other development activities that have significant effects on air and water resources at a regional or national scale. The highway and the other development activities can reasonably be foreseen as "connected actions" (40 CFR § 1508.25).

Many times there is a mismatch between the scale at which environmental effects occur and the level at which decisions are made. Such mismatches present an obstacle to cumulative effects analysis. For example, while broad scale decisions are made at the program or policy level (e.g., National Energy Strategy, National Transportation Plan, Base Realignment and Closure Initiative), the environmental effects are generally assessed at the project level (e.g., coal-fired power plant, interstate highway connector, disposal of installation land). Cumulative effects analysis should be the tool for federal agencies to evaluate the implications of even project-level environmental assessments (EAs) on regional resources.

Federal agencies have struggled with preparing cumulative effects analyses since CEQ issued its regulations in 1978. They continue to find themselves in costly and time-consuming administrative proceedings and litigation over the proper scope of the analysis. Court cases throughout the years have affirmed CEQ's requirement to assess cumulative effects of projects but have added little in the way of guidance and direction. To date, there has not been a single, universally accepted conceptual approach, nor even general principles accepted by all scientists and managers. States and

other countries with "little NEPA" laws have experienced similar implementation problems.

A General Accounting Office (GAO) report on coastal pollution noted that state coastal managers raised concerns about the quality of cumulative effects analysis in environmental reviews for proposed federal activities (GAO 1991). In one case study, state coastal managers told GAO that the Environmental Impact Statement (EIS) for rerouting and expanding a highway did not consider that the project as proposed would have a significant growth-inducing effect that would exceed state planning limitations by 100 percent. The Department of Commerce acknowledged the need to provide additional guidance on how to assess the indirect and cumulative effects of proposed actions in the coastal zone and recently published a cumulative impacts assessment protocol for managing cumulative coastal environmental impacts (Vestal et al. 1995).

The increased use of EAs rather than EISs in recent years could exacerbate the cumulative effects problem. Agencies today prepare substantially more EAs than EISs; in a typical year 45,000 EAs are prepared compared to 450 EISs. An agency's decision to prepare an EIS is important because an EIS tends to contain more rigorous analysis and more public involvement than an EA. EAs tend to save time and money because an EA generally takes less time to prepare. They are a cost-effective way to determine whether potentially significant effects are likely and whether a project can mitigate these effects. At the same time, because EAs focus on whether effects are significant, they tend to underestimate the cumulative effects of their projects. Given that so many more EAs are prepared than EISs, adequate consideration of cumulative effects requires that EAs address them fully. One study analyzed 89 EAs announced in the *Federal Register* between January 1, 1992, and June 30, 1992, to determine the extent to which treatment of cumulative effects met CEQ's requirements (Figure 1-2). Only 35 EAs (39%) mentioned cumulative

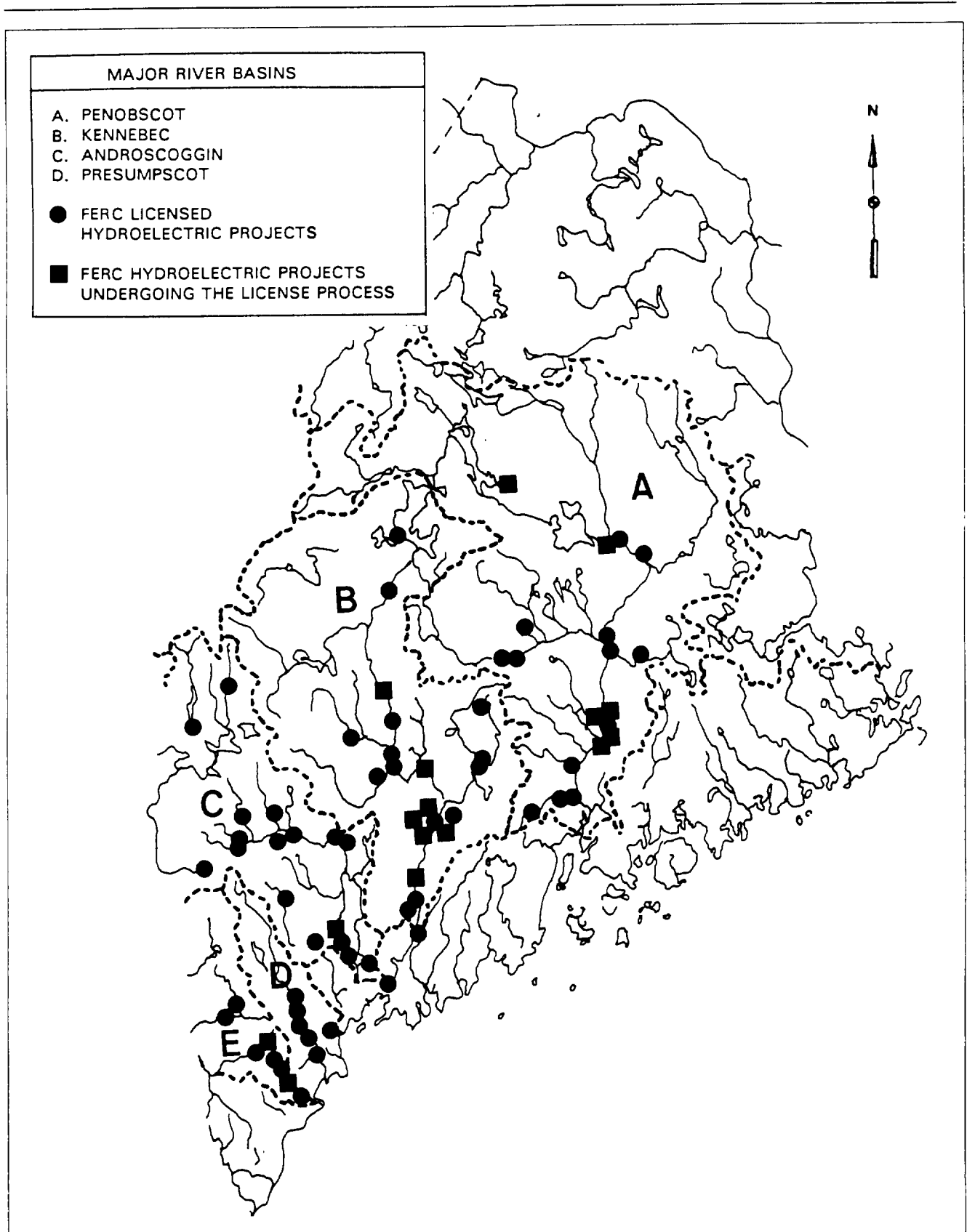
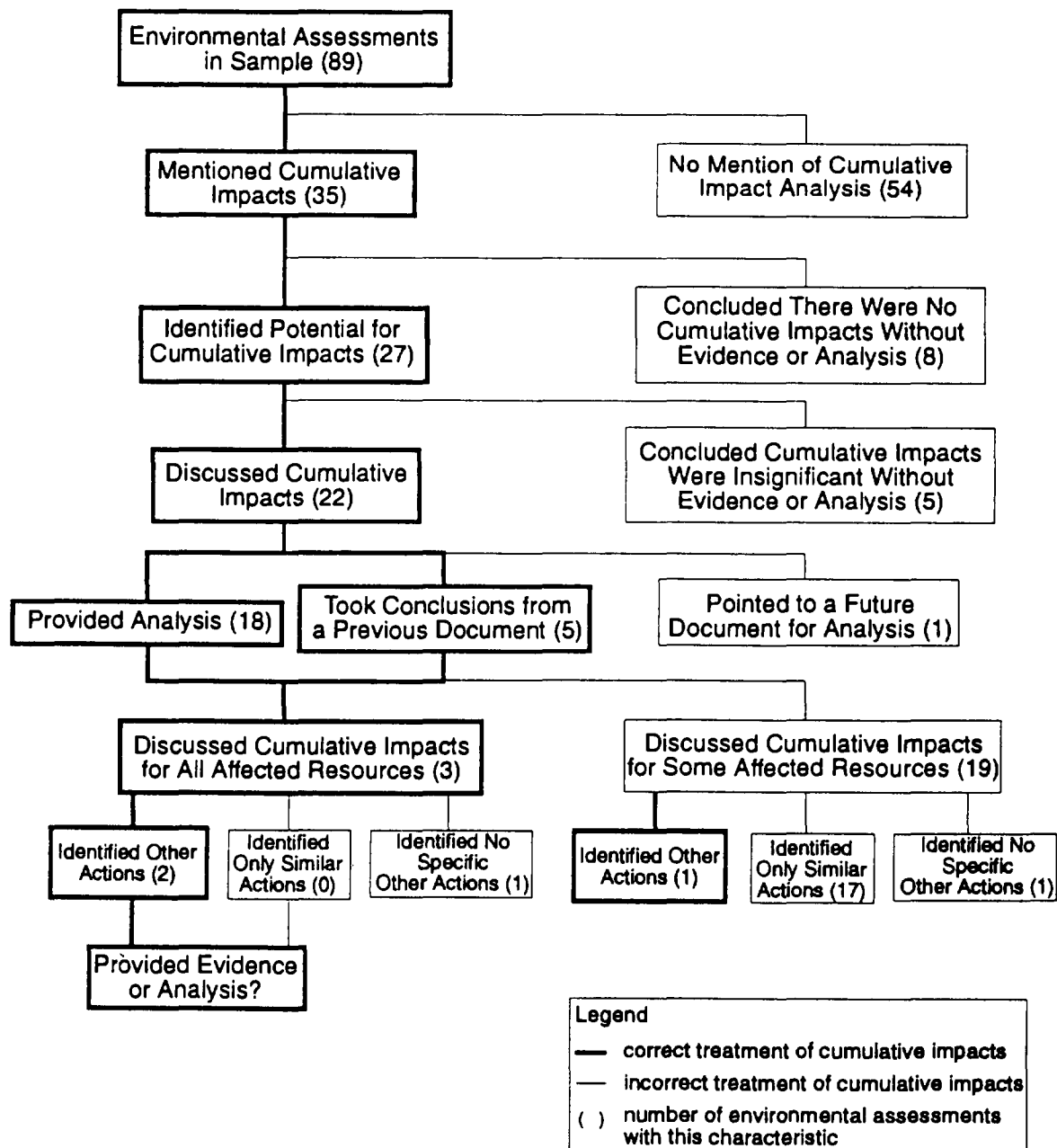


Figure 1-1. River basins and associated FERC related hydroelectric projects in Maine (undated)



For the 22 environmental assessments (EAs) that discussed cumulative impacts, the three treatments are not mutually exclusive. One EA in the sample provided analysis for some resources, took the conclusions from a previous document for one resource, and pointed to a future document for another resource. For this reason, the numbers in the boxes sum to 24 instead of 22.

Figure 1-2. Consideration of cumulative effects in environmental assessments (McCold and Holman 1995)

effects. Nearly half of those failed to present evidence to support their conclusions concerning cumulative effects (McCold and Holman 1995).

PRINCIPLES OF CUMULATIVE EFFECTS ANALYSIS

Increasingly, decisionmakers are recognizing the importance of looking at their projects in the context of other development in the community or region (i.e., of analyzing the cumulative effects). Direct effects continue to be most important to decisionmakers, in part because they are more certain. Nonetheless, the importance of acid rain, climate change, and other cumulative effects problems has resulted in many efforts to undertake and improve the analysis of cumulative effects. Although no universally accepted framework for cumulative effects analysis exists, general principles have gained acceptance (Table 1-2).

Each of these eight principles illustrates a property of cumulative effects analysis that differentiates it from traditional environmental impact assessment. By applying these principles to environmental analysis of all kinds, cumulative effects will be better considered, and the analysis will be complete. A critical principle states that cumulative effects analysis should be conducted within the context of resource, ecosystem, and human community thresholds—levels of stress beyond which the desired condition degrades. The magnitude and extent of the effect on a resource depends on whether the cumulative effects exceed the capacity of the resource to sustain itself and remain productive. Similarly, the natural ecosystem and the human community have maximum levels of cumulative effects that they can

withstand before the desired conditions of ecological functioning and human quality of life deteriorate.

Determining the threshold beyond which cumulative effects significantly degrade a resource, ecosystem, and human community is often problematic. Without a definitive threshold, the NEPA practitioner should compare the cumulative effects of multiple actions with appropriate national, regional, state, or community goals to determine whether the total effect is significant. These thresholds and desired conditions can best be defined by the cooperative efforts of agency officials, project proponents, environmental analysts, non-governmental organizations, and the public through the NEPA process. Ultimately, cumulative effects analysis under NEPA should be incorporated into the agency's overall environmental planning and the regional planning of other federal agencies and stakeholders.

HOW ENVIRONMENTAL EFFECTS ACCUMULATE

Cumulative effects result from spatial (geographic) and temporal (time) crowding of environmental perturbations. The effects of human activities will accumulate when a second perturbation occurs at a site before the ecosystem can fully rebound from the effect of the first perturbation. Many researchers have used observations or environmental change theory to categorize cumulative effects into different types. The diversity of sources, processes, and effects involved has prevented the research and assessment communities from agreeing on a standard typology. Nonetheless, it is useful to review the eight scenarios for accumulating effects shown in Table 1-3.

Table 1-2. Principles of cumulative effects analysis

- 1. Cumulative effects are caused by the aggregate of past, present, and reasonably foreseeable future actions.**

The effects of a proposed action on a given resource, ecosystem, and human community include the present and future effects added to the effects that have taken place in the past. Such cumulative effects must also be added to effects (past, present, and future) caused by all other actions that affect the same resource.
- 2. Cumulative effects are the total effect, including both direct and indirect effects, on a given resource, ecosystem, and human community of all actions taken, no matter who (federal, nonfederal, or private) has taken the actions.**

Individual effects from disparate activities may add up or interact to cause additional effects not apparent when looking at the individual effects one at a time. The additional effects contributed by actions unrelated to the proposed action must be included in the analysis of cumulative effects.
- 3. Cumulative effects need to be analyzed in terms of the specific resource, ecosystem, and human community being affected.**

Environmental effects are often evaluated from the perspective of the proposed action. Analyzing cumulative effects requires focusing on the resource, ecosystem, and human community that may be affected and developing an adequate understanding of how the resources are susceptible to effects.
- 4. It is not practical to analyze the cumulative effects of an action on the universe; the list of environmental effects must focus on those that are truly meaningful.**

For cumulative effects analysis to help the decisionmaker and inform interested parties, it must be limited through scoping to effects that can be evaluated meaningfully. The boundaries for evaluating cumulative effects should be expanded to the point at which the resource is no longer affected significantly or the effects are no longer of interest to affected parties.
- 5. Cumulative effects on a given resource, ecosystem, and human community are rarely aligned with political or administrative boundaries.**

Resources typically are demarcated according to agency responsibilities, county lines, grazing allotments, or other administrative boundaries. Because natural and sociocultural resources are not usually so aligned, each political entity actually manages only a piece of the affected resource or ecosystem. Cumulative effects analysis on natural systems must use natural ecological boundaries and analysis of human communities must use actual sociocultural boundaries to ensure including all effects.
- 6. Cumulative effects may result from the accumulation of similar effects or the synergistic interaction of different effects.**

Repeated actions may cause effects to build up through simple addition (more and more of the same type of effect), and the same or different actions may produce effects that interact to produce cumulative effects greater than the sum of the effects.
- 7. Cumulative effects may last for many years beyond the life of the action that caused the effects.**

Some actions cause damage lasting far longer than the life of the action itself (e.g., acid mine drainage, radioactive waste contamination, species extinctions). Cumulative effects analysis needs to apply the best science and forecasting techniques to assess potential catastrophic consequences in the future.
- 8. Each affected resource, ecosystem, and human community must be analyzed in terms of its capacity to accommodate additional effects, based on its own time and space parameters.**

Analysts tend to think in terms of how the resource, ecosystem, and human community will be modified given the action's development needs. The most effective cumulative effects analysis focuses on what is needed to ensure long-term productivity or sustainability of the resource.

Table 1-3. Examples of cumulative effects (modified from NRC 1986 and Spaling 1995)		
Type	Main characteristics	Example
1. Time crowding	Frequent and repetitive effects on an environmental system	Forest harvesting rate exceeds regrowth
2. Time lags	Delayed effects	Exposure to carcinogens
3. Space crowding	High spatial density of effects on an environmental system	Pollution discharges into streams from nonpoint sources
4. Cross-boundary	Effects occur away from the source	Acidic precipitation
5. Fragmentation	Change in landscape pattern	Fragmentation of historic district
6. Compounding effects	Effects arising from multiple sources or pathways	Synergism among pesticides
7. Indirect effects	Secondary effects	Commercial development following highway construction
8. Triggers and thresholds	Fundamental changes in system behavior or structure	Global climate change

In simplest terms, cumulative effects may arise from single or multiple actions and may result in additive or interactive effects. Interactive effects may be either countervailing—where the net adverse cumulative effect is less than the sum of the individual effects—or

synergistic—where the net adverse cumulative effect is greater than the sum of the individual effects. This combination of two kinds of actions with two kinds of processes leads to four basic types of cumulative effects (Table 1-3; see Peterson et al. 1987 for a similar typology).

Table 1-4. Types of cumulative effects		
	Additive Process	Interactive Process
Single Action	Type 1 — Repeated “additive” effects from a single proposed project. Example: Construction of a new road through a national park, resulting in continual draining of road salt onto nearby vegetation.	Type 2 — Stressors from a single source that interact with receiving biota to have an “interactive” (nonlinear) net effect. Example: Organic compounds, including PCBs, that biomagnify up food chains and exert disproportionate toxicity on raptors and large mammals.
Multiple Actions	Type 3 — Effects arising from multiple sources (projects, point sources, or general effects associated with development) that affect environmental resources additively. Example: Agricultural irrigation, domestic consumption, and industrial cooling activities that all contribute to drawing down a groundwater aquifer.	Type 4 — Effects arising from multiple sources that affect environmental resources in an interactive (i.e., countervailing or synergistic) fashion. Example: Discharges of nutrients and heated water to a river that combine to cause an algal bloom and subsequent loss of dissolved oxygen that is greater than the additive effects of each pollutant.

ROADMAP TO THE HANDBOOK

The chapters that follow discuss the incorporation of cumulative effects analysis into the components of environmental impact assessment: scoping (Chapter 2), describing the affected environment (Chapter 3), and determining the environmental consequences (Chapter 4). Although cumulative effects analysis is an iterative process, basic steps that

to be accomplished can be identified in each component of the NEPA process; each chapter focuses on its constituent steps (Table 1-4). The last chapter of this report discusses developing a cumulative effects analysis methodology that draws upon existing methods, techniques, and tools to analyze cumulative effects. Appendix A provides brief descriptions of 11 cumulative effects analysis methods.

Table 1-5. Steps in cumulative effects analysis (CEA) to be addressed in each component of environmental impact assessment (EIA)

EIA Components	CEA Steps
Scoping	1. Identify the significant cumulative effects issues associated with the proposed action and define the assessment goals. 2. Establish the geographic scope for the analysis. 3. Establish the time frame for the analysis. 4. Identify other actions affecting the resources, ecosystems, and human communities of concern.
Describing the Affected Environment	5. Characterize the resources, ecosystems, and human communities identified in scoping in terms of their response to change and capacity to withstand stresses. 6. Characterize the stresses affecting these resources, ecosystems, and human communities and their relation to regulatory thresholds. 7. Define a baseline condition for the resources, ecosystems, and human communities.
Determining the Environmental Consequences	8. Identify the important cause-and-effect relationships between human activities and resources, ecosystems, and human communities. 9. Determine the magnitude and significance of cumulative effects. 10. Modify or add alternatives to avoid, minimize, or mitigate significant cumulative effects. 11. Monitor the cumulative effects of the selected alternative and adapt management.

2

SCOPING FOR CUMULATIVE EFFECTS

PRINCIPLES

- Include past, present, and future actions.
- Include all federal, nonfederal, and private actions.
- Focus on each affected resource, ecosystem, and human community.
- Focus on truly meaningful effects.

Expanding environmental impact assessment to incorporate cumulative effects can only be accomplished by the enlightened use of the scoping process. The purpose of scoping for cumulative effects is to determine (1) whether the resources, ecosystems, and human communities of concern have already been affected by past or present activities and (2) whether other agencies or the public have plans that may affect the resources in the future. This is best accomplished as an iterative process, one that goes beyond formal scoping meetings and consultations to include creative interactions with all the stakeholders. Scoping should be used in both the planning and project development stage (i.e., whenever information on cumulative effects will contribute to a better decision).

Scoping information may come from agency consultations, public comments, the analyst's own knowledge and experience, planning activities, the proponent's statements of purpose and need, underlying studies in support of the project proposal, expert opinion,

or other NEPA analyses. This information supports all the steps in cumulative effects analysis, including identifying data for establishing the environmental baseline (see Chapter 3) and identifying information related to impact significance (see Chapter 4). Most importantly, however, scoping for cumulative effects should include the following steps:

Step 1

Identify the significant cumulative effects issues associated with the proposed action and define the assessment goals.

Step 2

Establish the geographic scope for the analysis.

Step 3

Establish the time frame for the analysis.

Step 4

Identify other actions affecting the resources, ecosystems, and human communities of concern.

IDENTIFYING CUMULATIVE EFFECTS ISSUES

Identifying the major cumulative effects issues of a project involves defining the following:

- the direct and indirect effects of the proposed action,
- which resources, ecosystems, and human communities, are affected, and
- which effects on these resources are important from a cumulative effects perspective.

The proposed action may affect several resources either directly or indirectly. Resources can be elements of the physical environment, species, habitats, ecosystem parameters and functions, cultural resources, recreational opportunities, human community structure, traffic patterns, or other economic and social conditions. In a broad sense, all the impacts on affected resources are probably cumulative; however, the role of the analyst is to narrow the focus of the cumulative effects analysis to important issues of national, regional, or local significance. This narrowing can occur only after thorough scoping. The analyst should ask basic questions such as whether the proposed action will have effects similar to other actions in the area and whether the resources have been historically affected by cumulative actions (Table 2-1). Many significant cumulative effects issues are well known. Public interest groups, natural resource and land management agencies, and regulatory agencies regularly deal with cumulative effects. Newspapers and scientific journals frequently publish letters and comments dealing with these issues.

Not all potential cumulative effects issues identified during scoping need to be included in an EA or an EIS. Some may be irrelevant or inconsequential to decisions about the proposed action and alternatives. Cumulative effects analysis should "count what counts", not produce superficial analyses of a long laundry list of issues that have little relevance to the effects of the proposed action or the eventual decisions. Because cumulative effects can result from the activities of other agencies or persons, they may have already been analyzed by others and the importance of the issue determined. For instance, an agency proposing an action with minor effects on wetlands should not unilaterally decide that cumulative effects on wetlands is not an important issue. Cumulative effects analysis should consider the concerns of agencies managing and regulating wetlands,

as well as the regional history of cumulative wetland losses and degradation, and the presence of other proposals that would produce future wetland losses or degradation.

BOUNDING CUMULATIVE EFFECTS ANALYSIS

Once the study goals of the cumulative effects analysis are established, the analyst must decide on the specific content of the study that will meet those requirements. Analyzing cumulative effects differs from the traditional approach to environmental impact assessment because it requires the analyst to expand the geographic boundaries and extend the time frame to encompass additional effects on the resources, ecosystems, and human communities of concern.

Identifying Geographic Boundaries

For a project-specific analysis, it is often sufficient to analyze effects within the immediate area of the proposed action. When analyzing the contribution of this proposed action to cumulative effects, however, the geographic boundaries of the analysis almost always should be expanded. These expanded boundaries can be thought of as differences in hierarchy or scale. Project-specific analyses are usually conducted on the scale of counties, forest management units, or installation boundaries, whereas cumulative effects analysis should be conducted on the scale of human communities, landscapes, watersheds, or airsheds. Choosing the appropriate scale to use is critical and will depend on the resource or system. Figure 2-1 illustrates the utility of using the ecologically relevant watershed boundary of the Anacostia River basin rather than the political boundaries of local governments to develop restoration plans.

A useful concept in determining appropriate geographic boundaries for a cumulative effects analysis is the **project impact zone**.

Table 2-1. Identifying potential cumulative effects issues related to a proposed action

1. What is the value of the affected resource or ecosystem? Is it:
 - protected by legislation or planning goals?
 - ecologically important?
 - culturally important?
 - economically important?
 - important to the well-being of a human community?
2. Is the proposed action one of several similar past, present, or future actions in the same geographic area? (Regions may be land management units, watersheds, regulatory regions, states, ecoregions, etc.) *Examples: timber sales in a national forest; hydropower development on a river; incinerators in a community.*
3. Do other activities (whether governmental or private) in the region have environmental effects similar to those of the proposed action? *Example: release of oxidizing pollutants to a river by a municipality, an industry, or individual septic systems.*
4. Will the proposed action (in combination with other planned activities) affect any natural resources; cultural resources; social or economic units; or ecosystems of regional, national, or global public concern? *Examples: release of chlorofluorocarbons to the atmosphere; conversion of wetland habitat to farmland located in a migratory waterfowl flyway.*
5. Have any recent or ongoing NEPA analyses of similar actions or nearby actions identified important adverse or beneficial cumulative effect issues? *Examples: National Forest Plan EIS; Federal Energy Regulatory Commission Basinwide EIS or EA.*
6. Has the impact been historically significant, such that the importance of the resource is defined by past loss, past gain, or investments to restore resources? *Example: mudflat and salt-marsh habitats in San Francisco Bay.*
7. Might the proposed action involve any of the following cumulative effects issues?
 - long range transport of air pollutants resulting in ecosystem acidification or eutrophication
 - air emissions resulting in degradation of regional air quality
 - release of greenhouse gases resulting in climate modification
 - loading large water bodies with discharges of sediment, thermal, and toxic pollutants
 - reduction or contamination of groundwater supplies
 - changes in hydrological regimes of major rivers and estuaries
 - long-term containment and disposal of hazardous wastes
 - mobilization of persistent or bioaccumulated substances through the food chain
 - decreases in the quantity and quality of soils
 - loss of natural habitats or historic character through residential, commercial, and industrial development
 - social, economic, or cultural effects on low-income or minority communities resulting from ongoing development
 - habitat fragmentation from infrastructure construction or changes in land use
 - habitat degradation from grazing, timber harvesting, and other consumptive uses
 - disruption of migrating fish and wildlife populations
 - loss of biological diversity

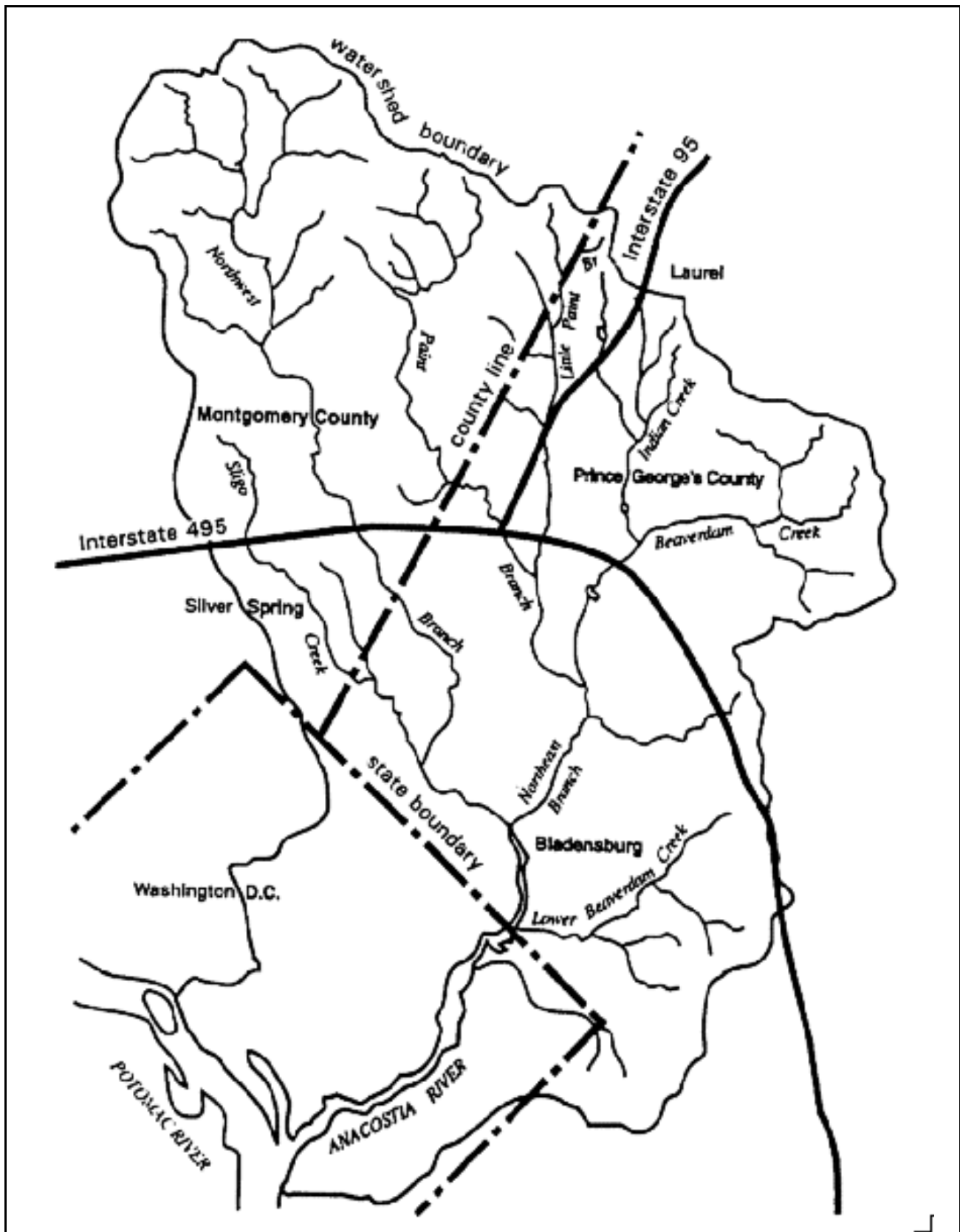


Figure 2-1. Juxtaposition of natural and political boundaries surrounding the Anacostia River

For a proposed action or reasonable alternative, the analysts should

- Determine the area that will be affected by that action. That area is the project impact zone.
- Make a list of the resources within that zone that could be affected by the proposed action.
- Determine the geographic areas occupied by those resources outside of the project impact zone. In most cases, the largest of these areas will be the appropriate area for the analysis of cumulative effects.
- Determine the affected institutional jurisdictions, both for the proposing agency and other agencies or groups.

Project impact zones for a proposed action are likely to vary for different resources and environmental media. For water, the project impact zone would be limited to the hydrologic system that would be affected by the proposed action. For air, the zone may be the physiographic basin in which the proposed action would be located. Land-based effects may occur within some set distance from the proposed action. In addition, the boundaries for an individual resource should be related to the resource's dependence on different environmental media. Table 2-2 provides some possible geographic boundaries for different resources. This list is *not* inclusive. The applicable geographic scope needs to be defined case by case.

Table 2-2. Geographic areas that could be used in a cumulative effects analysis	
Resource	Possible Geographic Areas for Analysis
Air quality	Metropolitan area, airshed, or global atmosphere
Water quality	Stream, watershed, river basin, estuary, aquifer, or parts thereof
Vegetative resources	Watershed, forest, range, or ecosystem
Resident wildlife	Species habitat or ecosystem
Migratory wildlife	Breeding grounds, migration route, wintering areas, or total range of affected population units
Fishery resources	Stream, river basin, estuary, or parts thereof; spawning area and migration route
Historic resources	Neighborhood, rural community, city, state, tribal territory, known or possible historic district
Sociocultural resources	Neighborhood, community, distribution of low-income or minority population, or culturally valued landscape
Land use	Community, metropolitan area, county, state, or region
Coastal zone	Coastal region or watershed
Recreation	River, lake, geographic area, or land management unit
Socioeconomics	Community, metropolitan area, county, state, or country

One way to evaluate geographic boundaries is to consider the distance an effect can travel. For instance, air emissions can travel substantial distances and are an important part of regional air quality. Air quality regions are defined by the EPA, and these regions are an appropriate boundary for assessment of the cumulative effects of releases of pollutants to the atmosphere. For water resources, an appropriate regional boundary may be a river basin or parts thereof. Watershed boundaries are useful for cumulative effects analysis because (1) pollutants and material released in the watershed may travel downstream to be mingled with other pollutants and materials; (2) migratory fish may travel up and down the river system during their life cycle; and (3) resource agencies may have basin-wide management and planning goals. For land-based effects, an appropriate regional boundary may be a "forest or range," a watershed, an ecological region (ecoregion), or socioeconomic region (for evaluating effects on human communities). Which boundary is the most appropriate depends both on the accumulation characteristics of the effects being assessed and an evaluation of the management or regulatory interests of the agencies involved.

Identifying Time Frames

The time frame of the project-specific analysis should also be evaluated to determine its applicability to the cumulative effects analysis. This aspect of the cumulative effects analysis may at first seem the most troublesome to define. CEQ's regulations define cumulative effects as the "incremental effect of the action when added to other past, present, and reasonably foreseeable future actions" (40 CFR § 1508.7). In determining how far into the future to analyze cumulative effects, the analyst should first consider the time frame of the project-specific analysis. If the effects of the proposed action are projected to last five years, this time frame may be the most appropriate for

the cumulative effects analysis. The analyst should attempt to identify actions that could reasonably be expected to occur within that period.

There may be instances when the time frame of the project-specific analysis will need to be expanded to encompass cumulative effects occurring further into the future (Figure 2-2). For instance, even though the effects of a proposed action may linger or decrease slowly through time, the time frame for the project-specific analysis usually does not extend beyond the time when project-specific effects drop below a level determined to be significant. These project-specific effects, however, may combine with the effects of other actions beyond the time frame of the proposed action and result in significant cumulative effects that must be considered.

IDENTIFYING PAST, PRESENT, AND REASONABLY FORESEEABLE FUTURE ACTIONS

As described above, identifying past, present, and future actions is critical to establishing the appropriate geographic and time boundaries for the cumulative effects analysis. Identifying boundaries and actions should be iterative within the scoping process.

A schematic diagram showing the area in which the proposed action is located, the location of resources, and the location of other facilities (existing or planned), human communities, and disturbed areas can be useful for identifying actions to be included in the cumulative effects analysis (Figure 2-3). A geographic information system (GIS) or a manual map overlay system can be used to depict this information (see Appendix A for a description of map overlays and GIS). Such a diagram is useful for determining project-specific impact zones and their overlap with areas affected by other nonproject actions.

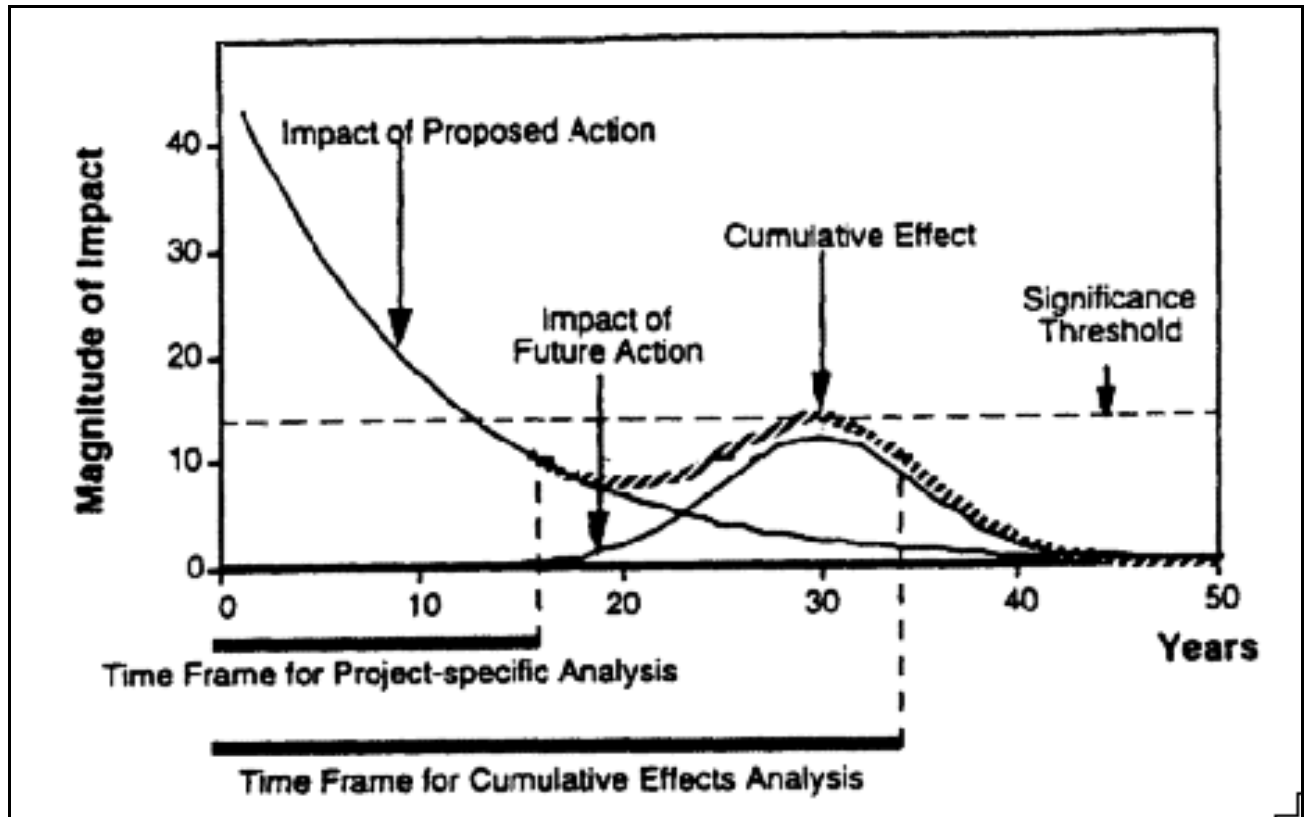


Figure 2-2. Time frames for project-specific and cumulative effects analyses

By examining the overlap of impact zones on the areas occupied by resources, it should be possible to refine the list of projects or activities (past, present, or future) to be included in the analysis. Proximity of actions may not be sufficient justification to include them in the analysis. In the example shown in Figure 2-3, the cumulative effects analysis for trout should consider the effects of the existing mine and the planned logging activity, because these activities would have either present or future effects on the trout spawning area below the proposed power plant facility. Although an agricultural area is nearby, it can be excluded from the analysis because its sediment loading effects occur downstream of the trout spawning area. Proximity of other actions to the proposed action is not the decisive factor for including these actions in an analysis; these actions must have some influence on the resources affected by the proposed action. In other words, these other actions should be included in analysis when

their impact zones overlap areas occupied by resources affected by the proposed action.

Completing the geographic or schematic diagram depending on applying cause-and-effect models that link human actions and the resources or ecosystems. This too is an iterative process. Identifying other activities contributing to cumulative effects could result in the addition of new effect pathways to the cause-and-effect model. In the example, addition of an existing mine to the cumulative effects analysis could require adding a pathway for the effects of chemical pollution on trout. Chapters 4 and 5 and Appendix A discuss cause-and-effect modeling and network analysis.

The availability of data often determines how far back past effects are examined. Although certain types of data (e.g., forest cover) may be available for extensive periods in the past (i.e., several decades), other data (e.g., water quality data) may be available only for

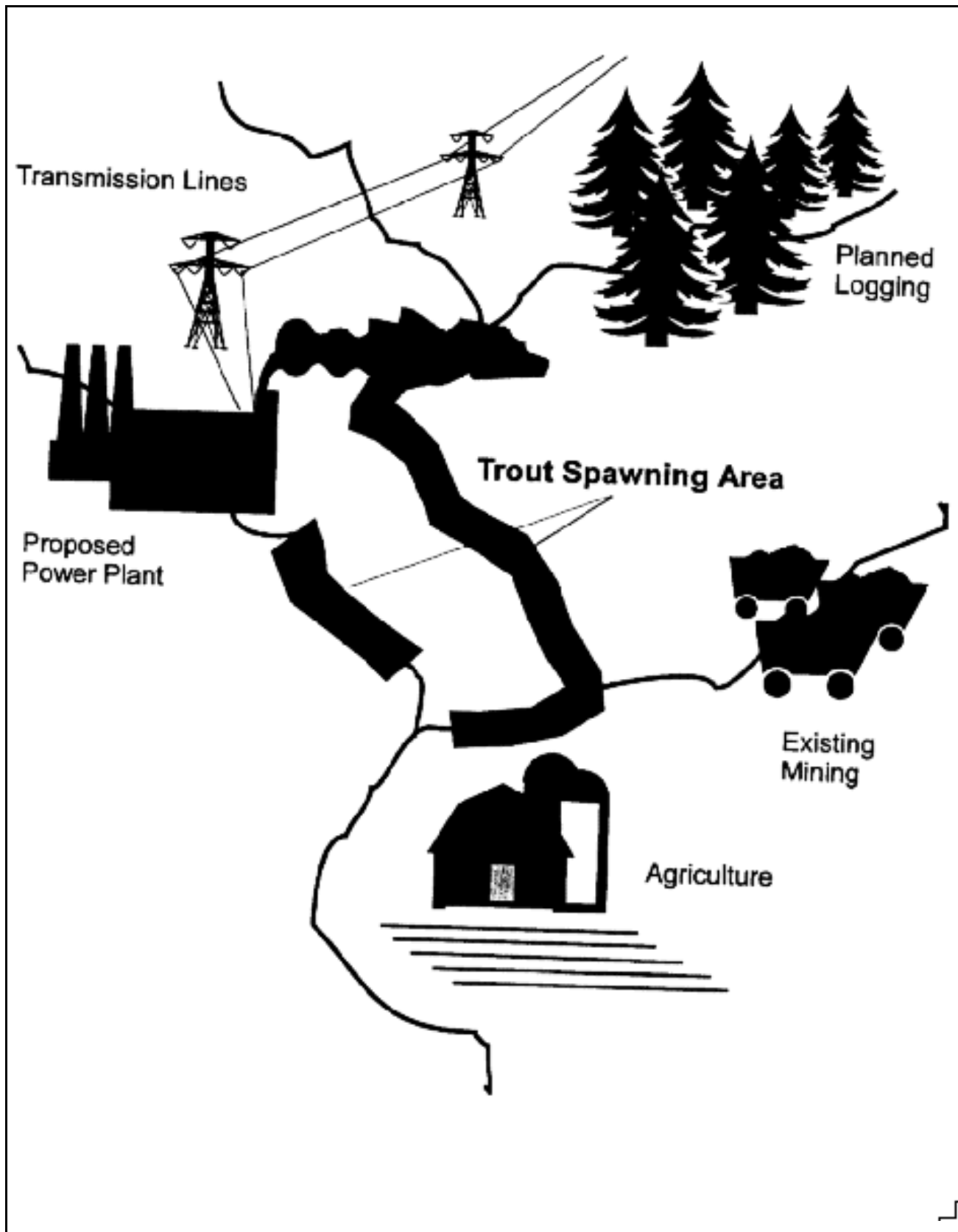


Figure 2-3. Impact zones of proposed and existing development relative to a trout population

much shorter periods. Because the data describing past conditions are usually scarce, the analysis of past effects is often qualitative.

Identifying similar actions presently underway is easier than identifying past or future actions, but it is by no means simple. Because most of the analytical effort in an environmental impact assessment deals with the proposed action, the actions of other agencies and private parties are usually less well known. Effective cumulative effects analysis requires close coordination among agencies to ensure that even all present actions, much less past and future actions, are considered.

The first step in identifying future actions is to investigate the plans of the proponent agency and other agencies in the area. Commonly, analysts only include those plans for actions which are funded or for which other NEPA analysis is being prepared. This approach does not meet the letter or intent of CEQ's regulations. It underestimates the number of future projects, because many viable actions may be in the early planning stage. On the other hand, some actions in the planning, budgeting, or execution phase may not go forward. To include all proposals ever considered as other actions would most likely overestimate the future effects of cumulative effects on the resources, ecosystems, and human communities; therefore, the analyst should develop guidelines as to what constitutes "reasonably foreseeable future actions" based on the planning process within each agency. Specifically, the analyst should use the best available information to develop scenarios that predict which future actions might reasonably be expected as a result of the proposal. Such scenarios are generally based on experience obtained from similar projects located elsewhere in the region. Including future actions in the study is much easier if an agency has already developed a planning document that identifies proposed future actions and has communicated these plans to other federal agencies and governmental bodies in the affected region.

When identifying future actions to include in the cumulative effects analysis, reasonably

foreseeable actions by private organizations or individuals are usually more difficult to identify than those of federal or other governmental entities. In many cases, local government planning agencies can provide useful information on the likely future development of the region, such as master plans. Local zoning requirements, water supply plans, economic development plans, and various permitting records will help in identifying reasonably foreseeable private actions (see Chapter 3 for other sources of information). In addition, some private landowners or organizations may be willing to share their plans for future development or land use. These plans can be considered in the analysis, but it is important to indicate in the NEPA analysis whether these plans were presented by the private party responsible for originating the action. Whenever speculative projections of future development are used, the analyst should provide an explicit description of the assumptions involved. If the analyst is uncertain whether to include future actions, it may be appropriate to bound the problem by developing several scenarios with different assumptions about future actions.

In general, future actions can be excluded from the analysis of cumulative effects if

- the action is outside the geographic boundaries or time frame established for the cumulative effects analysis;
- the action will not affect resources that are the subject of the cumulative effects analysis; or
- including of the action would be arbitrary.

At the same time, NEPA litigation [*Scientists' Institute for Public Information, Inc., v. Atomic Energy Commission* (481 F.2d 1079 D.C. Cir.1073)] has made it clear that "reasonable forecasting" is implicit in NEPA and that it is the responsibility of federal agencies to predict the environmental effects of proposed actions before they are fully known. CEQ's regulations provide for including these uncertainties in the environmental impact assessment where the

foreseeable future action is not planned in sufficient detail to permit complete analysis. Specifically, CEQ's regulations state

[w]hen an agency is evaluating reasonably foreseeable significant adverse effects on the human environment in an environmental impact statement and there is incomplete or unavailable information, ... [that] cannot be obtained because the overall costs of obtaining it are exorbitant or the means to obtain it are not known,... the agency shall include... the agency's evaluation of such impacts based upon theoretical approaches or research methods generally accepted in the scientific community (40 CFR § 1502.22).

Even when the decisionmaker does not select the environmentally preferable alternative, including the cumulative effects of future actions in the analysis serves the important NEPA function of informing the public and potentially influencing future decisions.

AGENCY COORDINATION

Because the actions of other agencies are part of cumulative effects analysis, greater emphasis should be placed on consulting with other agencies than is commonly practiced. Fortunately, when federal agencies adopt the ecosystem approach to management (espoused by the Interagency Ecosystem Management Task Force) such consultation probably will be enhanced (see box). During scoping, periodic coordination with other agencies may enhance the cumulative effects analysis process. As described above, a cumulative effects analysis might

- include an assessment of another agency's proposed action,
- include an assessment of the effects of another agency's completed actions,
- evaluate another agency's resource management practices and goals, or

- evaluate another agency's future plans.

Ecosystem Management

Vice President Gore's National Performance Review called for the agencies of the federal government to adopt "a proactive approach to ensuring a sustainable economy and a sustainable environment through ecosystem management." The Interagency Ecosystem Management Task Force (IEMTF 1995) was established to carry out this mandate. The ecosystem approach espoused by IEMTF and a wide range of government, industry, and private interest groups is a method for sustaining or restoring natural systems in the face of the cumulative effects of many human actions. In addition to using the best science, the ecosystem approach to management is based on a collaboratively developed vision of desired future conditions that integrates ecological, economic, and social factors. Achieving this shared vision requires developing partnerships with nonfederal stakeholders and improving communication between federal agencies and the public. Many ecosystem management initiatives are underway across the United States. The lessons learned from these experiences should be incorporated into the scoping process under NEPA to address cumulative effects more effectively. The IEMTF specifically recommends that agencies develop regional ecosystem plans to coordinate their review activities under NEPA. These ecosystem plans can provide a framework for evaluating the environmental status quo and the combined cumulative effects of individual projects.

The success of any of these activities is enhanced by coordination with the affected agency. At a minimum, the analyst should establish an ongoing process of periodic consultation and coordination with other agencies early in the scoping process whenever there are significant cumulative effects issues. Where appropriate, the lead agency should pursue cooperating agency status for affected agencies to facilitate reviewing drafts, supplying information, writing sections of the document, and using the

document to support more than one agency's programs.

SCOPING SUMMARY

Scoping for cumulative effects analysis is a proactive and iterative process. It involves a thorough evaluation of the proposed action and its environmental context. During the scoping process, the analyst should

- consult with agencies and other interested persons concerning cumulative effects issues;
- evaluate the agency's planning as well as the proposed action and reasonable alternatives (including the no-action alternative) to identify potential cumulative effects;
- evaluate the importance of the cumulative effects issues associated with a proposed action to identify additional resources, ecosystems, and human communities that should be included in the EA or EIS;
- identify the geographic boundaries for analysis of the cumulative effects on each resource, ecosystem, and human community;

- identify a time frame for the analysis of the cumulative effects on each resource, ecosystem, and human community; and
- determine which other actions should be included in the analysis and agree among interested parties on the scope of the data to be gathered, the methods to be used, the way the process will be documented, and how the results will be reviewed.

At the end of the scoping process, there should be a list of cumulative effects issues to be assessed, a geographic boundary and time frame assigned for each resource analysis, and a list of other actions contributing to each cumulative effects issue. In addition, during scoping the analyst should obtain information and identify data needs related to the affected environment (Chapter 3) and environmental consequences (Chapter 4) of cumulative effects, including resource capabilities, thresholds, standards, guidelines, and planning goals.

3

DESCRIBING THE AFFECTED ENVIRONMENT

PRINCIPLES

- Use natural boundaries.
- Focus on each affected resource, ecosystem, and human community.

Characterizing the affected environment in a NEPA analysis that addresses cumulative effects requires special attention to defining baseline conditions. These baseline conditions provide the context for evaluating environmental consequences and should include historical cumulative effects to the extent feasible. The description of the affected environment relies heavily on information obtained through the scoping process (Chapter 2) and should include all potentially affected resources, ecosystems, and human communities. Determining the cumulative environmental consequences based on the baseline conditions will be discussed in Chapter 4. The affected environment section serves as a "bridge" between the identification during scoping of cumulative effects that are likely to be important and the analysis of the magnitude and significance of these cumulative effects. Specifically, describing the environment potentially affected by

cumulative effects should include the following steps:

Step 5

Characterize the resources, ecosystems, and human communities identified during scoping in terms of their response to change and capacity to withstand stresses.

Step 6

Characterize the stresses affecting these resources, ecosystems, and human communities and their relation to regulatory thresholds.

Step 7

Define a baseline condition for the resources, ecosystems, and human communities.

Describing the affected environment when considering cumulative effects does not differ greatly from describing the affected environment as part of project-specific analyses; however, analyses and supporting data should be extended in terms of geography, time, and the potential for resource or system interactions. In project-specific NEPA analysis, the description of the affected environment is based on a list of resources that may be directly or indirectly affected by the proposed project. In cumulative effects analysis, the analyst must attempt to identify and characterize effects of other actions on these same resources. The affected environment for a cumulative effects analysis,

therefore, may require wider geographic boundaries and a broader time frame to consider these actions (see the discussion on bounding cumulative effects analysis in Chapter 2).

COMPONENTS OF THE AFFECTED ENVIRONMENT

To address cumulative effects adequately, the description of the affected environment should contain four types of information:

- data on the **status** of important natural, cultural, social, or economic **resources and systems**;
- data that characterize important environmental or social **stress factors**;
- a description of pertinent **regulations, administrative standards, and development plans**; and
- data on environmental and socioeconomic **trends**.

The analyst should begin by evaluating the existing resources likely to be cumulatively affected, including one or more of the following: soils, geology and geomorphology, climate and rainfall, vegetative cover, fish and wildlife water quality and quantity, recreational uses, cultural resources, and human community structure within the area of expected project effects. The analyst should also review social and economic data (including past and present land uses) closely associated with the status of the resources, ecosystems, and human communities of concern. The description of the affected environment should focus on how the existing conditions of key resources, ecosystems, and human communities have been altered by human activities. This historical context should include important human stress factors and pertinent environmental regulations and standards. Where possible, trends in the condition of resources, ecosystems, and human communities should be identified. The

description of the affected environment will not only provide the baseline needed to evaluate environmental consequences, but also it will help identify other actions contributing to cumulative effects. While describing the affected environment, the analyst should pay special attention to common natural resource and socioeconomic issues that arise as a result of cumulative effects. The following list describes many issues but is by no means exhaustive:

Air

- Human health hazards and poor visibility from the cumulative effects of emissions that lower ambient air quality by elevating levels of ozone, particulates, and other pollutants.
- Regional and global atmospheric alterations from cumulative additions of pollutants that contribute to global warming, acidic precipitation, and reduced ultraviolet radiation absorption following stratospheric ozone depletion.

Surface Water

- Water quality degradation from multiple point-source discharges.
- Water quality degradation from land uses that result in nonpoint-source pollution within the watershed.
- Sediment delivery to a stream or estuary from multiple sources of soil erosion caused by road construction, forestry practices, and agriculture.
- Water shortages from unmanaged or unmonitored allocations of the water supply that exceed the capacity of the resource.
- Deterioration of recreational uses from nonpoint-source pollution, competing uses for the water body, and overcrowding.

Ground Water

- Water quality degradation from nonpoint- and multiple-point sources of pollution that infiltrate aquifers.
- Aquifer depletion or salt water intrusion following the overdraught of ground-water for numerous uncoordinated uses.

Lands and Soils

- Diminished land fertility and productivity through chemical leaching and salinization resulting from unsustainable agricultural practices.
- Soil loss from multiple, uncoordinated activities such as agriculture on excessive gradients, overharvesting in forestry, and highway construction.

Wetlands

- Habitat loss and diminished flood control capacity resulting from dredging and filling individual tracts of wetlands.
- Toxic sediment contamination and reduced wetlands functioning resulting from irrigation and urban runoff.

Ecological Systems

- Habitat fragmentation from the cumulative effects of multiple land clearing activities, including logging, agriculture, and urban development.
- Degradation of sensitive ecosystems (e.g., old growth forests) from incremental stresses of resource extraction, recreation, and second-home development.
- Loss of fish and wildlife populations from the creation of multiple barriers to migration (e.g., dams and highways).

Historic and Archaeological Resources

- Cultural site degradation resulting from streambank erosion, construction, plowing and land leveling, and vandalism.

- Fragmentation of historic districts as a result of uncoordinated development and poor zoning.

Socioeconomics

- Over-burdened social services due to sudden, unplanned population changes as a secondary effect of multiple projects and activities.
- Unstable labor markets resulting from changes in the pool of eligible workers during "boom" and "bust" phases of development.

Human Community Structure

- Disruption of community mobility and access as a result of infrastructure development.
- Change in community dynamics by incremental displacement of critical community members as part of unplanned commercial development projects.
- Loss of neighborhoods or community character, particularly those valued by low-income and minority populations, through incremental development.

The cumulative effects analyst should determine if the resources, ecosystems, and human communities identified during scoping include all that could potentially be affected when cumulative effects are considered. This means reviewing the list of selected resources in terms of their expanded geographic boundaries and time frames. It also requires evaluating the system interactions that may identify additional resources subject to potential cumulative effects. If scoping addresses a limited set of resources and fails to consider those with which they interact, the analyst should evaluate the need to consider additional resources. The analyst should return to the list of resources frequently and be willing to modify it as necessary; furthermore, the analyst should be able to identify and discuss conflicts between

the resources (such as competition for regulated instream flows between fishery interests and the whitewater boating community).

Status of Resources, Ecosystems, and Human Communities

Determining the status of the affected environment depends on obtaining data about the resources, ecosystems, and human communities of concern. The availability of information continues to vary, but the number of useful indicators of ecological condition has increased greatly in recent years. In particular, indicators of the health or integrity of biological communities are in widespread use by water resource management agencies (Southerland and Stribling 1995). The concept of "indices of biotic integrity" (Karr et al. 1986; Karr 1991) is a powerful tool for evaluating the cumulative effects on natural systems, because biological communities act as integrators of multiple stresses over time. By using biological indicators in conjunction with reference or minimally affected sites, investigators have described the baseline conditions of entire regions. This approach has been applied to many freshwater and estuarine environments. Figure 3-1 describes the status of benthic communities of estuarine organisms in the Chesapeake Bay (Ranasinghe et al. 1994). This kind of information can be used to describe the baseline conditions at both the site and regional scales.

A second major innovation in indicators of resource or ecosystem condition is the development of landscape metrics. The discipline of landscape ecology recognizes that critical ecological processes such as habitat fragmentation require a set of indicators (e.g., habitat pattern shape, dominance, connectivity, configuration) at the landscape scale (Forman and Godron 1986; Risser et al. 1984). Investigators at the Oak Ridge National Laboratory and elsewhere have developed several indicators that can be used in conjunction with remote sensing and GIS technologies to describe the environmental baseline for sites or regions (O'Neill et al. 1988, 1994). The comprehensive spatial coverage and

multiple characterizations over time available from remote sensing make linking these measures to known environmental conditions one of the most promising approaches for assessing status and trends in resources and ecosystems.

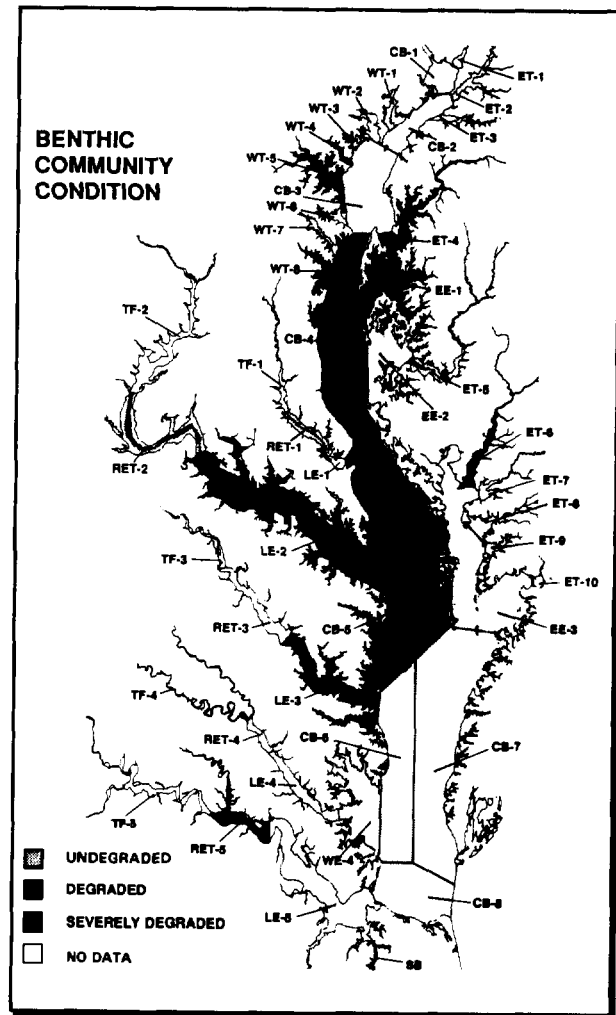


Figure 3-1. Status of benthic communities as a baseline of ecological conditions in the Chesapeake Bay (Ranasinghe et al. 1994)

Indicators have also been developed to gauge the well-being of human communities. Concern about human health and environmental conditions in minority and low-income communities has resulted in directives and guidelines for addressing environmental justice (see box). The structure, or societal setting, of human communities is analogous to the

structure of a natural ecosystem. Human communities are integrated entities with characteristic compositions, structures, and functioning. The community profile draws upon indicators of these aspects to describe the integrity of the community (FHWA 1996). Community indicators can range from general variables such as "social service provision" to specific indicators such as "distance to nearest hospital." Indicators can also be composites of different factors. For example, the familiar "quality of life" indicator is an attempt to merge key economic,

Environmental Justice

In 1994, President Clinton issued Executive Order 12898, "Federal Actions to Address Environmental Justice in Minority Populations and Low-Income Populations," requiring federal agencies to adopt strategies to address environmental justice concerns within the context of agency operations. In an accompanying memorandum, the President emphasizes that existing laws, including NEPA, provide opportunities for federal agencies to address this issue. The U.S. EPA has stated that addressing environmental justice concerns is entirely consistent with NEPA and that disproportionately high and adverse human health or environmental effects on minority or low-income populations should be analyzed with the same tools currently intrinsic to the NEPA process. Specifically, the analysis should focus on smaller areas or communities within the affected area to identify significant effects that may otherwise have been diluted by an examination of a larger population or area. Demographic, geographic, economic, and human health and risk factors all contribute to whether the populations of concern face disproportionately high and adverse effects. Public involvement is particularly important for identifying the aspects of minority and low-income communities that need to be addressed. Early and sustained communications with the affected community throughout the NEPA process is an essential aspect of environmental justice.

cultural, and environmental factors into an overall characterization of community well-being.

Characterization of Stress Factors

Environmental impact assessment is an attempt to characterize the relationship between human activities and the resultant environmental and social effects; therefore, the next step in describing the affected environment is to compile data on stress factors pertaining to each resource, ecosystem, and human community. Table 3-1 lists 26 activities (both existing and proposed), in addition to the proposed action, that may cumulatively affect resources of concern for the Castle Mountain Mining Project (U.S. BLM 1990). For each activity in this example, anticipated cumulative effects are identified for each of 12 resource issues. The primary locations of expected effects are also listed. The analyst should use this kind of stress information to summarize the overall adverse effect on the environment. Analogously, other activities that benefit the environment (e.g., restoration projects) should be included to determine the overall net (adverse or beneficial) effect on the environment. Where activities contributing to cumulative effects are less well defined, a general stress level can be described. For instance, the affected environment discussion need not address every farm in the watershed, but it should note the presence of substantial agricultural activity.

Two types of information should be used to describe stress factors contributing to cumulative effects. First, the analyst should identify the types, distribution, and intensity of key social and economic activities within the region. Data on these socioeconomic "driving variables" can identify cumulative effects problems in the project area (McCabe et al. 1991). For example, population growth is strongly associated with habitat loss. A federal proposal that would contribute to substantial population growth in a specific region (e.g., a highway project traversing a remote area) should be viewed as a likely driving variable for environmental effects.

Table 3-1. Other activities (existing and proposed) that may cumulatively affect resources of concern for the Castle Mountain Mining Project (U.S. BLM 1990)

Description/Responsible Agency	Status	Anticipated Environmental Issues That Could Be Cumulative	Primary Impact Location
Utilities/Services			
1 AT&T Communication cable upgrading (BLMN)	E,P	4,1	IV
2 PacBell microwave sites (BLMN)	E,P	4,1	IV
3 Bio Gen power plant (SBC)	E	2	IV
4 Additional utility lines (1-15 corridor) (BLMN)	P	4,4	IV
5 Whiskey Pete's airstrip/waterline (BLMN)	P	4	IV
6 Solid waste landfill (UP Tracks near state line) (BLMN)	P	4,12	IV
7 Waste water ponds (Ivanpah Lake) (BLMN)	E	4,9	IV
8 Nipton waste site (BLMN)	P	4,9	IV
9 LA-Las Vegas bullet train (BLMN)	P	4,9,10	IV
Commercial and Residential			
10 Nipton land exchange (BLMN)	P	4,6,12	IV
11 Scattered residential units (BLMN)	E,P	--	LV
Recreation			
12 Ivanpah Lake landsailing (BLMN)	E	4,5,10	IV
13 Barstow to Vegas ORV race (BLMN)	E	4,5,10	IV
14 East Mojave Heritage Trail use (BLMN)	E	4,5,10	IV,LV,PV
15 Mojave Road use (BLMN)	E	4,5,10	IV,LV,PV
16 Clark Country Road A68P use (BLMS,CC)	E	4,5,10	PV
Mining			
17 Proposed Action/Alternative - precious metals (BLMN)	P	3,4,5,8,9	LV
18 Colosseum Mine - precious metals (BLMN)	E	3,4,5,8,9	IV
19 Caltrans borrow pits - aggregates (BLMN)	E	4,5	IV
20 Morning Star Mine - precious metals (BLMN)	E	3,4,5,8,9	IV
21 Vanderbilt - precious metals mill site (BLMN)	E	3,4,5,8,9	IV
22 Golden Quail Mine - precious metals (BLMN)	E	3,4,5,8,9	LV
23 Hart District Clay Pits (BLMN)	E	4,9	LV
24 Mountain Pass Mine - rare earth materials (BLMN)	E	3,4,5,8,9	IV
25 Exploratory activities (BLMN, BLMS)	E,P	4,5,9	LV,PV
Grazing			
26 Grazing leases (BLMN, BLMS)	E	4,5	IV,V,PV
Source of Information BLMN: BLM Needles BLMS: BLM Stateline SBC: San Bernardino County, Planning Department CC: Clark County, Planning Department	Status E: Existing P: Proposed	Issues 1 Earth 2 Air 3 Water 4 Wildlife 5 Vegetation 6 Transportation 7 Public Service/Utilities 8 Health/Safety 9 Visual Resources 10 Recreation 11 Cultural Resources 12 Land Use	Location PV: Piute Valley IV: Ivanpah Valley LV: Lanfair Valley

Second, the analyst should look for individual indicators of stress on specific resources, ecosystems, and human communities. Like the familiar "canary in the coal mine," changes in certain resources can serve as an early warning of impending environmental or social degradation (Reid et al. 1991). Indicators of environmental stress can be either exposure-oriented (e.g., contamination levels) or effects-oriented (e.g., loss or degradation of a fishery). High sediment loads and the loss of stable stream banks are both common indicators of cumulative effects from urbanization.

The goal of characterizing stresses is to determine whether the resources, ecosystems, and human communities of concern are approaching conditions where additional stresses will have an important cumulative effect. Simple maps (Figure 3-2) of existing and planned activities can indicate likely cumulative effects, as in the example of Seattle's Southwest Harbor (USACE et al. 1994). Regulatory, administrative, and planning information can also help define the condition of the region and the development pressures occurring within it. Lastly, trends analysis of change in the extent and magnitude of stresses is critical for projecting the future cumulative effect.

Regulations, Administrative Standards, and Regional Plans

Government regulations and administrative standards (e.g., air and water quality criteria) can play an important role in characterizing the regional landscape. They often influence developmental activity and the resultant cumulative stress on resources, ecosystems, and human communities. They also shape the manner in which a project may be operated, the amount of air or water emissions that can be released, and the limits on resource harvesting or extraction. For example, designation of a "Class I" air quality area can restrict some types of development in a region because the Prevention of Significant Deterioration (PSD) requirement establishes a threshold of cumulative air quality degradation.

In the United States, agencies at many different levels of government share responsibilities for resource use and environmental protection. In general, the federal government is charged with functions such as national standard-setting, whereas state governments manage implementation by issuing permits and monitoring compliance with regulatory standards. Each of the states handles environmental regulation and resource management in its own way. Most states have chartered specific agencies for environmental protection, resource management, or both. This information, along with contact names, can be obtained from the Council of State Governments (Brown and Marshall 1993). States usually have discretion under federal law to set standards more stringent than national ones. Land-use decisions are usually made by local governments. Local control may take the form of authority to adopt comprehensive land use plans; to enact zoning ordinances and subdivision regulations; or to restrict shoreline, floodplain, and wetland development. Data on local government issues and programs can be obtained through relevant local government agencies.

The affected environment section of a NEPA analysis should include as many regulations, criteria, and plans as are relevant to the cumulative effects problems at hand. Federal, state, and local resource and comprehensive plans guiding development activities should be reviewed and, where relevant, used to complete characterization of the affected environment. Agencies' future actions and plans pertaining to the identified resources of concern should be included if they are based on authorized plans or permits issued by a federal, state, or other governmental agency; highly speculative actions should not be included. Agency or regional planning documents can provide the analyst with a reasonable projection of future activities and their modes of operation. How project effects fit within the goals of governmental regulations and planning is an important measure of cumulative effects on the resources, ecosystems, and human communities of the region.

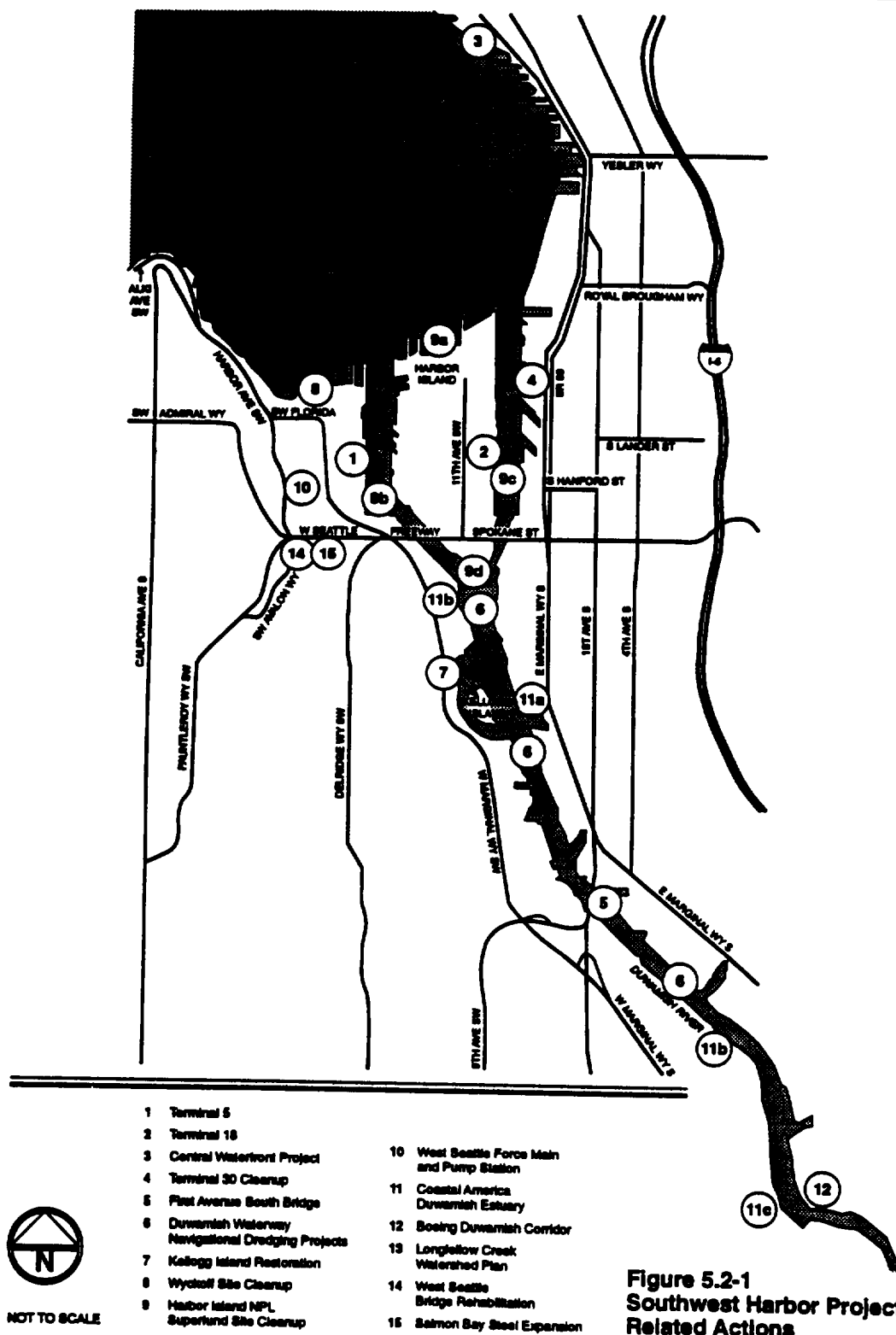


Figure 3-2. Regional map of projects and activities contributing to cumulative effects in Seattle's Southwest Harbor (USACE et al. 1994)

Trends

Cumulative effects occur through the accumulation of effects over varying periods of time. For this reason, an understanding of the historical context of effects is critical to assessing the direct, indirect, and cumulative effects of proposed actions. Trends data can be used in three ways: (1) to establish the baseline for the affected environment more accurately (i.e., by incorporating variation over time), (2) to evaluate the significance of effects relative to historical degradation (i.e., by helping to estimate how close the resource is to a threshold of degradation), and (3) to predict the effects of the action (i.e., by using the model of cause and effects established by past actions).

The ability to identify trends in conditions of resources or in human activities depends on available data. Although data on existing conditions can sometimes be obtained for cumulative effects analysis, analysts can rarely go back in time to collect data (in some cases, lake sediment cores or archaeological excavations can reconstruct relevant historical conditions). Improved technologies for cost-effectively accessing and analyzing data that have been collected in the recent past, however, have been developed. Historical photographs and remotely sensed satellite information can be efficiently analyzed on geographic information systems to reveal trends. The analyst may use these tools to characterize the condition of a resource before contemporary human influences, or the condition at the period when resource degradation was first identified. As shown in Figure 3-3, remote sensing imagery was used to record the change in the condition of the Jemez Mountains, New Mexico (Allen 1994). The 1935 map (left) shows the location of railroads, dirt roads, and primitive roads in the landscape surrounding the Bandelier National Monument. By 1981 (right) the increase in roads and the appearance of several townsites is striking.

This 12-fold increase in total road length is an effective measure of cumulative environmental degradation resulting from the accompanying fire suppression, motorized disturbance of wildlife, creation of habitat edge in forest interiors, and introduction of weedy species along road corridors. The U.S. Forest Service has been using this landscape-scale GIS and remotely sensed information in planning efforts for the Bandelier's headwaters area to ensure that desired forest conditions are maintained (e.g., area and distribution of old growth and densities of snags).

OBTAINING DATA FOR CUMULATIVE EFFECTS ANALYSIS

Obtaining information on cumulative effects issues is often the biggest challenge for the analyst. Gathering data can be expensive and time consuming. Analysts should identify which data are needed for their specific purpose and which are readily available. In some cases, federal agencies or the project proponent will have adequate data; in other cases, local or regional planning agencies may be the best source of information. Public involvement can often direct the analyst to useful information or, itself, serve as an invaluable source of information, especially about the societal setting, which is critical for evaluating effects on human communities. In any case, when information is not available from traditional sources, analysts must be resourceful in seeking alternative sources. Table 3-2 lists some of the possible types and sources of information that may be of use for cumulative effects analysis.

Although most information needed to describe the affected environment must be obtained from regional and local sources, several national data centers are important. Census Bureau publications and statistical abstracts are commonly used for addressing demographic, housing, and general socioeconomic issues, as are several commercial business databases. Currently, an extensive inventory of environmental data coordinated by

The Nature Conservancy through state Natural Heritage Programs (NHPs) and Conservation Data Centers (CDCs) provides the most comprehensive information available about the abundance and distribution of rare species and communities (Jenkins 1988). NHPs and CDCs are continually updated, computer-assisted inventories of the biological and ecological features (i.e., biodiversity elements) of the region in which they are located. These data centers are designed to assist in conservation planning, natural resource management, and environmental impact assessment. Another promising source of data is the U.S. Geological Survey's Biological Resources Division, created

by the consolidation of biological research, inventory and monitoring, and information transfer programs of seven Department of Interior bureaus. The mission of the Division is to gather, analyze, and disseminate the biological information necessary to support sound management of the nation's resources. The U.S. Geological Survey itself was originally created in response to the demands of industry and conservationists for accurate baseline data. Although substantial information can already be obtained from USGS, the implementation of the National Biodiversity Information Infrastructure (NAS 1993) may provide even greater access to comprehensive biological data.

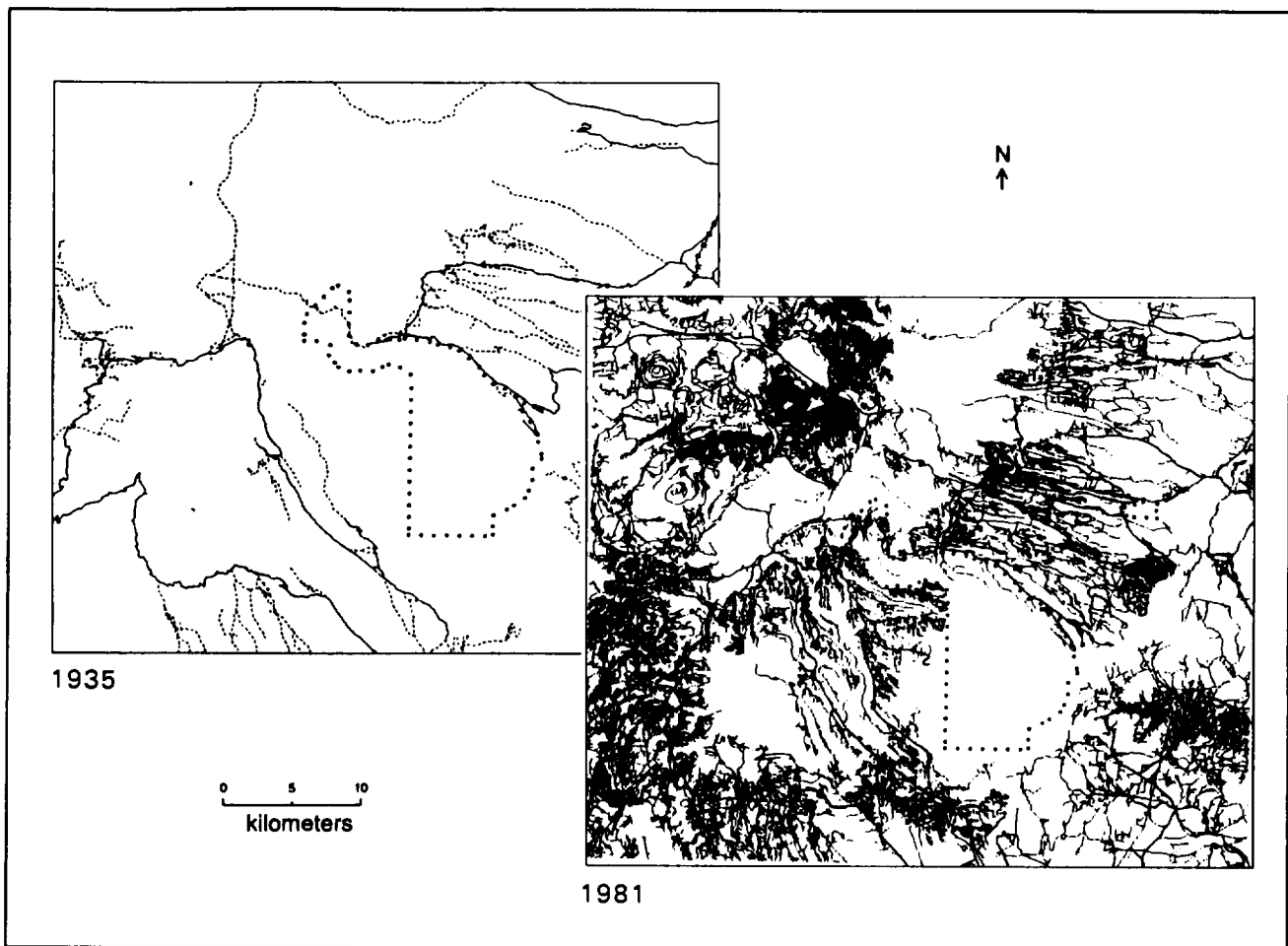


Figure 3-3. Remote sensing imagery illustrating the cumulative increase in roads between 1935 and 1981 across the same 187,858 ha of the Jemez Mountains, New Mexico. The crosshatched line is a railroad; the solid lines are dirt roads; the thin dashed lines are primitive roads' and dotted lines show the current boundary of Bandelier National Monument (Allen 1994).

Table 3-2. Possible sources of existing data for cumulative effects analysis	
Individuals	▪ former and present landholders ▪ long-time residents ▪ long-time resource users ▪ long-time resource managers
Historical societies	Local, state, and regional societies provide: ▪ personal journals ▪ photos ▪ newspapers ▪ individual contacts
Schools and universities	▪ central libraries ▪ natural history or cultural resources collections or museums ▪ field stations ▪ faculty in history and natural and social sciences
Other collections	Private, city, state, or federal collections in : ▪ archaeology ▪ botany ▪ zoology ▪ natural history
Natural history surveys	▪ private ▪ state ▪ national
Private organizations	▪ land preservation ▪ habitat preservation ▪ conservation ▪ cultural resources history ▪ religious institutions ▪ chambers of commerce ▪ voluntary neighborhood organizations
Government agencies	▪ local park districts ▪ local planning agencies ▪ local records-keeping agencies ▪ state and federal land management agencies ▪ state and federal fish, wildlife, and conservation agencies ▪ state and federal regulatory agencies ▪ state planning agencies ▪ state and federal records-keeping agencies ▪ state and federal surveys ▪ state and federal agricultural and forestry agencies ▪ state historic preservation offices ▪ Indian tribal government planning, natural resource, and cultural resource offices
Project proponent	▪ project plans and supporting environmental documentation

Although federal data sources are critical for compiling baseline data, they have substantial limitations. For the most part, federal environmental data programs have evolved to support a specific agency's missions. They are not designed to capture the interconnections among environmental variables or generate information needed for analyses that cut across sectorial and disciplinary lines. The fact that federal databases are often generated by monitoring programs designed to track progress in meeting regulatory goals further inhibits

integration of data (Irwin and Rodes 1992). The only comprehensive effort to develop estimates of baseline ecological conditions across the United States has been the Environmental Monitoring and Assessment Program (EMAP). EMAP has successfully developed indicators for many resources and has applied them in regional demonstration programs to provide statistically rigorous estimates of the condition of ecosystems. Fully implemented, this program would be invaluable for analyzing cumulative effects (see box).

Defining Baseline Ecological Conditions Through EMAP

Over the last decade, EPA has led a multiagency effort to assess the condition of the nation's ecological resources (Messer et al. 1991). The Environmental Monitoring and Assessment Program (EMAP)'s goal is to identify the extent and magnitude of environmental problems on regional and national scales and to provide information that policy makers, scientists, and the public need to evaluate the success of environmental policies and programs (Thornton et al. 1994). EMAP has developed a scientifically rigorous monitoring design (Overton et al. 1990) within which appropriate indicators (Barber 1994) can be sampled to provide the types of information required to address these questions. EMAP has successfully field tested many of the indicators, sampling protocols, and assessment methods required to evaluate the condition of individual ecological resources (Larsen and Christie 1993; Summers et al. 1993; Weisberg et al. 1993; Lewis and Conkling 1994). Although estimates of the condition of certain resources have been developed for certain regions, EMAP has not yet been implemented on a large scale.

EMAP differs from other monitoring programs in the following ways:

- EMAP focuses on assessing ecological condition by measuring biological indicators. Biological indicators provide integrated measures of response to natural and human-induced stress that cannot be obtained from traditional chemical and physical indicators of environmental stresses such as pollutants and habitat modification. The program maintains a core set of indicators that are implemented nationally with uniform methodology and quality control.
- EMAP uses a statistically rigorous sampling design. By measuring indicators within a network of probability samples rather than from sites selected using subjective criteria, EMAP produces unbiased estimates of the status of and changes in indicators of ecological condition with known confidence.
- EMAP takes an ecosystem-oriented approach to monitoring by sampling several ecological resources. EMAP maintains monitoring efforts in agricultural lands, rangelands, forests, estuaries, and surface waters (i.e., lakes and streams). It also maintains cross-cutting activities in landscape characterization, indicator development, and atmospheric deposition.

These attributes make EMAP uniquely suited to addressing cumulative effects. Where regional estimates of ecological condition have been developed, they can be used as baseline conditions for evaluating the effects of new projects. Although EMAP monitoring is currently limited to a few regions of the country, the EMAP approach is being applied to state monitoring efforts that will establish baseline conditions (see Southerland and Weisberg 1995 for application to Maryland streams).

AFFECTED ENVIRONMENT SUMMARY

The description of the affected environment helps the decisionmaker understand the current conditions and the historical context of the important resources, ecosystems, and human communities. The analyst uses this phase of the NEPA process to characterize the region and determine the methodological complexity required to adequately address cumulative

effects. In describing the affected environment, the cumulative effects analyst should

- identify common cumulative effects issues within the region;
- characterize the current status of the resources, ecosystems, and human communities identified during scoping;
- identify socioeconomic driving variables and indicators of stress on these resources;

-
- characterize the regional landscape in terms of historical and planned development and the constraints of governmental regulations and standards; and
 - define a baseline condition for the resources using historical trends.

The affected environment section should include data on resources, ecosystems, and human communities; environmental and socioeconomic stress factors; governmental regulations, standards, and plans; and environmental and social trends. This information will provide the analyst with the baseline and historical context needed to evaluate the environmental consequences of cumulative effects (Chapter 4).

2

SCOPING FOR CUMULATIVE EFFECTS

PRINCIPLES

- Include past, present, and future actions.
- Include all federal, nonfederal, and private actions.
- Focus on each affected resource, ecosystem, and human community.
- Focus on truly meaningful effects.

Expanding environmental impact assessment to incorporate cumulative effects can only be accomplished by the enlightened use of the scoping process. The purpose of scoping for cumulative effects is to determine (1) whether the resources, ecosystems, and human communities of concern have already been affected by past or present activities and (2) whether other agencies or the public have plans that may affect the resources in the future. This is best accomplished as an iterative process, one that goes beyond formal scoping meetings and consultations to include creative interactions with all the stakeholders. Scoping should be used in both the planning and project development stage (i.e., whenever information on cumulative effects will contribute to a better decision).

Scoping information may come from agency consultations, public comments, the analyst's own knowledge and experience, planning activities, the proponent's statements of purpose and need, underlying studies in support of the project proposal, expert opinion,

or other NEPA analyses. This information supports all the steps in cumulative effects analysis, including identifying data for establishing the environmental baseline (see Chapter 3) and identifying information related to impact significance (see Chapter 4). Most importantly, however, scoping for cumulative effects should include the following steps:

Step 1

Identify the significant cumulative effects issues associated with the proposed action and define the assessment goals.

Step 2

Establish the geographic scope for the analysis.

Step 3

Establish the time frame for the analysis.

Step 4

Identify other actions affecting the resources, ecosystems, and human communities of concern.

IDENTIFYING CUMULATIVE EFFECTS ISSUES

Identifying the major cumulative effects issues of a project involves defining the following:

- the direct and indirect effects of the proposed action,
- which resources, ecosystems, and human communities, are affected, and
- which effects on these resources are important from a cumulative effects perspective.

The proposed action may affect several resources either directly or indirectly. Resources can be elements of the physical environment, species, habitats, ecosystem parameters and functions, cultural resources, recreational opportunities, human community structure, traffic patterns, or other economic and social conditions. In a broad sense, all the impacts on affected resources are probably cumulative; however, the role of the analyst is to narrow the focus of the cumulative effects analysis to important issues of national, regional, or local significance. This narrowing can occur only after thorough scoping. The analyst should ask basic questions such as whether the proposed action will have effects similar to other actions in the area and whether the resources have been historically affected by cumulative actions (Table 2-1). Many significant cumulative effects issues are well known. Public interest groups, natural resource and land management agencies, and regulatory agencies regularly deal with cumulative effects. Newspapers and scientific journals frequently publish letters and comments dealing with these issues.

Not all potential cumulative effects issues identified during scoping need to be included in an EA or an EIS. Some may be irrelevant or inconsequential to decisions about the proposed action and alternatives. Cumulative effects analysis should "count what counts", not produce superficial analyses of a long laundry list of issues that have little relevance to the effects of the proposed action or the eventual decisions. Because cumulative effects can result from the activities of other agencies or persons, they may have already been analyzed by others and the importance of the issue determined. For instance, an agency proposing an action with minor effects on wetlands should not unilaterally decide that cumulative effects on wetlands is not an important issue. Cumulative effects analysis should consider the concerns of agencies managing and regulating wetlands,

as well as the regional history of cumulative wetland losses and degradation, and the presence of other proposals that would produce future wetland losses or degradation.

BOUNDING CUMULATIVE EFFECTS ANALYSIS

Once the study goals of the cumulative effects analysis are established, the analyst must decide on the specific content of the study that will meet those requirements. Analyzing cumulative effects differs from the traditional approach to environmental impact assessment because it requires the analyst to expand the geographic boundaries and extend the time frame to encompass additional effects on the resources, ecosystems, and human communities of concern.

Identifying Geographic Boundaries

For a project-specific analysis, it is often sufficient to analyze effects within the immediate area of the proposed action. When analyzing the contribution of this proposed action to cumulative effects, however, the geographic boundaries of the analysis almost always should be expanded. These expanded boundaries can be thought of as differences in hierarchy or scale. Project-specific analyses are usually conducted on the scale of counties, forest management units, or installation boundaries, whereas cumulative effects analysis should be conducted on the scale of human communities, landscapes, watersheds, or airsheds. Choosing the appropriate scale to use is critical and will depend on the resource or system. Figure 2-1 illustrates the utility of using the ecologically relevant watershed boundary of the Anacostia River basin rather than the political boundaries of local governments to develop restoration plans.

A useful concept in determining appropriate geographic boundaries for a cumulative effects analysis is the **project impact zone**.

Table 2-1. Identifying potential cumulative effects issues related to a proposed action

1. What is the value of the affected resource or ecosystem? Is it:
 - protected by legislation or planning goals?
 - ecologically important?
 - culturally important?
 - economically important?
 - important to the well-being of a human community?
2. Is the proposed action one of several similar past, present, or future actions in the same geographic area? (Regions may be land management units, watersheds, regulatory regions, states, ecoregions, etc.) *Examples: timber sales in a national forest; hydropower development on a river; incinerators in a community.*
3. Do other activities (whether governmental or private) in the region have environmental effects similar to those of the proposed action? *Example: release of oxidizing pollutants to a river by a municipality, an industry, or individual septic systems.*
4. Will the proposed action (in combination with other planned activities) affect any natural resources; cultural resources; social or economic units; or ecosystems of regional, national, or global public concern? *Examples: release of chlorofluorocarbons to the atmosphere; conversion of wetland habitat to farmland located in a migratory waterfowl flyway.*
5. Have any recent or ongoing NEPA analyses of similar actions or nearby actions identified important adverse or beneficial cumulative effect issues? *Examples: National Forest Plan EIS; Federal Energy Regulatory Commission Basinwide EIS or EA.*
6. Has the impact been historically significant, such that the importance of the resource is defined by past loss, past gain, or investments to restore resources? *Example: mudflat and salt-marsh habitats in San Francisco Bay.*
7. Might the proposed action involve any of the following cumulative effects issues?
 - long range transport of air pollutants resulting in ecosystem acidification or eutrophication
 - air emissions resulting in degradation of regional air quality
 - release of greenhouse gases resulting in climate modification
 - loading large water bodies with discharges of sediment, thermal, and toxic pollutants
 - reduction or contamination of groundwater supplies
 - changes in hydrological regimes of major rivers and estuaries
 - long-term containment and disposal of hazardous wastes
 - mobilization of persistent or bioaccumulated substances through the food chain
 - decreases in the quantity and quality of soils
 - loss of natural habitats or historic character through residential, commercial, and industrial development
 - social, economic, or cultural effects on low-income or minority communities resulting from ongoing development
 - habitat fragmentation from infrastructure construction or changes in land use
 - habitat degradation from grazing, timber harvesting, and other consumptive uses
 - disruption of migrating fish and wildlife populations
 - loss of biological diversity

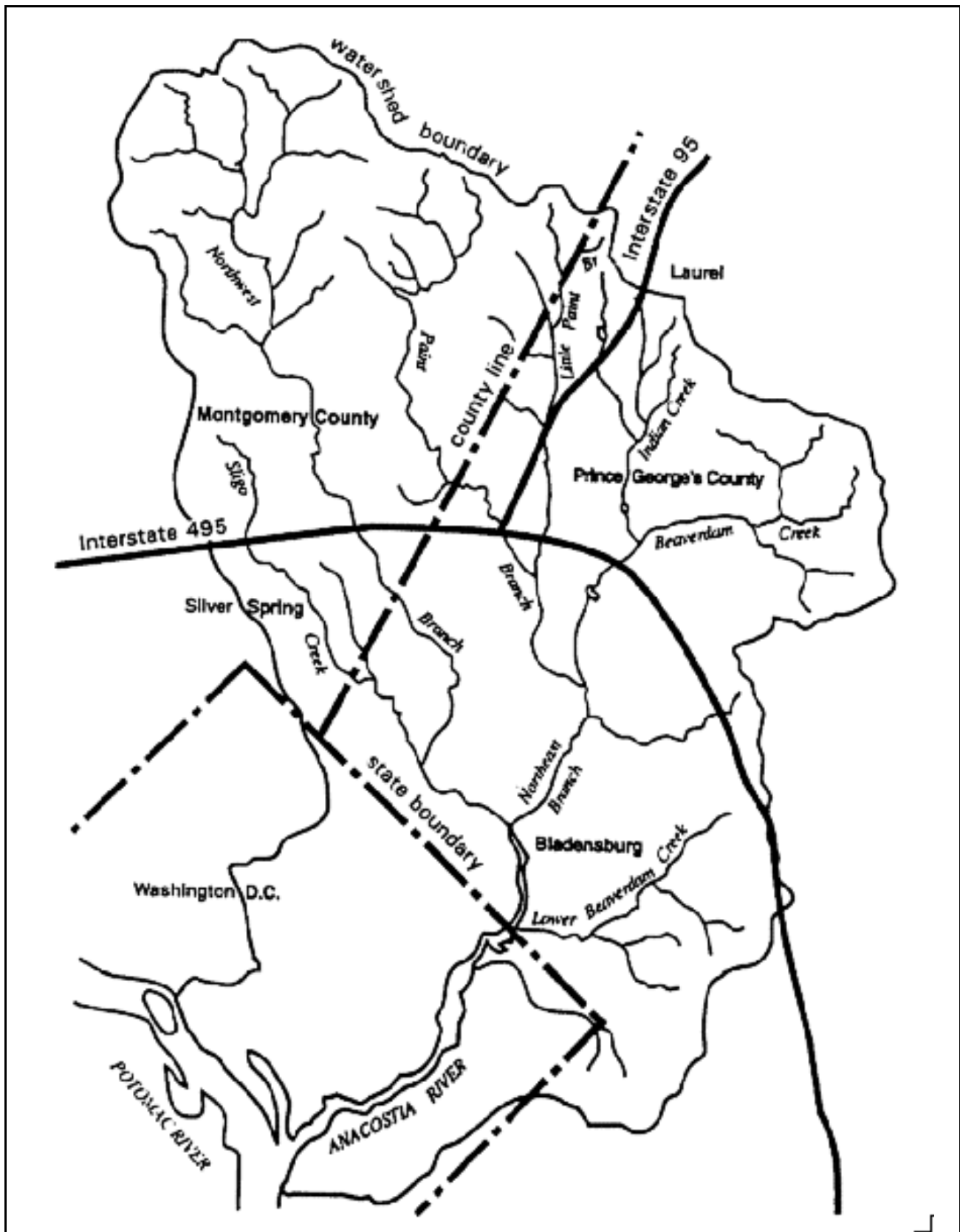


Figure 2-1. Juxtaposition of natural and political boundaries surrounding the Anacostia River

For a proposed action or reasonable alternative, the analysts should

- Determine the area that will be affected by that action. That area is the project impact zone.
- Make a list of the resources within that zone that could be affected by the proposed action.
- Determine the geographic areas occupied by those resources outside of the project impact zone. In most cases, the largest of these areas will be the appropriate area for the analysis of cumulative effects.
- Determine the affected institutional jurisdictions, both for the proposing agency and other agencies or groups.

Project impact zones for a proposed action are likely to vary for different resources and environmental media. For water, the project impact zone would be limited to the hydrologic system that would be affected by the proposed action. For air, the zone may be the physiographic basin in which the proposed action would be located. Land-based effects may occur within some set distance from the proposed action. In addition, the boundaries for an individual resource should be related to the resource's dependence on different environmental media. Table 2-2 provides some possible geographic boundaries for different resources. This list is *not* inclusive. The applicable geographic scope needs to be defined case by case.

Table 2-2. Geographic areas that could be used in a cumulative effects analysis	
Resource	Possible Geographic Areas for Analysis
Air quality	Metropolitan area, airshed, or global atmosphere
Water quality	Stream, watershed, river basin, estuary, aquifer, or parts thereof
Vegetative resources	Watershed, forest, range, or ecosystem
Resident wildlife	Species habitat or ecosystem
Migratory wildlife	Breeding grounds, migration route, wintering areas, or total range of affected population units
Fishery resources	Stream, river basin, estuary, or parts thereof; spawning area and migration route
Historic resources	Neighborhood, rural community, city, state, tribal territory, known or possible historic district
Sociocultural resources	Neighborhood, community, distribution of low-income or minority population, or culturally valued landscape
Land use	Community, metropolitan area, county, state, or region
Coastal zone	Coastal region or watershed
Recreation	River, lake, geographic area, or land management unit
Socioeconomics	Community, metropolitan area, county, state, or country

One way to evaluate geographic boundaries is to consider the distance an effect can travel. For instance, air emissions can travel substantial distances and are an important part of regional air quality. Air quality regions are defined by the EPA, and these regions are an appropriate boundary for assessment of the cumulative effects of releases of pollutants to the atmosphere. For water resources, an appropriate regional boundary may be a river basin or parts thereof. Watershed boundaries are useful for cumulative effects analysis because (1) pollutants and material released in the watershed may travel downstream to be mingled with other pollutants and materials; (2) migratory fish may travel up and down the river system during their life cycle; and (3) resource agencies may have basin-wide management and planning goals. For land-based effects, an appropriate regional boundary may be a "forest or range," a watershed, an ecological region (ecoregion), or socioeconomic region (for evaluating effects on human communities). Which boundary is the most appropriate depends both on the accumulation characteristics of the effects being assessed and an evaluation of the management or regulatory interests of the agencies involved.

Identifying Time Frames

The time frame of the project-specific analysis should also be evaluated to determine its applicability to the cumulative effects analysis. This aspect of the cumulative effects analysis may at first seem the most troublesome to define. CEQ's regulations define cumulative effects as the "incremental effect of the action when added to other past, present, and reasonably foreseeable future actions" (40 CFR § 1508.7). In determining how far into the future to analyze cumulative effects, the analyst should first consider the time frame of the project-specific analysis. If the effects of the proposed action are projected to last five years, this time frame may be the most appropriate for

the cumulative effects analysis. The analyst should attempt to identify actions that could reasonably be expected to occur within that period.

There may be instances when the time frame of the project-specific analysis will need to be expanded to encompass cumulative effects occurring further into the future (Figure 2-2). For instance, even though the effects of a proposed action may linger or decrease slowly through time, the time frame for the project-specific analysis usually does not extend beyond the time when project-specific effects drop below a level determined to be significant. These project-specific effects, however, may combine with the effects of other actions beyond the time frame of the proposed action and result in significant cumulative effects that must be considered.

IDENTIFYING PAST, PRESENT, AND REASONABLY FORESEEABLE FUTURE ACTIONS

As described above, identifying past, present, and future actions is critical to establishing the appropriate geographic and time boundaries for the cumulative effects analysis. Identifying boundaries and actions should be iterative within the scoping process.

A schematic diagram showing the area in which the proposed action is located, the location of resources, and the location of other facilities (existing or planned), human communities, and disturbed areas can be useful for identifying actions to be included in the cumulative effects analysis (Figure 2-3). A geographic information system (GIS) or a manual map overlay system can be used to depict this information (see Appendix A for a description of map overlays and GIS). Such a diagram is useful for determining project-specific impact zones and their overlap with areas affected by other nonproject actions.

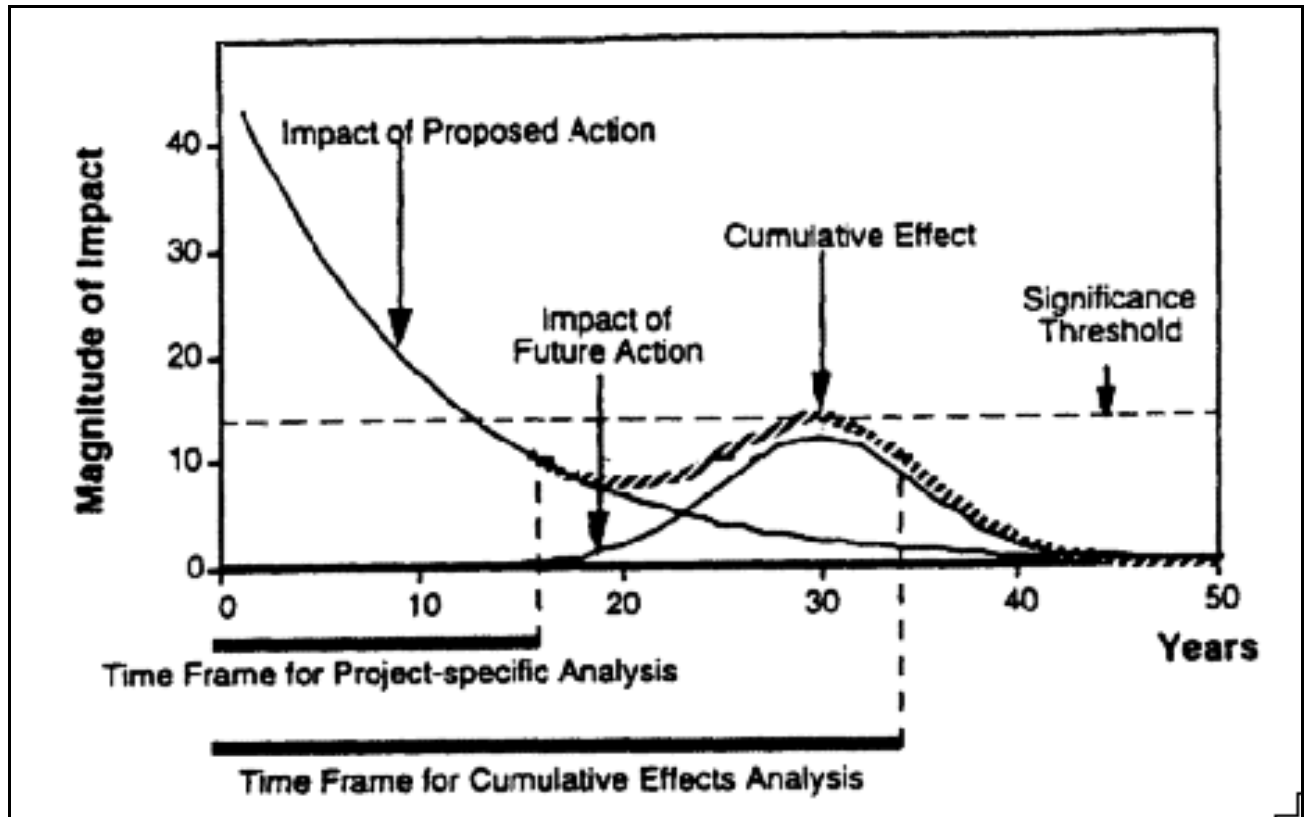


Figure 2-2. Time frames for project-specific and cumulative effects analyses

By examining the overlap of impact zones on the areas occupied by resources, it should be possible to refine the list of projects or activities (past, present, or future) to be included in the analysis. Proximity of actions may not be sufficient justification to include them in the analysis. In the example shown in Figure 2-3, the cumulative effects analysis for trout should consider the effects of the existing mine and the planned logging activity, because these activities would have either present or future effects on the trout spawning area below the proposed power plant facility. Although an agricultural area is nearby, it can be excluded from the analysis because its sediment loading effects occur downstream of the trout spawning area. Proximity of other actions to the proposed action is not the decisive factor for including these actions in an analysis; these actions must have some influence on the resources affected by the proposed action. In other words, these other actions should be included in analysis when

their impact zones overlap areas occupied by resources affected by the proposed action.

Completing the geographic or schematic diagram depending on applying cause-and-effect models that link human actions and the resources or ecosystems. This too is an iterative process. Identifying other activities contributing to cumulative effects could result in the addition of new effect pathways to the cause-and-effect model. In the example, addition of an existing mine to the cumulative effects analysis could require adding a pathway for the effects of chemical pollution on trout. Chapters 4 and 5 and Appendix A discuss cause-and-effect modeling and network analysis.

The availability of data often determines how far back past effects are examined. Although certain types of data (e.g., forest cover) may be available for extensive periods in the past (i.e., several decades), other data (e.g., water quality data) may be available only for

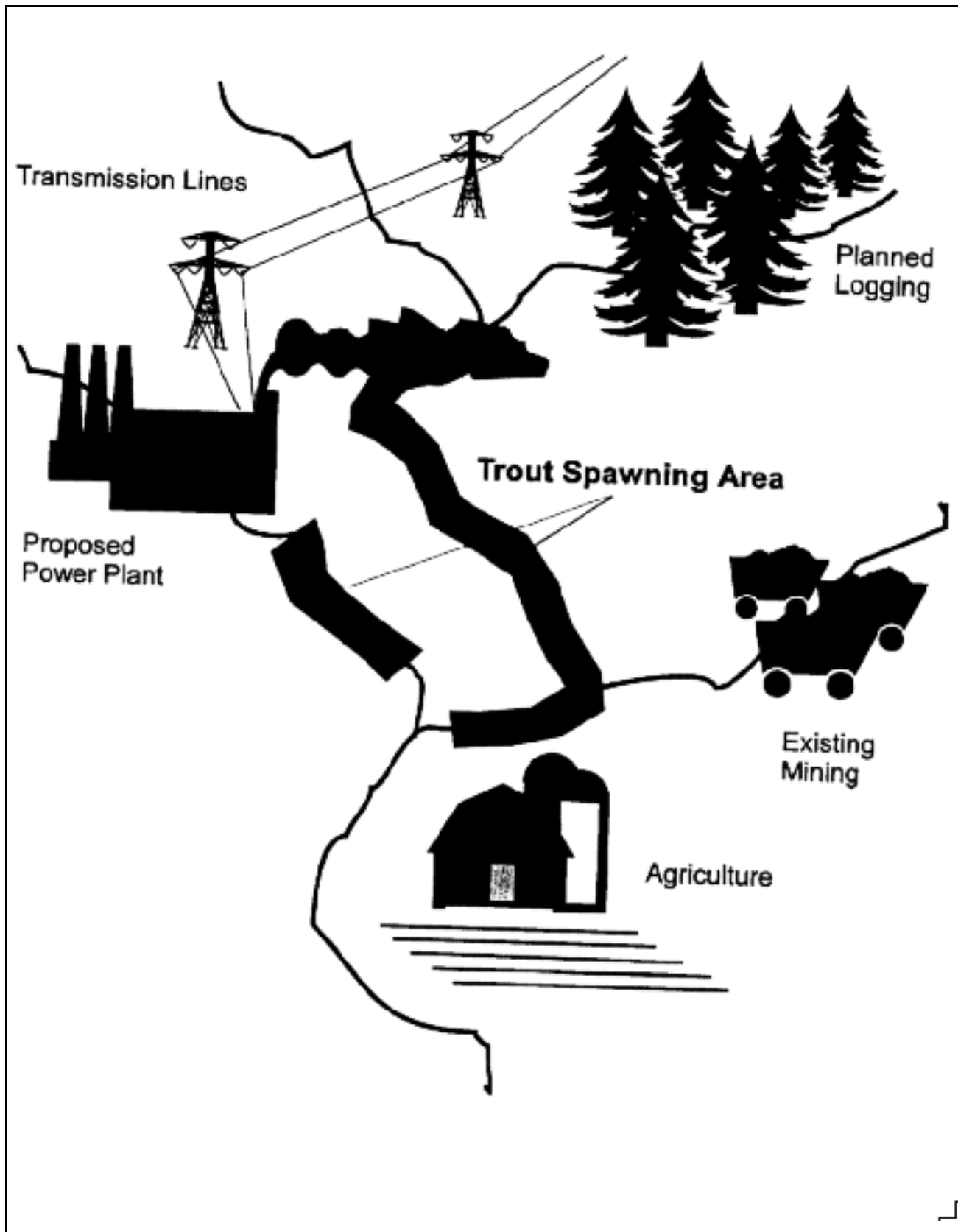


Figure 2-3. Impact zones of proposed and existing development relative to a trout population

much shorter periods. Because the data describing past conditions are usually scarce, the analysis of past effects is often qualitative.

Identifying similar actions presently underway is easier than identifying past or future actions, but it is by no means simple. Because most of the analytical effort in an environmental impact assessment deals with the proposed action, the actions of other agencies and private parties are usually less well known. Effective cumulative effects analysis requires close coordination among agencies to ensure that even all present actions, much less past and future actions, are considered.

The first step in identifying future actions is to investigate the plans of the proponent agency and other agencies in the area. Commonly, analysts only include those plans for actions which are funded or for which other NEPA analysis is being prepared. This approach does not meet the letter or intent of CEQ's regulations. It underestimates the number of future projects, because many viable actions may be in the early planning stage. On the other hand, some actions in the planning, budgeting, or execution phase may not go forward. To include all proposals ever considered as other actions would most likely overestimate the future effects of cumulative effects on the resources, ecosystems, and human communities; therefore, the analyst should develop guidelines as to what constitutes "reasonably foreseeable future actions" based on the planning process within each agency. Specifically, the analyst should use the best available information to develop scenarios that predict which future actions might reasonably be expected as a result of the proposal. Such scenarios are generally based on experience obtained from similar projects located elsewhere in the region. Including future actions in the study is much easier if an agency has already developed a planning document that identifies proposed future actions and has communicated these plans to other federal agencies and governmental bodies in the affected region.

When identifying future actions to include in the cumulative effects analysis, reasonably

foreseeable actions by private organizations or individuals are usually more difficult to identify than those of federal or other governmental entities. In many cases, local government planning agencies can provide useful information on the likely future development of the region, such as master plans. Local zoning requirements, water supply plans, economic development plans, and various permitting records will help in identifying reasonably foreseeable private actions (see Chapter 3 for other sources of information). In addition, some private landowners or organizations may be willing to share their plans for future development or land use. These plans can be considered in the analysis, but it is important to indicate in the NEPA analysis whether these plans were presented by the private party responsible for originating the action. Whenever speculative projections of future development are used, the analyst should provide an explicit description of the assumptions involved. If the analyst is uncertain whether to include future actions, it may be appropriate to bound the problem by developing several scenarios with different assumptions about future actions.

In general, future actions can be excluded from the analysis of cumulative effects if

- the action is outside the geographic boundaries or time frame established for the cumulative effects analysis;
- the action will not affect resources that are the subject of the cumulative effects analysis; or
- including of the action would be arbitrary.

At the same time, NEPA litigation [*Scientists' Institute for Public Information, Inc., v. Atomic Energy Commission* (481 F.2d 1079 D.C. Cir.1073)] has made it clear that "reasonable forecasting" is implicit in NEPA and that it is the responsibility of federal agencies to predict the environmental effects of proposed actions before they are fully known. CEQ's regulations provide for including these uncertainties in the environmental impact assessment where the

foreseeable future action is not planned in sufficient detail to permit complete analysis. Specifically, CEQ's regulations state

[w]hen an agency is evaluating reasonably foreseeable significant adverse effects on the human environment in an environmental impact statement and there is incomplete or unavailable information, ... [that] cannot be obtained because the overall costs of obtaining it are exorbitant or the means to obtain it are not known,... the agency shall include... the agency's evaluation of such impacts based upon theoretical approaches or research methods generally accepted in the scientific community (40 CFR § 1502.22).

Even when the decisionmaker does not select the environmentally preferable alternative, including the cumulative effects of future actions in the analysis serves the important NEPA function of informing the public and potentially influencing future decisions.

AGENCY COORDINATION

Because the actions of other agencies are part of cumulative effects analysis, greater emphasis should be placed on consulting with other agencies than is commonly practiced. Fortunately, when federal agencies adopt the ecosystem approach to management (espoused by the Interagency Ecosystem Management Task Force) such consultation probably will be enhanced (see box). During scoping, periodic coordination with other agencies may enhance the cumulative effects analysis process. As described above, a cumulative effects analysis might

- include an assessment of another agency's proposed action,
- include an assessment of the effects of another agency's completed actions,
- evaluate another agency's resource management practices and goals, or

- evaluate another agency's future plans.

Ecosystem Management

Vice President Gore's National Performance Review called for the agencies of the federal government to adopt "a proactive approach to ensuring a sustainable economy and a sustainable environment through ecosystem management." The Interagency Ecosystem Management Task Force (IEMTF 1995) was established to carry out this mandate. The ecosystem approach espoused by IEMTF and a wide range of government, industry, and private interest groups is a method for sustaining or restoring natural systems in the face of the cumulative effects of many human actions. In addition to using the best science, the ecosystem approach to management is based on a collaboratively developed vision of desired future conditions that integrates ecological, economic, and social factors. Achieving this shared vision requires developing partnerships with nonfederal stakeholders and improving communication between federal agencies and the public. Many ecosystem management initiatives are underway across the United States. The lessons learned from these experiences should be incorporated into the scoping process under NEPA to address cumulative effects more effectively. The IEMTF specifically recommends that agencies develop regional ecosystem plans to coordinate their review activities under NEPA. These ecosystem plans can provide a framework for evaluating the environmental status quo and the combined cumulative effects of individual projects.

The success of any of these activities is enhanced by coordination with the affected agency. At a minimum, the analyst should establish an ongoing process of periodic consultation and coordination with other agencies early in the scoping process whenever there are significant cumulative effects issues. Where appropriate, the lead agency should pursue cooperating agency status for affected agencies to facilitate reviewing drafts, supplying information, writing sections of the document, and using the

document to support more than one agency's programs.

SCOPING SUMMARY

Scoping for cumulative effects analysis is a proactive and iterative process. It involves a thorough evaluation of the proposed action and its environmental context. During the scoping process, the analyst should

- consult with agencies and other interested persons concerning cumulative effects issues;
- evaluate the agency's planning as well as the proposed action and reasonable alternatives (including the no-action alternative) to identify potential cumulative effects;
- evaluate the importance of the cumulative effects issues associated with a proposed action to identify additional resources, ecosystems, and human communities that should be included in the EA or EIS;
- identify the geographic boundaries for analysis of the cumulative effects on each resource, ecosystem, and human community;

- identify a time frame for the analysis of the cumulative effects on each resource, ecosystem, and human community; and
- determine which other actions should be included in the analysis and agree among interested parties on the scope of the data to be gathered, the methods to be used, the way the process will be documented, and how the results will be reviewed.

At the end of the scoping process, there should be a list of cumulative effects issues to be assessed, a geographic boundary and time frame assigned for each resource analysis, and a list of other actions contributing to each cumulative effects issue. In addition, during scoping the analyst should obtain information and identify data needs related to the affected environment (Chapter 3) and environmental consequences (Chapter 4) of cumulative effects, including resource capabilities, thresholds, standards, guidelines, and planning goals.

4

DETERMINING THE ENVIRONMENTAL CONSEQUENCES OF CUMULATIVE EFFECTS

PRINCIPLES

- Address additive, countervailing, and synergistic effects.
- Look beyond the life of the action.
- Address the sustainability of resources, ecosystems, and human communities.

The diversity of proposed federal actions and the environments in which they occur make it difficult to develop or recommend a single method or approach to cumulative effects analysis. In this chapter, we attempt to provide insight into and general guidelines for performing analyses needed to determine the environmental consequences of cumulative effects. We assume the analysis has already been scoped, including stipulating geographic and time boundaries (see Chapter 2), and that appropriate data have been gathered for the resources, ecosystems, and human communities of concern (see Chapter 3). Reference is made, when appropriate, to specific cumulative effects analysis methods described in Chapter 5 and Appendix A.

The analyst must ensure that the resources identified during scoping encompass all those needed for an analysis of cumulative effects. The analyst must also ensure that the relevant past, present, and reasonably foreseeable future

actions have been identified. As an iterative process, cumulative effects analysis often identifies additional resources or actions involved in cumulative effects during the analysis phase. In addition to confirming the resources and actions to be considered, the analyst should complete the following specific steps to determine the environmental consequences of the cumulative effects:

Step 8

Identify the important cause-and-effect relationships between human activities and resources, ecosystems, and human communities.

Step 9

Determine the magnitude and significance of cumulative effects.

Step 10

Modify or add alternatives to avoid, minimize, or mitigate significant cumulative effects.

Step 11

Monitor the cumulative effects of the selected alternative and adapt management.

CONFIRMING THE RESOURCES AND ACTIONS TO BE INCLUDED IN THE CUMULATIVE EFFECTS ANALYSIS

Even though scoping has identified likely important cumulative effects, the analyst should include other important cumulative effects that arise from more detailed consider-

ation of environmental consequences. In addition, as the proposed action is modified or other alternatives are developed (usually to avoid or minimize adverse effects), additional or different cumulative effects issues may arise. Specifically, the proposed action and reasonable alternatives (including the no-action alternative) could affect different resources and could affect them in different ways. For instance, hydroelectric facilities primarily affect aquatic resources by blocking fish migration routes, altering thermal regimes, and eroding stream channels as releases fluctuate. Reasonable alternatives for proposed hydroelectric facilities often include various types of power generating facilities that affect the environment in different ways. For example, the effects of coal-fired electric plants are most often related to coal-mining activities, the release of heated water to nearby water bodies in the cooling process, and the release of a variety of pollutants (including greenhouse gases) to the air during combustion. Nuclear plants also release heated water but they release radioactive materials to the air instead of greenhouse gases. Other past, present, or future actions also should be included in the analysis if evaluation of the cause-and-effect relationships identifies additional stresses affecting resources, ecosystems, and human communities of concern.

IDENTIFYING AND DESCRIBING CAUSE-AND-EFFECT RELATIONSHIPS FOR RESOURCES, ECOSYSTEMS, AND HUMAN COMMUNITIES

In preparing any assessment, the analyst should gather information about the cause-and-effect relationships between stresses and resources. The relationship between the percent of fine sediment in a stream bed and the emergence of salmon fry (Figure 4-1) is an example of a model of cause and effect that can be useful for identifying the cumulative effects on a selected resource. Such a model describes the response of the resource to a change in its environment. To determine the consequences of

the proposed action on the resource, the analyst must determine which cumulative environmental changes (e.g., higher sediment load) will result from the proposed action and other actions.

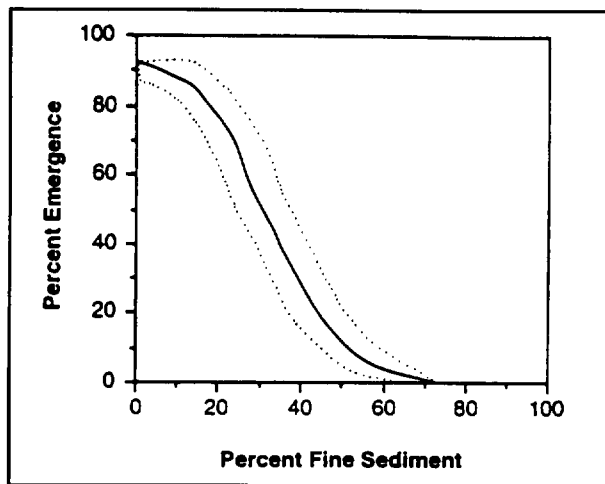


Figure 4-1. Empirical cause and effect relationship between emergence of salmon fry and percent of fine sediment in the stream bottom (Stowell et al. 1983)

Determining the Environmental Changes that Affect Resources

Using information gathered to describe the affected environment, the factors that affect resources (i.e., the causes in the cause-and-effect relationships) can be identified and a conceptual model of cause and effect developed. Networks and system diagrams are the preferred methods of conceptualizing cause-and-effect relationships (see Appendix A). The analyst can develop this model without knowing precisely how the resource responds to environmental change (i.e., the mechanism of the cause-and-effect relationship). If all pathways are identified, the model will be quite complex (Figure 4-2). Such a complex model can seldom be fully analyzed because sufficient data usually are not available to quantify each pathway. Because of this, the model should be simplified to include only important relationships that can be supported by information (Figure 4-3).

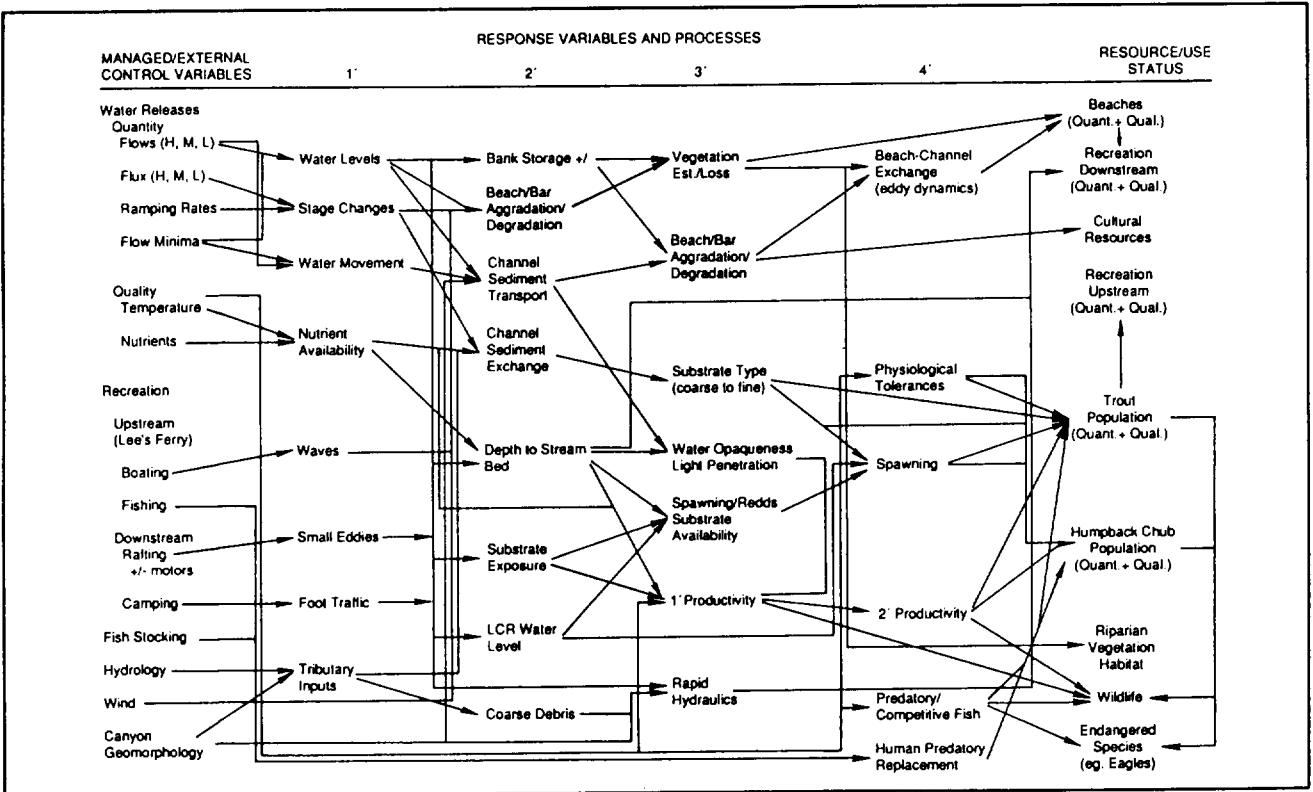


Figure 4-2. Example of a complex model of cause and effect

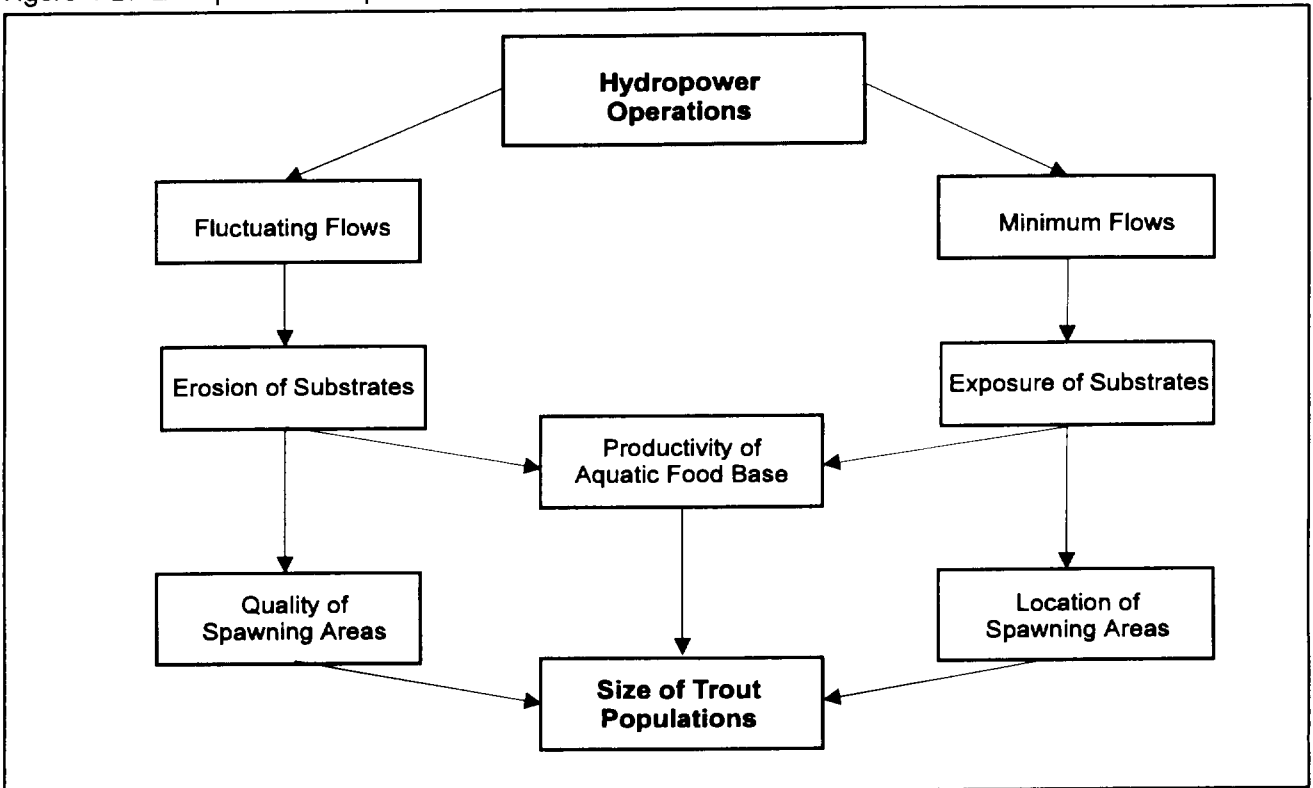


Figure 4-3. Example of a simplified model of cause and effect

The cause-and-effect model can aid in the identification of past, present, and future actions that should be considered in the analysis. In the example shown in Figure 4-3, the analyst should determine if there are other projects in the area that would affect any of the cause-and-effect pathways. The cause-and-effect model for the cumulative effects analysis will often include pathways that would not be needed for a project-specific analysis. Thus, as in defining boundaries, analyzing the consequences of cumulative effects requires broader thinking about the interactions among the activities and resources that affect environmental change.

Determining the Response of the Resource to Environmental Change

Once all of the important cause-and-effect pathways are identified, the analyst should determine how the resource responds to environmental change (i.e., what the effect is). The cause-and-effect relationships for each resource are used to determine the magnitude of the cumulative effect resulting from all actions included in the analysis.

Cause-and-effect relationships can be simple or complex. The magnitude of an effect on a species may depend simply on the amount of habitat that is disturbed. Similarly, effects on archaeological sites may be quantified by enumerating the sites that are disturbed. Other responses may be more complex. The example shown in Figure 4-1 demonstrated that the successful hatching of salmon eggs depends on the percentage of fine particles in the stream bottom in a complex but predictable fashion. Socio-economic models can be applied in a similar way to determine the effects of changes in immigration and emigration rates on the financial condition of a human community.

A wide variety of cause-and-effect evaluation techniques have been described in the literature (see Chapter 5). Techniques for evaluating ecological resources include the set of Habitat Suitability Index Models (HSI;

Schamberger et al. 1982; Hayes 1989) developed by the U.S. Fish and Wildlife Service for its Habitat Evaluation Procedures (HEP; U.S. Fish and Wildlife Service 1980). These models use cause-and-effect relationships for several key environmental variables to determine the suitability of different habitats for a variety of species. The change in number of habitat units (i.e., the ability of an area to support a species) as a result of multiple actions is a useful measure of cumulative effects. Species habitat models also drive the Habitat Evaluation System of the U.S. Army Corps of Engineers (1980). For wetland habitat designations, the Wetland Evaluation Technique is often used (Adamus et al. 1987). Other methods for linking measures of environmental change to effects on resources include developing relationships between loss in wetland area and functions such as flood storage, water quality, and life support (Preston and Bedford 1988; Leibowitz et al. 1992) and linking hydrology first to vegetation and then to wildlife habitat (Nestler 1992).

Nonlinear cause-and-effect relationships among several environmental changes pose an additional challenge for the analyst. A common example is the synergistic effect on fish populations that results from the combination of direct mortality losses to hydropower turbines and increased predation losses that occur as predators are attracted to dead and stunned fish. The analyst may also have to predict additional fish mortality from disease as a result of reductions in immune responses caused by toxic contamination. A third example of a common cumulative cause-and-effect problem is the combined effect on dissolved oxygen levels of excessive algal growth resulting from both increased nutrient loading and higher temperatures.

One of the most useful approaches for determining the likely response of the resource, ecosystem, and human community to environmental change is to evaluate the historical effects of activities similar to those under consideration. In the case of road construction through a

forest, the effects of similar past actions such as the construction of pipelines and power lines may provide a basis for predicting the likely effects of the proposed road construction. The residual effects of constructing and operating these linear facilities include fragmentation of forest tracts and the creation of homogeneous vegetation in the rights-of-way. Trends analysis (see Appendix A) can be used to model the effects of linear facilities over time and extrapolate the effects of a road construction project into the future.

If cause-and-effect relationships cannot be quantified, or if quantification is not needed to adequately characterize the consequences of each alternative, qualitative evaluation procedures can be used. The analyst may categorize the magnitude of effects into a set number of classes (e.g., high, medium, or low) or provide a descriptive narrative of the types of effects that may occur. Often, the analyst will be limited to qualitative evaluations of effects because cause-and-effect relationships are poorly understood or because few site-specific data are available. Even when the analyst cannot quantify cumulative effects, a useful comparison of relative effects can enable a decisionmaker to choose among alternatives.

DETERMINING THE MAGNITUDE AND SIGNIFICANCE OF CUMULATIVE EFFECTS

The analyst's primary goal is to determine the magnitude and significance of the environmental consequences of the proposed action in the context of the cumulative effects of other past, present, and future actions. To accomplish this, the analyst must use a conceptual model of the important resources, actions, and their cause-and-effect relationships. The critical element in this conceptual model is defining an appropriate baseline or threshold condition of the resource, ecosystem, and human community beyond which adverse or beneficial change would cause significant degradation or enhancement of the resource, respectively.

The concept of a baseline against which to compare predictions of the effects of the proposed action and reasonable alternatives is critical to the NEPA process. The no-action alternative is an effective construct for this purpose, but its characterization is often inadequate for analyzing cumulative effects. Much of the environment has been greatly modified by human activities, and most resources, ecosystems, and human communities are in the process of change as a result of cumulative effects. The analyst must determine the realistic potential for the resource to sustain itself in the future and whether the proposed action will affect this potential; therefore, the baseline condition of the resource of concern should include a description of how conditions have changed over time and how they are likely to change in the future without the proposed action.

The potential for a resource, ecosystem, and human community to sustain its structure and function depends on its resistance to stress and its ability to recover (i.e., its resilience). Determining whether the condition of the resource is within the range of natural variability or is vulnerable to rapid degradation is frequently problematic. Ideally, the analyst can identify a threshold beyond which change in the resource condition is detrimental. More often, the analyst must review the history of that resource and evaluate whether past degradation may place it near such a threshold. For example, the loss of 50% of historical wetlands within a watershed may indicate that further losses would significantly affect the capacity of the watershed to withstand floods. It is often the case that when a large proportion of a resource is lost, the system nears collapse as the surviving portion is pressed into service to perform more functions.

The baseline condition should also include other present (ongoing) actions. For example, the National Ambient Air Quality Standards (NAAQS) inventory represents the universe of

present actions used in air quality analyses to determine whether new emission sources will exceed air quality standards. The NAAQS inventory includes all existing emission sources, sources with Prevention of Significant Deterioration (PSD) permits that have not yet begun to operate, and applicants for whom a PSD permit has not yet been issued. The NAAQS analysis requires explicitly modeling all existing nearby sources (as far away as 50 kilometers) be for air quality effects. In the analysis of the cause-and-effect relationships related to the anticipated impacts, each source represents a cause, and their combined emissions create an effect on air quality, the significance of which can be determined by comparing the concentration of pollutants emitted to threshold concentrations specified in the NAAQS. The NAAQS thresholds are concentrations known to cause significant human health or other environmental effects.

The historical context and full suite of ongoing actions are not only critical for evaluating cumulative effects, but also for developing potential restoration as well. The first step in developing a river restoration plan is to understand how past actions (e.g., contributions of contaminants to the watershed) have contributed to the current condition of the water body. The historical trends in resource condition and its current potential for sustained structure and function are an essential frame of reference for developing mitigation and enhancement measures.

Determining Magnitude

Initially, the analyst will usually determine the separate effects of past actions, present actions, the proposed action (and reasonable alternatives), and other future actions. Once each group of effects is determined, cumulative effects can be calculated. The cumulative effects on a specific resource, however, will not necessarily be the sum of the effects of all

actions. Knowing how a particular resource responds to environmental change (i.e., the cause-and-effect relationship) is essential for determining the cumulative effect of multiple actions. Will the effects of two or more actions be additive, i.e., if one project would result in the death of 25% of a trout population (within a given level of uncertainty) and another the death of 10% of the trout, would the two projects together result in the loss of 35% of the trout? Although this is sometimes the case, there are often instances where the cause-and-effect relationship is more complex, i.e., the cumulative effect of two projects may be greater than the sum of the effects of each (in the trout example, more than 35% of the trout would die) or less than their sum (less than 35% of the trout would die). In some cases, the resource may better withstand additional adverse effects as stress increases, while in others, the resource may crash once a threshold is reached.

Once effects are identified using one of the methodologies described in Chapter 5, a table can be used to itemize effects into categories of past, present, proposed, and future actions. Tables 4-1, 4-2, and 4-3 show how these tables can be constructed using the results from different types of analyses. Regardless of the degree of quantification used, such tables are useful tools for putting the effects of the proposed action and alternatives into proper context. Table 4-1 illustrates the net cumulative effects of combining fish population increases from the proposed action with population losses from past and future actions. The table could be expanded to include the countervailing effect of sulfate aerosols on global warming (because they compensate for greenhouse gases) at the same time they are degrading ambient air quality. A series of such tables (one for each alternative) enables the analyst to compare alternatives meaningfully.

Table 4-1. Example table using quantitative description of effects (within a given level of uncertainty) on various resources					
Resource	Past Actions	Present Actions	Proposed Action	Future Actions	Cumulative Effect
Air Quality	No effect on SO ₂	20% increase in SO ₂	10% increase in SO ₂	5% increase in SO ₂	35% increase in SO ₂
Fish	50% of 1950 population lost	2% of fish population lost	5% increase in fish population	1% of fish population lost	48% of 1950 fish population lost
Wetlands	78% of presettlement wetlands lost	1% of existing wetlands lost annually for 5 years	0.5% of existing wetlands lost	1.5% of existing wetlands lost annually for 10 years	95% of presettlement wetlands lost in 10 years

The separation of effects into those attributable to the proposed action or a reasonable alternative versus those attributable to past and future actions also allows the analyst to determine the incremental contribution of each alternative. Situations can arise where an incremental effect that exceeds the threshold of concern for cumulative effects results, not from the proposed action, but from reasonably foreseeable but still uncertain future actions. Although this situation is generally unexplored, the decisionmaker is faced with determining whether to forgo or modify the proposed action to permit other future actions. Identifying incremental effects, therefore, is an important part of informing the decisionmaker.

Most cumulative effects analyses will identify varying levels of beneficial and adverse effects depending on the resource and the individual action. Aquatic species will experience entirely different effects from terrestrial ones. A warm water fishery (e.g., largemouth bass) may benefit from a change that is detrimental to a cold water fishery (e.g., trout), and effects that are beneficial to the well being of a human community (e.g., provision of social services) may be detrimental to natural systems (e.g., wetlands lost during construction of a hospital).

Because of this mixture of beneficial and adverse effects, the decisionmaker is often hard pressed to determine which alternative is environmentally preferred. To overcome this problem, indices of overall cumulative effect can be developed. Some of the matrix methods used in cumulative effects analysis were developed specifically to address this need. These methods use unitless measures of effect (e.g., scales or ranks) to get around the problem of combining results from a variety of resources.

Presentation of overall cumulative effects can be controversial. Intentional or unintentional manipulation of assumptions can dramatically alter the results of aggregated indices (Bisset 1983), and experience indicates that complex quantitative methods for evaluating cumulative effects make it more difficult for the public to understand and accept the results. Effects on resources are usually presented separately, and professional judgment is used in determining the reasonable alternative with the greatest net positive cumulative effect. The U.S. EPA has developed guidelines for addressing specific kinds of risks (including cancer risks and the risks posed by chemical mixtures) and for comparing disparate kinds of risks (U.S. EPA 1993).

Table 4-2. Example table using qualitative description of effects on various resources, with impact ranks assigned a value from 1 to 5 (least to greatest)

Resource	Past Actions	Present Actions	Proposed Action	Future Actions	Cumulative Effect
Air Quality	1	2	1	1	2
Fish	3	2	1	1	4
Wetlands	4	1	1	1	4

Table 4-3. Example table using narrative description of effects on various resources

Resource	Past Actions	Present Actions	Proposed Action	Future Actions	Cumulative Effect
Air Quality	Impacts dissipated	Noticeable deterioration in visibility during summer, but standards met	Visibility affected during operations, but standards met	Increase in auto emissions expected	Standards possibly violated
Fish	Decrease in numbers and species diversity	Occasional documented fish kills	Increase in number of fish kills	Loss of cold-water species due to change in temperature	Significant decline in numbers and species diversity
Wetlands	Large reduction in acreage of wetlands	Loss of small amount of wetland annually	Disturbance of a 5 acre wetland	Continued loss of wetlands	Significant cumulative loss of wetlands

Determining Significance

The significance of effects should be determined based on context and intensity. In its implementing regulations for NEPA, CEQ states that "the significance of an action must be analyzed in several contexts such as society as a whole (human, national), the affected region, the affected interests, and the locality" (40 CFR § 1508.27). Significance may vary with the setting of the proposed action.

Intensity refers to the severity of effect (40 CFR § 1508.27). Factors that have been used to define the intensity of effects include the

magnitude, geographic extent, duration, and frequency of the effects. As discussed above, the **magnitude** of an effect reflects relative size or amount of an effect. **Geographic extent** considers how widespread the effect might be. **Duration and frequency** refers to whether the effect is a one-time event, intermittent, or chronic. Where a quantitative evaluation is possible, specific criteria for significance should be explicitly identified and described. These criteria should reflect the resilience of the resource, ecosystem, and human community to the effects that are likely to occur.

Thresholds and criteria (i.e., levels of acceptable change) used to determine the significance of effects will vary depending on the type of resource being analyzed, the condition of the resource, and the importance of the resource as an issue (as identified through scoping). Criteria can be quantitative units of measure such as those used to determine threshold values in economic impact modeling, or qualitative units of measure such as the perceptions of visitors to a recreational area. No matter how the criteria are derived, they should be directly related to the relevant cause-and-effect relationships. The criteria used, including quantitative thresholds if appropriate, should be clearly stated in the assessment document.

Determinations of significance in an EA or an EIS are the focus of analysis because they lead to additional (more costly) analysis or to inclusion of additional mitigation (or a detailed justification for not implementing mitigation). The significance of adverse cumulative effects is a sensitive issue because the means to modify contributing actions are often outside the purview of the proponent agency. Currently, agencies are attempting to deal with this difficult issue by improving their analysis of historical trends in resource and ecosystem condition. Even where cumulative effects are not deemed to be significant, better characterization of historical changes in the resource can lead to improved designs for resource enhancement. Where projected adverse effects remain highly uncertain, agencies can implement adaptive management—flexible project implementation that increases or decreases mitigation based on monitoring results.

AVOIDING, MINIMIZING, AND MITIGATING SIGNIFICANT CUMULATIVE EFFECTS

If it is determined that significant cumulative effects would occur as a result of a proposed action, the project proponent should avoid,

minimize, or mitigate adverse effects by modifying or adding alternatives. The proponent should not overlook opportunities to enhance resources when adverse cumulative effects are not significant. The separation of responsibilities for actions contributing to cumulative effects makes designing appropriate mitigation especially difficult. In the case of the Lackawanna Industrial Highway, the Federal Highway Administration and Pennsylvania Department of Transportation sponsored development of a comprehensive plan for the valley that provides a mechanism for ensuring that secondary development accompanying construction of the highway would protect valued resources, ecosystems, and human communities (see box).

By analyzing the cause-and-effect relationships resulting in cumulative effects, strategies to mitigate effects or enhance resources can be developed. For each resource, ecosystem, and human community of concern, the key to developing constructive mitigation strategies is determining which of the cause-and-effect pathways results in the greatest effect. Mitigation and enhancement strategies that focus on those pathways will be the most effective for reducing cumulative effects.

It is sometimes more cost-effective to mitigate significant effects after they occur. This might involve containing and cleaning up a spill, or restoring a wetland after it has been degraded. In most cases, however, avoidance or minimization are more effective than remediating unwanted effects. For example, attempting to remove contaminants from air or water is much less effective than preventing pollution discharges into an airshed or watershed. Although such preventative approaches can be the most (or only) effective means of controlling cumulative effects, they may require extensive coordination at the regional or national scale (e.g., federal pollution control statutes).

Mitigating the Secondary and Cumulative Effects of the Lackawanna Valley Industrial Highway

Cumulative effects analysis conducted as part of the EIS for construction of a 16-mile-long, multi-lane, limited access highway in the Lackawanna Valley of Pennsylvania predicted substantial secondary environmental consequences from the expected (and desired) economic development in the valley. Specifically, additional industrial, commercial, and housing development would accompany the economic activity, producing higher demands on the valley's circulation system as well as on central water and sewer services and on other types of community services as well. To ensure that the development occurring as a result of the highway's construction would take place in an environmentally-sensitive manner, the Lackawanna Valley Corridor Plan was developed. This plan was a cooperative study sponsored by the Federal Highway Administration, Pennsylvania Department of Transportation, Pennsylvania Department of Community Affairs, and Lackawanna County through the Lackawanna County Regional Planning Commission (1996). The study produced an overall framework for the future development of the valley, including a Land Use Plan and a Circulation Plan, and a series of land development regulations that may be implemented by valley municipalities to ensure that new development protects community values and environmental resources. By undertaking the Lackawanna Valley Corridor Plan as part of the environmental decisionmaking process for the Lackawanna Valley Industrial Highway, the responsible federal and state agencies provided a concrete mechanism to avoid, minimize, and mitigate potentially adverse cumulative effects from secondary actions beyond their direct control.

ADDRESSING UNCERTAINTY THROUGH MONITORING AND ADAPTIVE MANAGEMENT

The complexity of cumulative effects problems ensures that even rigorous analyses will contain substantial uncertainties about predicted environmental consequences (Carpenter 1995a). Risk assessment methods offer effective ways of presenting the uncertainties to decisionmakers (Carpenter 1995b), and increased scientific knowledge and improved analytical capabilities using modern computers and GIS can help reduce this uncertainty. Nonetheless, both researchers and practitioners generally agree that monitoring is critical to assess the accuracy of predictions of effects and ensure the success of mitigations (Canter 1993). Monitoring provides the means to identify the need for modifying (increasing or decreasing) mitigation, and adaptive management provides the flexible program for achieving these changes. An efficient, cost-effective approach to adaptive management is to sequentially implement mitigation measures so that the measures can be changed as needed (Carpenter 1995c).

It is important to remember that the goal of the NEPA process is to reduce adverse environmental effects (or maximize the net beneficial effect), including cumulative effects. Cumulative effects analysis, therefore, should be an iterative process in which consequences are assessed repeatedly following incorporation of avoidance, minimization, and mitigation measures into the alternatives. In this way, monitoring is the last step in determining the cumulative effects that ultimately result from the action. Important components of a monitoring program for assessing cumulative effects include the following:

- measurable indicators of the magnitude and direction of ecological and social change,
- appropriate timeframe,

-
- appropriate spatial scale,
 - means of assessing causality,
 - means of measuring mitigation efficacy, and
 - provisions for adaptive management.

ENVIRONMENTAL CONSEQUENCES SUMMARY

Although cumulative effects analysis is similar in many ways to the analysis of project-specific effects, there are key differences. To determine the environmental, social, and economic consequences of cumulative effects, the analyst should

- Select the resources, ecosystems, and human communities considered in the project-specific analysis to be those that could be affected cumulatively.
- Identify the important cause-and-effect relationships between human activities and resources of concern using a network or systems diagram that focuses on the important cumulative effects pathways.
- Adjust the geographic and time boundaries of the analysis based on cumulative cause-and-effect relationships.
- Incorporate additional past, present, and reasonably foreseeable actions into the analysis as indicated by the cumulative cause-and-effect relationships.

- Determine the magnitude and significance of cumulative effects based on context and intensity and present tables comparing the effects of the proposed action and alternatives to facilitate decisionmaking.
- Modify or add alternatives to avoid, minimize, or mitigate cumulative effects based on the cause-and-effect pathways that contribute most to the cumulative effect on a resource.
- Determine cumulative effects of the selected alternative with mitigation and enhancement measures.
- Explicitly address uncertainty in communicating predictions to decisionmakers and the public, and reduce uncertainty as much as possible through monitoring and adaptive management.

Determining the environmental consequences entails describing the cause-and-effect relationships producing cumulative effects and summarizing the total effect of each alternative. These activities require developing a cumulative effects analysis methodology (Chapter 5) from available methods, techniques, and tools of analysis (Appendix A).

5

METHODS, TECHNIQUES, AND TOOLS FOR ANALYZING CUMULATIVE EFFECTS

Analyzing cumulative effects under NEPA is conceptually straightforward but practically difficult. Fortunately, the methods, techniques, and tools available for environmental impact assessment can be used in cumulative effects analysis. These methods are valuable in all phases of analysis and can be used to develop the conceptual framework for evaluating the cumulative environmental consequences, designing appropriate mitigations or enhancements, and presenting the results to the decisionmaker.

This chapter introduces the reader to the literature on cumulative effects analysis and discusses the incorporation of individual methods into an analytical methodology. Appendix A provides summaries of 11 methods for analyzing cumulative effects. The research and environmental impact assessment communities continue to make important contributions to the field. In addition to methods developed explicitly for environmental impact assessment, valuable new approaches to solving cumulative effects problems are being put forth by practitioners of ecological risk assessment (Suter 1993; U.S. EPA 1992; U.S. EPA 1996), regional risk assessment (Hunsaker et al. 1990), and environmental planning (Williamson 1993; Vestal et al. 1995). Analysts should use this chapter and Appendix A as a starting point for further research into methods, techniques, and tools that can be applied to their projects.

LITERATURE ON CUMULATIVE EFFECTS ANALYSIS METHODS

Several authors have reviewed the wide variety of methods for analyzing cumulative effects that have been developed over the last 25 years (see Horak et al. 1983; Witmer et al. 1985; Granholm et al. 1987; Lane and Wallace 1988; Williamson and Hamilton 1989; Irwin and Rodes 1992; Leibowitz et al. 1992; Hochberg et al. 1993; Burris 1994; Canter and Kamath 1995; Cooper 1995; Vestal et al. 1995). In a review of 90 individual methods, Granholm et al. (1987) determined that none of even the 12 most promising methods met all of the criteria for cumulative effects analysis. Most of the methods were good at describing or defining the problem, but they were poor at quantifying cumulative effects. No one method was deemed appropriate for all types or all phases of cumulative effects analysis. In general, these authors grouped existing cumulative effects analysis methods into the following categories:

- those that describe or model the cause-and-effect relationships of interest, often through matrices or flow diagrams (see Bain et al. 1986; Armour and Williamson 1988; Emery 1986; Patterson and Whillans 1984);

- those that analyze the trends in effects or resource change over time (see Contant and Ortolano 1985; Gosselink et al. 1990); and
- those that overlay landscape features to identify areas of sensitivity, value, or past losses (see McHarg 1969; Bastedo et al. 1984; Radbruch-Hall et al. 1987; Canters et al. 1991).

These methods address important aspects of considering multiple actions and multiple effects on resources of concern, but they do not constitute a complete approach to cumulative effects analysis. General analytical frameworks for analysis have been developed for the U.S. Army Corp of Engineers (Stakhiv 1991), U.S. Fish and Wildlife Service (Horak et al. 1983), Department of Energy (Stull et al. 1987), U.S. Environmental Protection Agency (Bedford and Preston 1988), and the Canadian Government (Lane and Wallace 1988). In addition, the U.S. EPA and the National Oceanic and Atmospheric Administration have developed two specific approaches to address the problems of cumulative wetlands loss (Leibowitz et al. 1992; Vestal et al. 1995).

These methods usually take one of two basic approaches to addressing cumulative effects (Spaling and Smit 1993; Canter 1994):

- **Impact assessment approach**, which analytically evaluates the cumulative effects of combined actions relative to thresholds of concern for resources or ecosystems.
- **Planning approach**, which optimizes the allocation of cumulative stresses on the resources or ecosystems within a region.

The first approach views cumulative effects analysis as an extension of environmental impact assessment (e.g., Bronson et al. 1991; Conover et al. 1985); the second approach regards cumulative effects analysis as a correlate of regional or comprehensive planning

(e.g., Bardecki 1990; Hubbard 1990; Stakhiv 1988; 1991). Although the impact assessment approach more closely parallels current NEPA practice, an optimizing approach based on a community-derived vision of future conditions may be preferable in the absence of reliable thresholds for the resources, ecosystems, and human communities of concern. In fact, the planning approach to cumulative effects analysis is becoming more common within agencies and intergovernmental bodies as they embrace the principles of ecosystem management (IEMTF 1995) and sustainable development. These two approaches are complementary and together constitute a more complete cumulative effects analysis methodology, one that satisfies the NEPA mandate to merge environmental impact assessment with the planning process.

IMPLEMENTING A CUMULATIVE EFFECTS ANALYSIS METHODOLOGY

Although the NEPA practitioner must draw from the available methods, techniques, and tools it is important to understand that a study-specific methodology is necessary. Designing a study-specific methodology entails using a variety of methods to develop a conceptual framework for the analysis. The conceptual framework should constitute a general causal model of cumulative effects that incorporates information on the causes, processes, and effects involved. A set of primary methods can be used to describe the cumulative effects study in terms of multiple causation, interactive processes, and temporally and spatially variable effects.

The **primary methods** for developing the conceptual causal model for a cumulative effects study are

1

Questionnaires, interviews, and panels to gather information about the wide range of actions and effects needed for a cumulative effects analysis.

2

Checklists to identify potential cumulative effects by reviewing important human activities and potentially affected resources.

- 3 **Matrices** to determine the cumulative effects on resources, ecosystems, and human communities by combining individual effects from different actions.
- 4 **Networks and system diagrams** to trace the multiple, subsidiary effects of various actions that accumulate upon resources, ecosystems, and human communities.
- 5 **Modeling** to quantify the cause-and-effect relationships leading to cumulative effects.
- 6 **Trends analysis** to assess the status of resources, ecosystems, and human communities over time and identify cumulative effects problems, establish appropriate environmental baselines, or project future cumulative effects.
- 7 **Overlay mapping and GIS** to incorporate locational information into cumulative effects analysis and help set the boundaries of the analysis, analyze landscape parameters, and identify areas where effects will be the greatest.

After developing the conceptual framework, the analyst must choose a method to determine and evaluate the cumulative effects of project actions. This method must provide a procedure for aggregating information across multiple resources and projects in order to draw conclusions or recommendations. The simplest method is the comparison of project (or program) alternatives qualitatively or quantitatively in tabular form.

Tables and matrices use columns and rows to organize effects and link activities (or alternatives) with resources, ecosystems, and human communities of concern. The relative effects of various activities can be determined by comparing the values in the cells of a table. The attributes of each cell can be descriptive or numerical. Tables are commonly used to present proposed actions and reasonable alternatives (including no-action) and their respective effects on resources of concern. Tables can be used to organize the full range of environmental, economic, and social effects. Depending on how the table is constructed, a cell may

represent a combination of activities and, therefore, be cumulative, or it may include a separate column for cumulative effects.

Cumulative effects are increasingly appearing as a separate column in EISs. In the case of the cumulative mining effects in the Yukon-Charley Rivers National Preserve, Alaska (National Park Service 1990), the estimated effect of the proposed mining actions on each resource (e.g., riparian wildlife habitat) was evaluated both as a direct effect and as a cumulative effect in combination with past mining losses. Quantitative short-term and long-term effects (in acres) were calculated (Table 5-1). In the case of the Pacific yew (U.S. Forest Service 1993), the potential direct, indirect, and cumulative effects on the genetic resource of the Pacific yew were summarized qualitatively (e.g., risk of genetic erosion at edge of range; Table 5-2).

Some tables are designed explicitly to aggregate effects across resources (including weighting different effects). Grand indices that combine effects include the Environmental Evaluation System (Dee et al. 1973) and ecological rating systems for wildlife habitat and other natural areas (e.g., Helliwell 1969, 1973). Such approaches have been relatively unsuccessful because intentional or unintentional manipulation of assumptions can dramatically alter the results of aggregated indices (Bisset 1983), and because complex quantitative methods for evaluating cumulative effects make it more difficult for the public to understand and accept the results. Westman (1985) concluded that aggregation and weighting of effects should be rejected in favor of providing information in a qualitative, disaggregated form. Although it may not be possible to combine highly disparate resource effects, different resource effects that cumulatively affect interconnected systems must be addressed in combination. In any case, greater efforts need to be made to present the full suite of adverse and beneficial effects to the decisionmaker so that comparisons are clear and understandable.

Table 5-1. Cumulative effects of mining on riparian habitat in Yukon-Charley National Preserve, Alaska (National Park Service 1990)

Study Area Drainage	Habitat (acres)		Long-Term Impacts (acres)			Short-Term Impacts (acres)	
	Premining	Existing (% Premining)	Past Mining Loss	Alternative A Loss	Cumulative Loss	Alternative A Loss	Cumulative Loss
Wood chopper	1,227	1,101(89.7)	126	30	156	26	182
Coal	2,081	1,376 (66.1)	705	20	725	14	739
Sam	1,158	1,148 (99.1)	10	20	30	11	41
TOTAL	4,446	3,615 (81.2)	841	70	911	51	962
Fourth of July	833	777 (93.3)	56	20	76	16	92
GRAND TOTAL	5,299	4,402 (83.1)	897	90	987	67	1,054

Table 5-2. Cumulative effects on the genetic resources of the Pacific yew (U.S. Forest Service 1993)

Alternative	Direct Effects on Existing Levels of Genetic Variation	Indirect Effects on Levels of Genetic Variation in Future Generations	Cumulative Effects
A	Risk of losing small populations at edge of range, thereby reducing existing levels.	Risk of losing small populations at edge of range, thereby reducing future levels.	Risk of genetic erosion at edge of range.
B	None.	None.	Would negate risk to small populations and halt genetic erosion.
C	Risk of slightly reducing levels within population for some populations. No effect on overall variation.	Risk of slightly reducing some populations. No effect on overall variation or values.	Would enhance gene variation.
D	Within population levels could be reduced more than in Alt. C. No effect on overall genetic variation.	Could be reduced more than in Alt. C. for some populations. No overall effect.	Same as Alt. C.
F	Within population levels could be reduced more than in Alt. D. Overall levels of variation would be reduced slightly.	Could be reduced more than in Alt D. Potential significant reduction in adaptability of some populations and some reduction in values.	Same as Alt. C.
G 1	Same as Alt. D.	Same as Alt. D.	Same as Alt. C
G 2	Same as Alt. D.	Same as Alt. D.	Gene conservation would not be well served because of fewer reserves.

Although tables and matrices are the most common method for evaluating the cumulative effect of alternatives, map overlays and modeling can be used to summarize and evaluate cumulative effects.

In general, the standard environmental impact assessment methods described above can be combined effectively to address cumulative effects (Figure 5-1). Two aspects of cumulative effects analysis, however, warrant special analysis methods: (1) the need to address resource sustainability, and (2) the need to focus on integrated ecosystems and human communities. By definition, cumulative effects analysis involves comparing the combined effect with the capacity of the resource, ecosystem, and human community to

withstand stress. **Carrying capacity analysis** has been applied to a wide range of resources to address cumulative effects. Cumulative effects are a more complex problem for whole ecosystems, because ecosystems are subject to the widest possible range of direct and indirect effects. Analyzing the cumulative effects on ecosystems requires a better understanding of the interworkings of ecological systems and a more holistic perspective. Specifically, **ecosystem analysis** entails new indicators of ecological conditions including landscape-scale measures. In addition to these two special methods, analyzing cumulative effects on human communities requires specific **economic impact analysis** and **social impact analysis methods**.

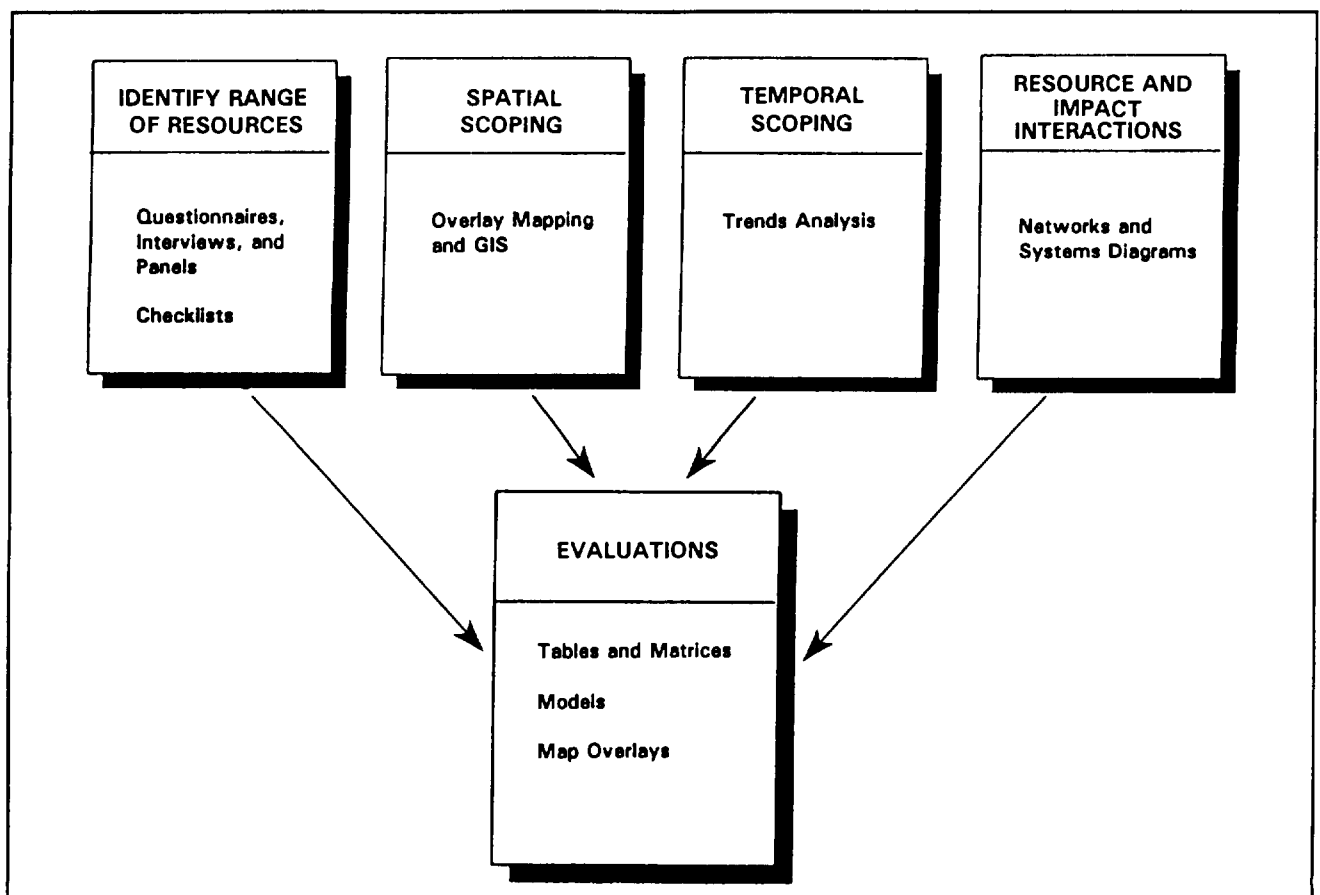


Figure 5-1. Conceptual model for combining primary methods into a cumulative effects analysis

In addition to the primary and special methods discussed above, there are several tools that can be used to conduct or illustrate cumulative effects analysis. The most important are modern computers with capabilities for storing, manipulating, and displaying large amounts of data. Although simple tables, graphs, and hand-drawn maps are adequate for many analyses, powerful computers can facilitate the use of multidimensional matrices and sophisticated models that require solving complex equations or conducting simulations. General tools for illustrating cumulative effects include dose-response curves, cumulative frequency distributions, maps, and videography. Video simulation, wherein an existing site is captured through imagery and electronically altered to show how the site will look after a proposed action is implemented, is a promising new technology for analyzing effects and communicating them to the public (Marlatt et al. 1993).

Most importantly, **geographic information systems (GIS)** can manipulate and display the location-specific data needed for cumulative effects analysis. GIS can be used to manage large data sets, overlay data and analyze development and natural resource patterns, analyze trends, use mathematical models of effect with locational data, perform habitat analysis, perform aesthetic analysis, and improve public consultation (Eedy 1995). GIS can incorporate a statistically reliable locational component into virtually any cumulative effects analysis. Unlike manual mapping systems, the scale can be adjusted and the data layers easily updated. Once a GIS has been developed, it can drastically reduce the effort needed to analyze the effects of future projects, i.e., each new development proposal can be readily overlain on existing data layers to evaluate cumulative effects (Johnston et al. 1988).

Effective use of the increased analytical and presentation capabilities of computers and GIS requires large amounts of data. Fortunately, available **remote sensing** technologies can provide locational information at varying levels of resolution for virtually all parts of the United States. Remote sensing applications (both photographic and satellite imagery) can help the analyst reveal the past status of environmental resources or ecological processes, determine existing environmental conditions, and quantitatively or qualitatively assess possible future trends in the environment. Although remote sensing is a relatively recent technological development, aerial photography available for most areas of the United States since the 1930s or 1940s, and space-based photographs and satellite imagery have been collected since the 1960s. For example, aerial photography from 1960, 1981, and 1990 (Figure 5-2) show change in the condition of small mountainous tributary streams to the North Fork Hoh River in the Olympic Peninsula. The photo taken in 1960 shows undisturbed old growth Sitka spruce-hemlock forest. The photos of the same location taken in 1981 and 1990 show extensive timber harvest and soil erosion. Each patch of harvested timber was approved under individual logging permits over a 30-year period. As a result of the cumulative timber harvest, the area has experienced severe landsliding and erosion, causing sedimentation in salmon spawning and rearing areas in the Hoh River and in lower portions of the tributary streams.

The combination of remote sensing and GIS has facilitated the development of a suite of landscape-scale indicators of ecosystem status that hold promise for quantifying ecological variables and improving the measurement of cumulative effects (Hunsaker and Carpenter 1990; Noss 1990; O'Neill et al. 1988, 1994).

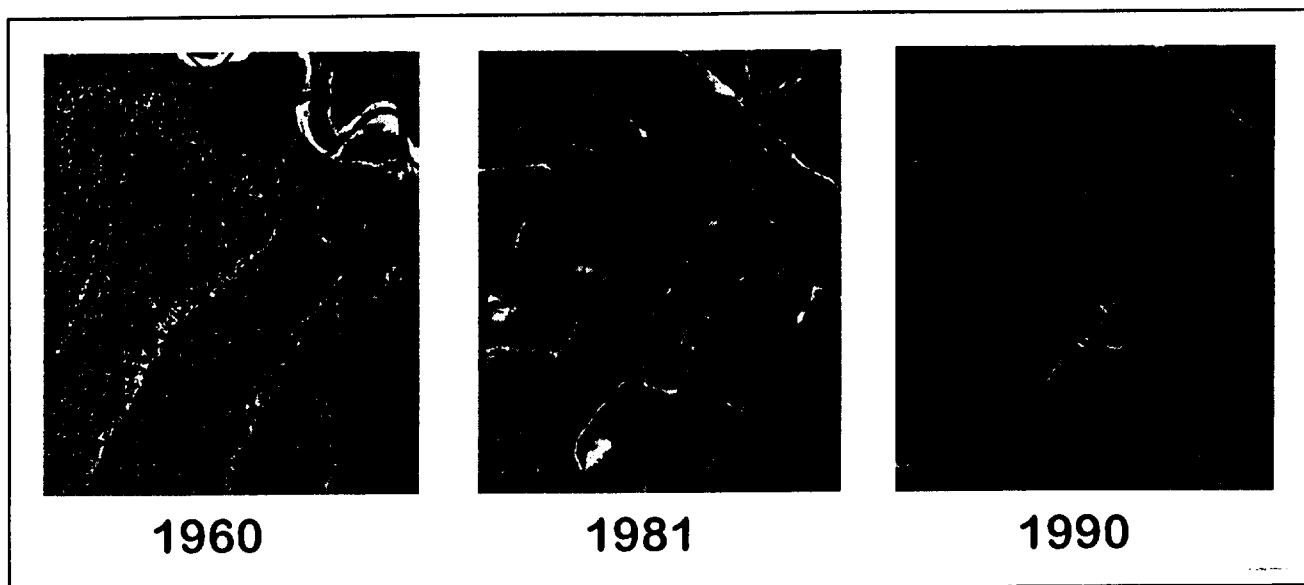


Figure 5-2. Deteriorating trend in watershed condition of the North Fork Hoh River, Washington as illustrated by a time-series of aerial photographs depicting cumulative loss of forest from individual timber sales (Dave Somers, The Tulalip Tribes, personal communication)

Table 5-3 summarizes the 11 important cumulative effects analysis methods discussed above. Appendix A provides standardized descriptions of these methods. Many cumulative effects analysis methods can be adapted for environmental or social impact assessment; the basic analytical frameworks and mathematical operations are often applicable to both social and environmental variables. Each of the 11 methods represents a general category that may contain more specific methods. When and where each method is appropriate for cumulative effects analysis depends on the following criteria:

- 1 Whether the method can assess
 - effects of same and different nature
 - temporal change
 - spatial characteristics
 - structural/functional relationships
 - physical/biological/human interactions

- additive and synergistic interactions
- delayed effects
- persistence of impacts

- 2 Whether the method can
 - quantify effects
 - synthesize effects
 - suggest alternatives
 - serve as a planning or decision-making tool
 - link with other methods, and

- 3 Whether the method is
 - validated
 - flexible
 - reliable and repeatable.

Table 5-3. Primary and special methods for analyzing cumulative effects

Primary Methods	Description	Strengths	Weaknesses
1. Questionnaires, Interviews, and Panels	Questionnaires, interviews, and panels are useful for gathering the wide range of information on multiple actions and resources needed to address cumulative effects. Brainstorming sessions, interviews with knowledgeable individuals, and group consensus building activities can help identify the important cumulative effects issues in the region.	- Flexible - Can deal with subjective information	- Cannot quantify - Comparison of alternatives is subjective
2. Checklists	Checklists help identify potential cumulative effects by providing a list of common or likely effects and juxtaposing multiple actions and resources; - potentially dangerous for the analyst that uses them as a shortcut to thorough scoping and conceptualization of cumulative effects problems.	- Systematic - Concise	- Can be inflexible - Do not address interactions or cause-effect relationships
3. Matrices	Matrices use the familiar tabular format to organize and quantify the interactions between human activities and resources of concern. Once even relatively complex numerical data are obtained, matrices are well-suited to combining the values in individual cells of the matrix (through matrix algebra) to evaluate the cumulative effects of multiple actions on individual resources, ecosystems, and human communities.	- Comprehensive presentation - Comparison of alternatives - Address multiple projects	- Do not address space or time - Can be cumbersome - Do not address cause-effect relationships
4. Networks and System Diagrams	Networks and system diagrams are an excellent method for delineating the cause-and-effect relationships resulting in cumulative effects; they allow the user to analyze the multiple, subsidiary effects of various actions and trace indirect effects to resources that accumulate from direct effects on other resources.	- Facilitate conceptualization - Address cause-effect relationships - Identify indirect effects	- No likelihood for secondary effects - Problem of comparable units - Do not address space or time
5. Modeling	Modeling is a powerful technique for quantifying the cause-and-effect relationships leading to cumulative effects, can take the form of mathematical equations describing cumulative processes such as soil erosion, or may constitute an expert system that computes the effect of various project scenarios based on a program of logical decisions.	- Can give unequivocal results - Addresses cause-effect relationships - Quantification - Can integrate time and space	- Need a lot of data - Can be expensive - Intractable with many interactions
6. Trends Analysis	Trends analysis assesses the status of a resource, ecosystem, and human community over time and usually results in a graphical projection of past or future conditions. Changes in the occurrence or intensity of stressors over the same time period can also be determined. Trends can help the analyst identify cumulative effects problems, establish appropriate environmental baselines, or project future cumulative effects.	- Addresses accumulation over time - Problem identification - Baseline determination	- Need a lot of data in relevant system - Extrapolation of system thresholds is still largely subjective
7. Overlay Mapping and GIS	Overlay mapping and geographic information systems (GIS) incorporate locational information, into cumulative effects analysis and help set the boundaries of the analysis, analyze landscape parameters, and identify areas where effects will be the greatest. Map overlays can be based on either the accumulation of stresses in certain areas or on the suitability of each land unit for development.	- Addresses spatial pattern and proximity of effects - Effective visual presentation - Can optimize development options	- Limited to effects based on location - Do not explicitly address indirect effects - Difficult to address magnitude of effects

Table 5-3. Continued

Special Methods	Description	Strengths	Weaknesses
8. Carrying Capacity Analysis	Carrying capacity analysis identifies thresholds (as constraints on development) and provides mechanisms to monitor the incremental use of unused capacity. Carrying capacity in the ecological context is defined as the threshold of stress below which populations and ecosystem functions can be sustained. In the social context, the carrying capacity of a region is measured by the level of services (including ecological services) desired by the populace.	▪ True measure of cumulative effects against threshold ▪ Addresses effects in system context ▪ Addresses time factors	▪ Rarely can measure capacity directly ▪ May be multiple thresholds ▪ Requisite regional data are often absent
9. Ecosystem Analysis	Ecosystem analysis explicitly addresses biodiversity and ecosystem sustainability. The ecosystem approach uses natural boundaries (such as watersheds and ecoregions) and applies new ecological indicators (such as indices of biotic integrity and landscape pattern). Ecosystem analysis entails the broad regional perspective and holistic thinking that are required for successful cumulative effects analysis.	▪ Uses regional scale and full range of components and interactions ▪ Addresses space and time ▪ Addresses ecosystem sustainability	▪ Limited to natural systems ▪ Often requires species surrogates for system ▪ Data intensive ▪ Landscape indicators still under development
10. Economic Impact Analysis	Economic impact analysis is an important component of analyzing cumulative effects because the economic well-being of a local community depends on many different actions. The three primary steps in conducting an economic impact analysis are (1) establishing the region of influence, (2) modeling the economic effects, and (3) determining the significance of the effects. Economic models play an important role in these impact assessments and range from simple to sophisticated.	▪ Addresses economic issues ▪ Models provide definitive, quantified results	▪ Utility and accuracy of results dependent on data quality and model assumptions ▪ Usually do not address nonmarket values
11. Social Impact Analysis	Social impact analysis addresses cumulative effects related to the sustainability of human communities by (1) focusing on key social variables such as population characteristics, community and institutional structures, political and social resources, individual and family changes, and community resources; and (2) projecting future effects using social analysis techniques such as linear trend projections, population multiplier methods, scenarios, expert testimony, and simulation modeling.	▪ Addresses social issues ▪ Models provide definitive, quantified results	▪ Utility and accuracy of results dependent on data quality and model assumptions ▪ Social values are highly variable

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APPENDIX A

SUMMARIES OF CUMULATIVE EFFECTS ANALYSIS METHODS

1

QUESTIONS, INTERVIEWS, AND PANELS

Questionnaires, interviews, and panels are important information gathering techniques for analyzing cumulative effects. Such techniques are especially valuable to the analyst, because they *collect information on the wide range of actions and effects needed to address cumulative problems*. The analyst will often use brainstorming sessions, interviews with knowledgeable individuals, and group consensus building activities to identify the important cumulative effects issues in the region.

Questionnaires, interviews, and panels are applicable to both social and environmental effects and are used primarily in the scoping process. They are often the principal method for identifying potential efforts and can be used to help characterize spatial and cause-and-effect relationships. Rather than simply collecting data, these techniques can be used for "strategizing" (i.e., prioritizing issues and defining the scope of the study).

The choice of information gathering techniques draws upon the experience and professional judgement of the analysts. Simple brainstorming of experts and other interested parties can be an effective technique for

identifying potential cumulative effects problems. Information gathering can be expanded to include structured interviews with key opinion leaders, indigenous peoples, and technical experts. These activities are essential components of the scoping process and, in many cases, are sufficient for qualitative analysis.

A common feature of information gathering and strategizing is the use of a multi-disciplinary panel of experts. These panels can bring consensus to subjective judgements and are useful for designing the assessment method, evaluating the significance of effects, and comparing alternatives. The Delphi method (Linstone and Turoff 1975) provides a structured process for producing expert consensus and is applicable to groups of various compositions. Fuzzy set models provide another means of structuring subjective evaluations of cumulative effects issues (Harris et al. 1994; Wegner and Reng 1987). Panels or other group-decision methods often use evaluative techniques to score or rank effects during the decisionmaking process. In this way, panels can be used to estimate the importance of cumulative effects even though they are necessarily subjective and qualitative (Stull et al. 1987).

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1 EXAMPLES:

Information gathering is essential to all environmental impact assessment and can become especially involved when scoping for cumulative effects in an EIS. Primarily, the analyst will use questionnaires, interviews, and panels to build a comprehensive list of environmental problems that could accumulate. During preparation of an EIS on the Castle Mountain open heap leach gold mine project, the U.S. Bureau of Land Management (1990) compiled a wide range of information into a list of activities that, combined with the proposed action, might produce cumulative effects (Chapter 3, Table 3-1). For each of 26 individual activities, anticipated cumulative effects were identified for each of 12 resource issues. The status (existing or proposed) of these additional activities and the primary geographical location of effects were also listed.

The analyst will also use these information gathering techniques to help develop a community vision for the region when the cumulative effect of a suite of actions will restore resources. The Restoration Plan for the Exxon Valdez Oil Spill in Alaska involved identifying many individual restoration options that, when combined as an alternative, would have the cumulative beneficial effect of mitigating natural resource damages resulting from the spill. The Restoration Plan required an extremely high level of coordination among federal and state agencies, as well as commercial fishermen, local businesses, and Native American communities. The Restoration Team had the formidable task of determining whether the cumulative effect of a set of restoration

options (an alternative) would meet the public's expectations for restoration of resources. To accomplish this, a scientific conference and many public meetings were held, producing a "Restoration Framework" that served as a scoping document under NEPA (EVOS Trustee Council 1992, 1993). In addition, a questionnaire was distributed to the public along with a summary of the draft Restoration Plan (EVOS Restoration Office 1993) as a means of soliciting public comment on the critical issues addressed by the Restoration Plan.

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2 CHECKLISTS

Checklists can help the analyst identify potential environmental effects by providing a list of common or likely effects. Checklists are especially valuable for analyzing cumulative effects because they *provide a format for juxtaposing multiple actions and resources in a way that highlights potential cumulative effects*. Checklists are potentially dangerous for the analyst who uses them as a shortcut to thorough scoping.

The strength of checklists is that they structure the analysis and reduce the likelihood that major effects will be overlooked; however, checklists are incomplete, they may cause important effects to be omitted. Because of the standard checklist format, checklists are more repeatable than ad hoc methods. They also provide a means of concisely presenting effects. At the same time, the simplicity of the checklist format has disadvantages. A checklist may be either an incomplete compilation of effects or a huge, unwieldy list with many irrelevant

effects. In an attempt to be comprehensive, the checklist may also lead to "double counting" the same effect under different headings.

Many of these disadvantages are avoided by developing checklists for specific kinds of projects. Checklists can also be simplified by organizing potential effects into separate lists or hierarchical categories for each resource, ecosystem, and human community of concern. To address cumulative effects, checklists need to incorporate all of the activities associated with the proposed action and other past, present, and future actions affecting the resources. A promising approach is to use project-specific checklists (for each relevant past, present, and future action) to identify and quantify effects on resources and then transfer these effects to a cumulative checklist or interaction matrix (see Method 3). Two or more effects on a single resource indicate a potential cumulative effect; weighted effects can be summed to indicate the magnitude of the effect.

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2 EXAMPLES:

Specific checklists have been developed for many different classes of actions (e.g., housing projects, sewage treatment facilities, power plants, highways, airports). Several federal agencies have standard checklists for preparing EISs or EAs (e.g., U.S. DOE 1994). The California Department of Transportation (1993) has developed a checklist of 56 questions that must be answered for each state highway project. Question 55 specifically addresses cumulative effects:

Does the project have environmental effects which are individually limited, but cumulatively considerable? Cumulatively considerable means that the incremental effects of an individual project are considerable when viewed in connection with the effects of past projects, the effects of other current projects, and the effects of probable future projects. It includes the effects of other projects which interact with this project and, together, are considerable.

This kind of "simple" questionnaire checklist acts merely as a reminder to the analyst and does not include supplemental information about the likely kinds of effects that may arise. Canter and Kamath (1995) have developed a comprehensive, yet generic, questionnaire checklist that addresses the cumulative effects

of projects. "Descriptive" checklists expand on the checklist concept by including information on measuring and predicting effects (Canter 1996). A more elaborate descriptive checklist is the environmental impact computer system developed by the U.S. Army Construction Engineering Laboratory (Lee et al. 1974). This system identifies potential environmental effects from 9 functional areas of Army activities on 11 broad environmental categories (Jain and Kumar 1973). This computer system can produce checklists of potential effects arising from up to 2,000 Army activities on 1,000 environmental factors. The organization of activities and resources in the same table constitutes an interaction matrix as originally devised by Leopold and others (1971).

Checklists can also be modified to include qualitative terms for each identified effect, such as "adverse" or "beneficial," "short-term" or "long-term," and "no effect" or "significant effect." The hypothetical cumulative checklist in Table A-1 uses a qualitative symbol in place of the usual checkmark next to each potential effect on the list. In this example, the cumulative effects column reflects the number or magnitude of cumulative effects identified for that resource row. More sophisticated uses of this tabular approach are discussed in the matrices section that follows.

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Table A-1. Hypothetical checklist for identifying potential cumulative effects of a highway project

Potential Impact Area	Proposed Action			Past Actions	Other Present Actions	Future Actions	Cumulative Impact
	Construction	Operation	Mitigation				
Topography and Soils	**			*			**
Water Quality	**	*	+	*	*	*	***
Air Quality		**		*			**
Aquatic Resources	**	**	+	*		*	**
Terrestrial Resources	*	*		*			**
Land Use	*	***		*		*	***
Aesthetics	**	***	+	*			**
Public Services	*	+				+	+
Community Structure		*			*		*
Others							
KEY: * low adverse effect ** moderate adverse effect *** high adverse effect + beneficial effect □ no effect							

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3 MATRICES

Matrices are two-dimensional checklists that attempt to quantify the interactions between human activities and resources or ecosystems of concern. They were designed to assess the magnitude and importance of individual interactions between activities and resources (Leopold et al. 1971) but have been extended to consider the cumulative effects of multiple actions on resources (Bain et al. 1986; Stull et al. 1987; LaGory et al. 1993).

Matrices alone cannot quantify effects, but they are a useful means of presenting and manipulating quantitative results of modeling, mapping, and subjective techniques. Once even relatively complex numerical data are obtained, matrices are well-suited to *combining the values in individual cells in the matrix (through matrix algebra) to evaluate the cumulative effects of multiple actions on individual resources, ecosystems, and human communities*. Matrices have the advantage of being mathematically straightforward and readily amenable to interpretation because of their familiar tabular format. Matrices are commonly used in social science research and have the potential for increased application in social and economic analyses.

The values entered in a matrix can take one of several forms. The analyst may elect to simply note the presence or absence of an effect (i.e., a binary entry). This has the benefit of being straightforward and readily understandable; however, it fails to note the magnitude of

effects on various resources and does not allow the user to value resources differentially (e.g., through the use of numeric weights). Thus, a binary approach does not facilitate analyzing the cumulative effects on a resource, where the activities have consequences of varying degrees.

Analysts may instead choose to score effects based on factors such as magnitude, importance, duration, probability of occurrence, or feasibility of mitigation. The value entered may reflect some measurable value (e.g., soil loss may be expressed in tons/acre/ year), or it may reflect some relative ranking of the effect. Although complex weighting schemes allow the user to rank resource effects, the results may be difficult for others to understand, and the weighting schemes can be highly subjective. When using weighting schemes, analysts should enunciate the ranking criteria and consider whether it is scientifically reasonable to attempt a numeric comparison of cumulative effects on different resources.

The matrix concept can be extended to include stepped matrices that display resources against other resources (Canter 1996). Stepped matrices address secondary and tertiary effects of initiating actions and facilitate tracing effects through the environment. For example, action 1 causes changes in resource A which causes further changes in resource B. Stepped matrices are an intermediate method between simple matrices and networks and system diagrams (see Method 4).

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3 EXAMPLES:

Matrices were first formally proposed for environmental impact assessment by the U.S. Geological Survey (Leopold et al. 1971). Since that time a number of matrix methods have been proposed for analyzing cumulative effects. One such methodology is the Cluster Impact Assessment Procedure (CIAP) developed by the Federal Energy Regulatory Commission in the mid-1980s (FERC 1985, 1986a; Russo 1985). The methodology was developed specifically for use in assessing the cumulative effects of small hydroelectric facilities within single watersheds. The CIAP uses a matrix for each resource (e.g., salmon) consisting of relative effect ratings (on a scale from 1 to 5) arranged by project and resource components (e.g., for salmon, spawning habitat, migration). Each resource matrix table contains a summary column that represents the sum of effect ratings across components for each project (Figure A-1). An overall summary table is then developed that presents the effects of each project on all resources analyzed.

The CIAP does not incorporate or consider the possibility of synergistic interactions among projects that could result in nonadditive effects on resources; the effects of individual projects are simply added together to determine cumulative effects. This short-coming led to modification of the methodology to include interaction effects. With these modifications, cumulative

effects are viewed as being equivalent to the sum of the effects of individual projects plus any interaction between pairs of projects. Modified CIAP procedures include the approach used in the Salmon River and Snohomish River EISs for hydroelectric development in those basins (FERC 1986b, 1987; Irving and Bain 1993). Other matrix methodologies that incorporate interaction effects have been proposed (Bain et al. 1986; Stull et al. 1987; LaGory et al. 1993). Each represents a further development of the approach with an attempt to more accurately quantify cumulative impacts; consequently, each succeeding methodology attains additional complexity.

The Integrated Tabular Methodology (Stull et al. 1987; LaGory et al. 1993) uses the same matrix approach as Bain et al. (1986) but involves a systematic (albeit relatively complex) method of quantifying and developing interaction coefficients. To determine interaction coefficients, this method requires identification of the impact zones for all projects being evaluated as well as knowledge of the response of resources to environmental change. The methodology is designed to be flexible and can use a wide variety of data and models. For example, the methodology can use evaluative criteria such as effect ratings, habitat suitability indices (USFWS 1980; Bovee 1982), or quantitative population models.

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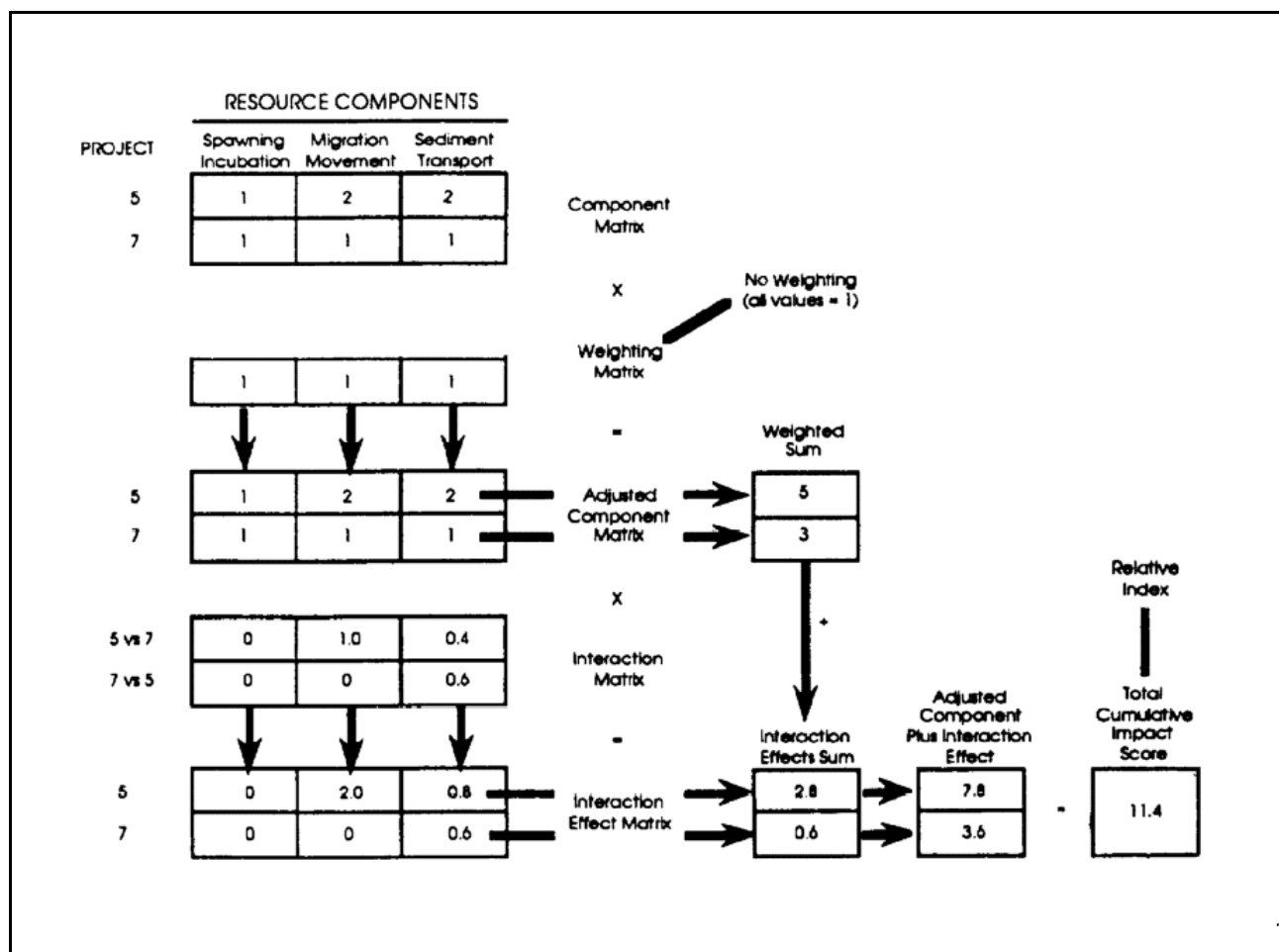


Figure A-1. Example of cumulative impact computations for a target resource with three resource components and two projects (FERC 1987).

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4

NETWORKS AND SYSTEM DIAGRAMS

Networks and system diagrams relate the components of an environmental or social system in a chain (network) or web (loop or system diagram) of causality and allow the user to trace cause and effect through a series of potential links. They allow the user to analyze the multiple, subsidiary effects of various actions and trace indirect effects on resources stemming from direct effects on other resources. In this way, the accumulation of multiple effects on individual resources, ecosystems, and human communities can be determined. *Networks and system diagrams are often the analyst's best method for identifying the cause-and-effect relationships that result in cumulative effects.*

Networks, loops, and system diagrams improve on the stepped matrix approach to illustrating the relationship among actions, effects, and environmental or socioeconomic conditions by using component boxes (or symbols) and linkage arrows (denoting processes). Networks and system diagrams concisely illustrate interactions among variables and secondary effects. Cumulative effects are identified whenever multiple sources affect the same resource, or when multiple effects of the same source affect a resource (via indirect pathways through other resource components). When quantitative measures are included, effects and their interactions can be evaluated using a common unit of measurement (usually energy flow). The use of a common scale distinguishes networks and system diagrams from other cumulative effects analysis methods but requires evaluating different classes of effects separately (e.g., ecological versus social impacts).

By definition, network analysis proceeds in only one direction (forward), whereas loops or system diagrams allow feedback of information output by one part of the system to any other part of the system. Networks also assume a strict hierarchical linkage among system variables and are thus not capable of showing all relationships among variables. In contrast, system diagrams are specifically designed to illustrate the interrelationships (and process pathways) among all components and thus are more realistic. The lack of an appropriate unit of measure for all system compartments can limit the analyst's ability to quantify system diagrams, but some success has been obtained by using the flow of water or energy flow as common units of measure (Gilliland and Risser 1977).

Expert systems can be used to implement network analysis. Expert systems are simply sets of logical rules that mirror the analysis process of an expert in some field. To identify cumulative effects, an expert system would (1) query the analyst about additional activities that might affect the resource in question and (2) carry the predicted effects through known causal links to reveal additional secondary effects on each resource. The line of questioning will take different courses, depending on the user's answers to questions along the way. The program used to work its way through the questions and answers is called an inference engine.

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4 EXAMPLES:

Since the introduction of network analysis for impact assessment by Sorensen (1971), networks and systems diagrams have been useful for describing cause-and-effect relationships in both natural and human-dominated systems. Figure A-2 illustrates how cumulative effects on socioeconomic conditions can be identified. The figure (modified from Rau and Wooten 1985) shows how the removal of both homes and businesses (following freeway construction) cumulatively results in an increase in property tax rate at the tetrinary level of effects. A comprehensive network (Figure A-3) illustrating all causes, perturbations, primary effects, and secondary effects related to coastal zone development was prepared for the

Australian (Commonwealth) Environmental Protection Agency (1994).

An example of the case of a single activity resulting in cumulative effects on a single resource through indirect effects is illustrated in Figure A-4 (Bisset 1983). This system diagram shows damage to fish spawning resulting from aerial application of herbicides through five different pathways resulting in low dissolved oxygen and high sediment stress. Low dissolved oxygen is caused by decreased plankton growth and increased oxygen consumption from debris pollution and erosion; increased sediment is also caused by debris pollution and increased erosion following the loss of riparian vegetation.

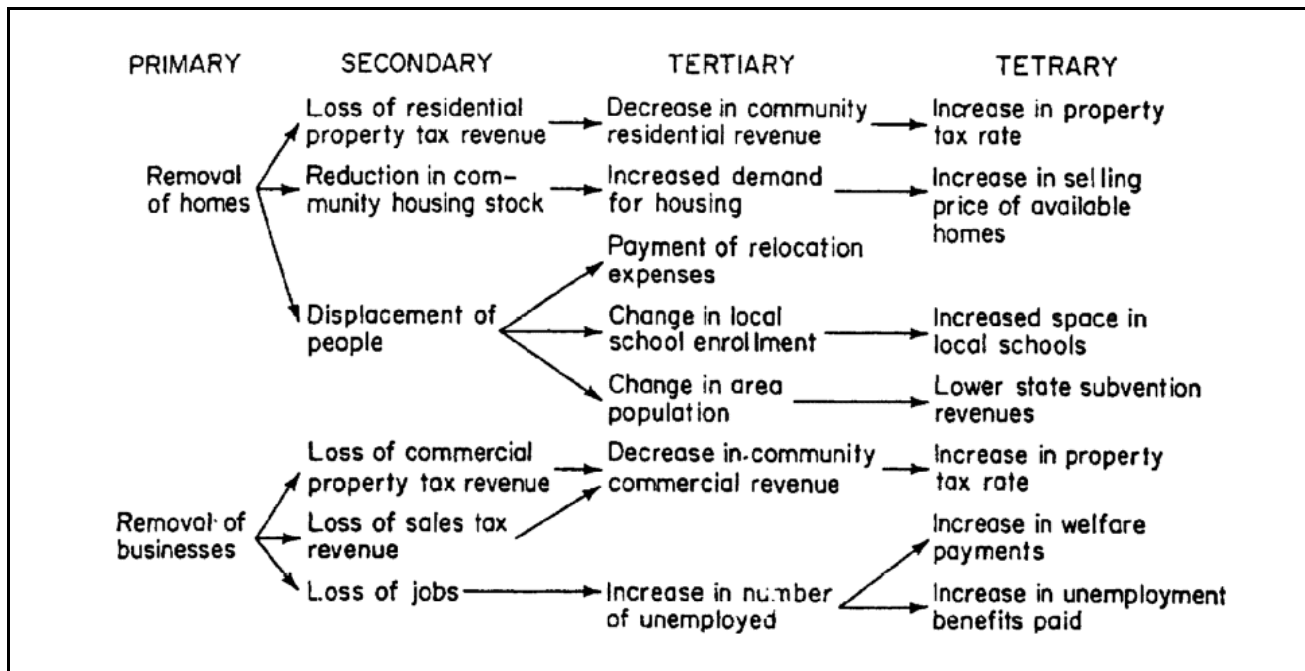


Figure A-2. Example of an "impact tree" for new freeway construction in an established downtown business district (modified from Rau and Wooten 1985)

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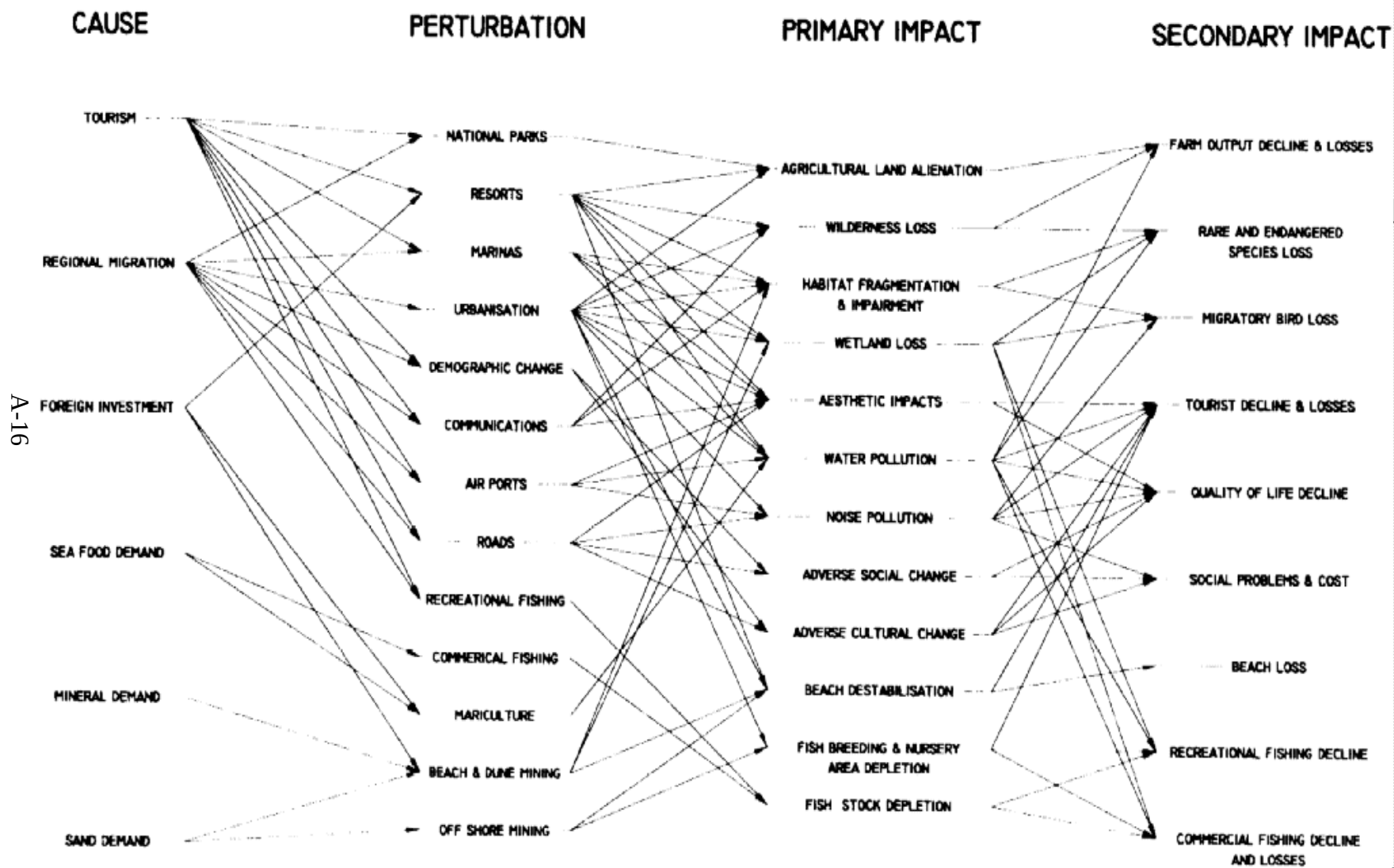


Figure A-3. A specific cause-and-effect network for coastal zone development cumulative impacts in Australia [Australian (Commonwealth) Environmental Protection Agency 1994]

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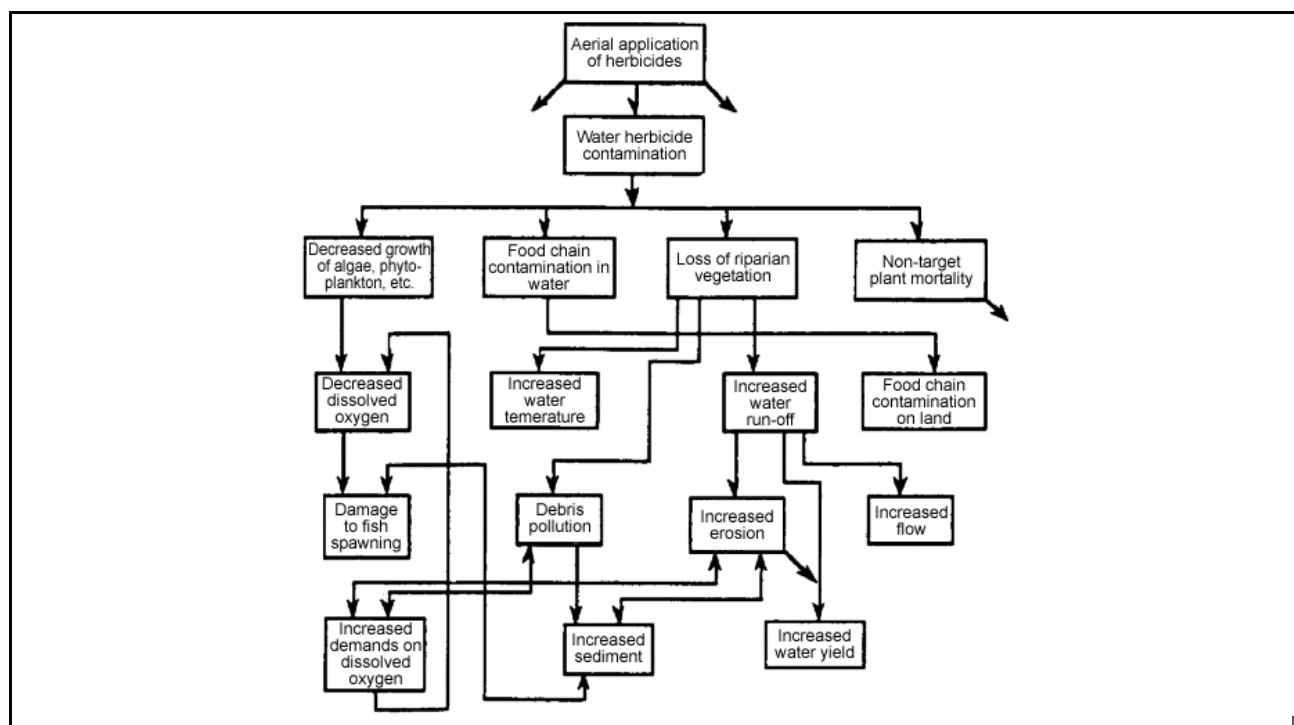


Figure A-4. System diagram showing cumulative indirect effects of aerial application of herbicide on an aquatic system (Bisset 1983).

As part of the Chesapeake Bay Restoration Plan, a cause-and-effect network analysis was conducted during a workshop charged with analyzing cumulative effects on the Bay (Williamson et al. 1987). This approach led the workshop away from focusing on development actions (near the start of the causal chains) or fish and wildlife species (near the end of the effect chains) to focusing on habitats as the hub of the cause-and-effect relationships contributing to cumulative effects on the Bay's living resources. This network analysis was instrumental in focusing the cumulative effects analysis on the appropriate ecological goals and remedial actions needed (Williamson 1993).

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5 MODELING

Modeling is a powerful technique for *quantifying the cause-and-effect relationships leading to cumulative effects*. Modeling can take the form of mathematical equations describing cumulative processes such as soil erosion, or it may constitute an expert system that computes the effect of various project scenarios based on a program of logical decisions. Modeling is also used in socioeconomic analyses, ranging from macroeconomic models to community-level demographics (see Methods 10 and 11).

Developing project-specific models requires substantial resources and time. For this reason, cumulative effects analysis will most often use or modify existing models. The lack of baseline data or project-specific data can also limit the use of sophisticated models. Nonetheless, modeling holds considerable promise for analyzing cumulative effects. In general, the use of models requires that an agency invest in (1) developing a given model or technique, or (2) obtaining baseline data for use in an existing model. The short-term investment usually reaps long-term benefits in analyzing cumulative effects. In some cases, the analyst may find a direct match between the model and the application to existing data. Examples where

cumulative effects are routinely modeled include the following:

- Air dispersion models
- Hydrologic regime models
- Oxygen sag models
- Soil erosion models
- Sediment transport models
- Species habitat models
- Regional economic models.

Models that are easily defended and generally recognized in the scientific community should be used. Thus, general models form the basis for most practical work under NEPA, whereas more sophisticated models are often used on a case-by-case basis. Rarely are models used to combine and evaluate cumulative effects of the proposed and other actions. Tables and matrices provide a more straightforward means of displaying alternatives and their cumulative effects on individual resources. Nonetheless, it is possible to develop an evaluative model that assigns resources to compartments and quantifies effects and relationships mathematically. Generally, the assumptions required by this approach are many, and the likelihood of public understanding and acceptance is low.

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5 EXAMPLES:

Concern for air quality has produced sophisticated air models that track local and regional emissions and estimate ambient (cumulative) pollutant concentrations. The original bubble concept in air pollution control was predicated on limiting the cumulative emissions at a site or region while allowing flexibility in the amount released by individual sources. Figure A-5 displays projected NO₂ concentration isopleths for the cumulative effects of an existing power plant and the proposed addition of a second generating unit in Healy, Alaska. This kind of model output can be combined with map overlay techniques to reveal potential adverse effects on mapped resources.

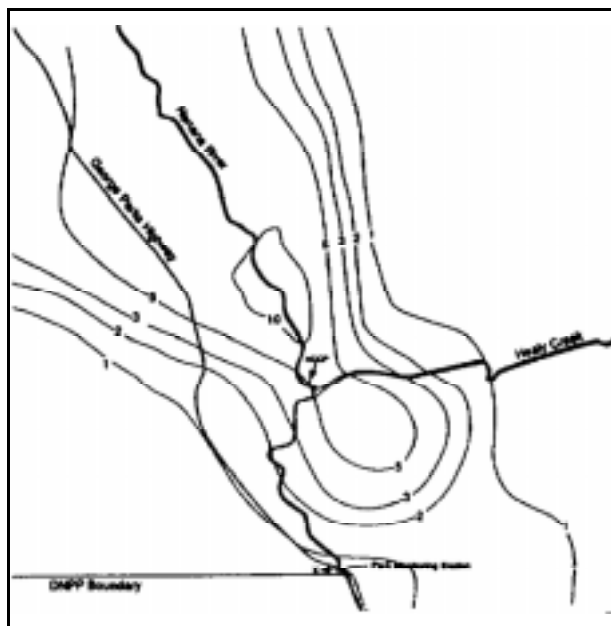


Figure A-5. Projected NO₂ concentration isopleths for combined HCCP and Unit 1 emissions, Healy, AK (Department of Energy 1993)

Water quality-based modeling is another approach to addressing cumulative effects of multiple discharges. Specifically, the cumulative effect of pollutant discharges into a waterbody can be determined through the wasteload allocation procedure under the National Pollution Discharge Elimination System (NPDES) permit process. The wasteload allocation uses a simple equation to incorporate receiving water dilution, background concentrations of pollutants, numeric water quality criteria or whole effluent toxicity information, and effluent volume for discharges into the stream of concern.

$$\text{waste load allocation} = \frac{WQC (Q_s + Q_e) - (Q_s C_s)}{Q_e}$$

- WQC = water quality criteria
- Q_s = upstream flow
- Q_e = effluent flow
- C_s = upstream concentration in toxic units

This wasteload allocation model sets the discharge limit so that the cumulative effect does not result in chronic toxicity to the aquatic biota of the stream. The most commonly used schemes for allocating waste loads among discharges are equal percent removal, equal effluent concentrations, and a hybrid method (where the criteria for waste reduction may not be the same for each point source).

Concerns over potential cumulative effects on aquatic resources resulting from decreases in dissolved oxygen (DO) concentrations prompted the Federal Energy Regulatory Commission (FERC) to model the DO in river reaches encompassing 19 potential hydroelectric generation sites in the Upper Ohio River Basin (FERC 1988). Although it is well known that introducing hydropower projects will affect DO

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concentrations by changing the amount of aeration that takes place at existing dams (from spillage over the dam), the cumulative effect on individual river reaches could only be determined by developing a simulation model (Figure A-6). This model first determined the amount of aeration provided by the dams, and then determined the change in DO caused by installing hydropower facilities. The amount of DO provided by dams was quantified by fitting field data to a statistical model. Then a mathematical model based on known biochemical oxygen demand (BOD) and hydraulic characteristics was developed to determine how changes in aeration at each dam where hydropower was proposed would affect DO concentrations over the entire study area. Ultimately, the effects of proposed hydropower projects on DO concentrations were analyzed under appropriate flow conditions, and the cumulative effects of different alternatives (combinations of projects) on target resources were defined.

The cumulative effects on species of concern can be modeled by quantifying specific mortality factors (e.g., entrainment of migrating species in the turbines of multiple hydropower facilities) or loss of suitable habitat. The cumulative effects of micro-hydro development on the fisheries of the Swan River drainage in Montana was modeled using the bull trout as the primary species of concern (Leathe and Enk 1985). A land-type-based watershed model was used to estimate future cumulative sediment loads resulting from a combination of forest management and micro-hydro development scenarios. The relationship of sediment load to substrate quality was determined and the substrate quality score was correlated with the number of bull trout. Based on these models, the cumulative effect on fisheries from scenarios containing 4 to 20 micro-hydro projects was estimated. Within the drainage, a 7% reduction in juvenile bull trout abundance was attributed to forest road construction; 13% to 24% losses were predicted for micro-hydro project development.

Truett et al. (1994) concluded that the best approach for assessing the cumulative effects on

wildlife is to focus on the habitat factors that control the distributions and abundances of

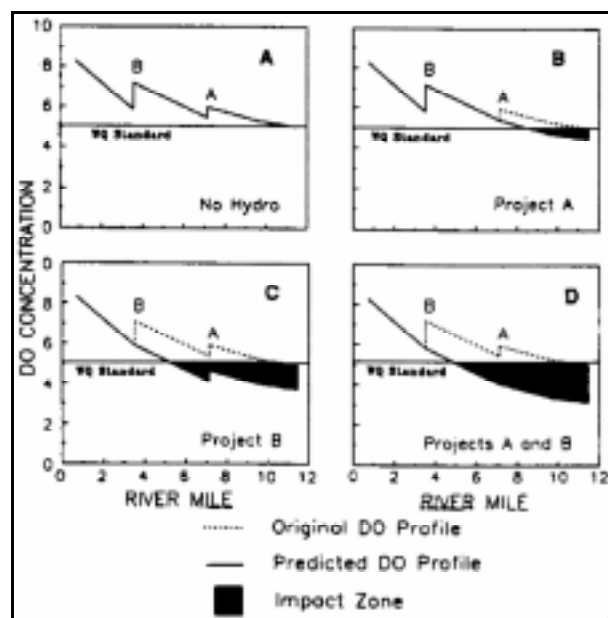


Figure A-6. Cumulative effects on dissolved oxygen caused by hydroelectric development, reduced spillages, and reduced aeration at dams (FERC 1988)

wildlife populations. The most commonly used models of resource-habitat relationships are the Habitat Evaluation Procedures (HEP; U.S. Fish and Wildlife Service 1980) and Instream Flow Incremental Methodology (IFIM; Armour et al. 1984) developed by the U.S. Fish and Wildlife Service. HEP uses Habitat Suitability Index (HSI) models to provide estimates of habitat quality (Schamberger et al. 1982; Hayes 1989). An HSI is developed for each species by aggregating functional values for specific habitat parameters known to support the species of interest. HSI models have also been developed for a few animal communities such as those found in shelterbelts (Schroeder 1986). The cumulative effect of multiple activities on a species can be determined by estimating the number of habitat units (combined HSIs for each habitat available to the species) affected in the area. HEP and IFIM models provide a common currency (habitat suitability) that can be debited by a wide variety of cumulative effects.

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Models are routinely used to assess regional economic effects. When the need to include socioeconomic considerations in NEPA analyses arose, the U.S. Army developed the Economic Impact Forecast System (EIFS) as a model that (1) was based in sound theory, (2) was accepted by the scientific community, and (3) could use readily available data. EIFS is discussed in more detail in the section on Economic Impact Analysis (Method 10).

Although the primary use of models in cumulative effects analysis is to quantify cause-and-effect relationships, optimization and simulation modeling can be used to evaluate among alternatives or against a predefined set of goals. Optimization methods (such as linear programming) address cumulative effects by explicitly incorporating multiple resources and seeking an optimum level for each resource relative to project objectives. Methods range from simple algebraic equations that are solved for variables of set ranges to complex versions including nonlinear functions, layers of optimizations, probabilities, and stochastic variables (Stull et al. 1987). Grygier and Stedinger (1985) used this technique to optimize energy production under the constraints of other goals including water supply, minimum flows, and reservoir levels. Simulation enables the practitioner to model an environmental or socioeconomic system, and simulate the effects of various actions on the system (as described by functional interactions among system components) over time and space. This is the most difficult of cumulative effects analysis methods, yet potentially most rewarding because it is capable of producing most nearly what a practitioner would want—a decisionmaking tool.

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6

TRENDS ANALYSIS

Trends analysis assesses the status of resources, ecosystems, and human communities over time and usually results in the graphical projection of past or future conditions. Changes in the occurrence or intensity of stress over time can also be determined. Trends analysis *provides the historical context that is critical to assessing the cumulative effects of proposed actions*. Specifically, trends analysis can assist the cumulative effects analyst by

- **Identifying cumulative effects problems.** When trends analysis demonstrates that a substantial amount of a resource has been lost, it usually reveals a cumulative effects problem that may be exacerbated by additional actions. For example, historical declines in a fishery resource may indicate that the fishery is near the threshold of population collapse.
- **Establishing appropriate environmental baselines.** When data on the current state of a resource are lacking (or too variable), trends data can be used to describe the existing condition. Trends information can also be used to develop historical baselines or regional goals against which to evaluate restoration efforts.
- **Projecting future cumulative effects.** Trends analysis can identify historical cause-and-effect relationships

between stresses and resources or ecosystems. Common cumulative effects relationships can be used to predict future effects whenever the environmental conditions are similar. Historical trends may also reveal threshold points where cumulative effects become significant or qualitatively different.

By documenting the cumulative effects on the condition of resources over time, trends analyses have been used as planners to assist with the orderly development of communities (by charting the course of economic development), and by wildlife managers to develop appropriate harvest guidelines (by recording populations trends in species). Changes in the condition of resources or ecosystems can be illustrated in both simple and complex forms. A simple trends analysis might produce a line graph showing decreasing numbers of animals from annual surveys. Changes in habitat pattern might be illustrated with a series of figures, or in a 3-dimensional graphic where the amount of change is portrayed on the vertical axis. Video simulations can be used to show complex changes in geographic or aesthetic resources. Time-series information from aerial photographs or satellite imagery are increasingly available for trends analysis across the United States.

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Trends identified from long-term data sets greatly enhance the evaluation of cumulative effects analyses on individual species. For example, the U.S. Fish and Wildlife Service's Breeding Bird Survey (BBS) has identified declining bird populations that may be at greater risk from future cumulative effects (Robbins et al. 1986). As is the case with most long-term records, data gaps in the BBS require

using advanced statistical methods to ensure accurate interpretation of trends. In this case, proportional trends for each survey route were estimated and then weighted to account for areal and data influences (Figure A-7). Trends analyses of bird surveys have identified a number of species with substantial declines in numbers, including many migratory songbirds (Atkins et al. 1990; Terborgh 1992).

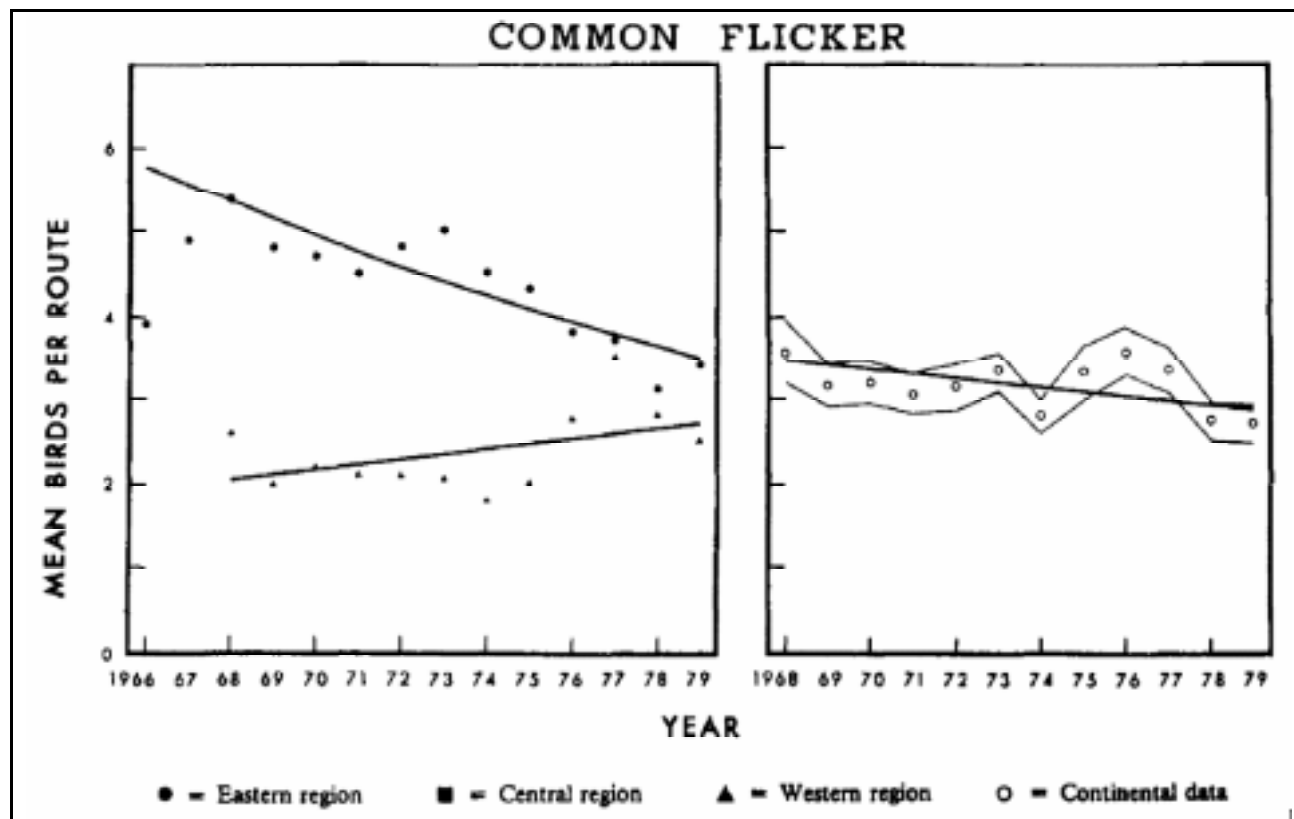


Figure A-7. Common flicker population trends (Robbins et al. 1986)

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Trends in the abundance and distribution of habitats are one of the most important indicators of cumulative effects problems. Figure A-8 dramatically illustrates the trend toward fragmentation of forested areas in Wisconsin (Curtis 1956 cited in Terborgh 1989). A recent study by the U.S. Army Corps of Engineers, in cooperation with U.S. EPA, Fish and Wildlife Service, and NOAA (1993), addressed historical trends in special aquatic habitats of Commencement Bay, WA, resulting from numerous dredge and fill activities since 1877. To address changes over 140 years, the trends analysis study combined historical literature with the photographic record. The use of remotely sensed photographic imagery allowed analysts to combine measures of the areal extent of spoil disposal with written information on the volume of material dredged, and produced a dramatic illustration of downward trends in the area of both intertidal mudflats and marshes (Table A-2).

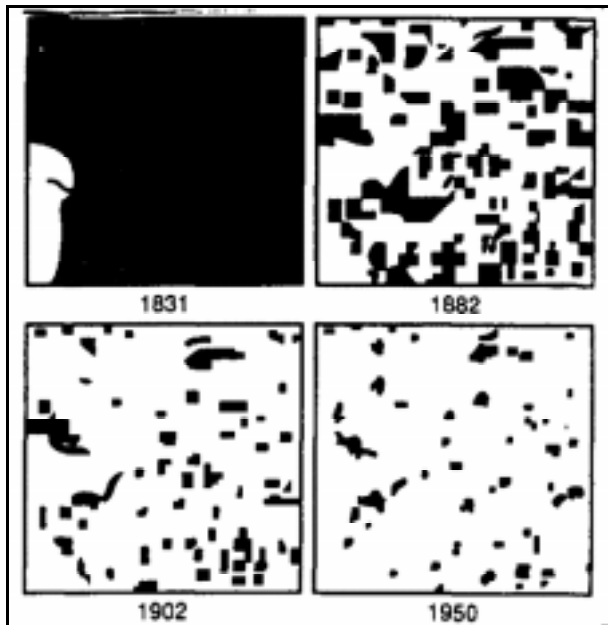


Figure A-8. Cadiz township forest fragmentation (Curtis 1956 cited in Terborgh 1989)

Many other examples of historical losses of wetlands have been reported by the U.S. Fish and Wildlife Service's National Wetlands Inventory (NWI; Dahl et al. 1991). In addition to identifying (and quantifying) this cumulative effects problem, the NWI trends analysis has produced statistics (such as the remaining acreage of different wetlands types) that can be used to predict thresholds where future wetlands losses will likely affect watershed functioning. The "synoptic approach" to cumulative effects analysis developed by the U.S. EPA Environmental Research Laboratory in Corvallis (Leibowitz et al. 1992) proposes to use this information as a quantitative means of comparing wetlands losses among watersheds and determining where future wetland losses will have the greatest effect.

Trends analysis can also be used to construct the environmental baseline for cumulative effects analysis when adequate data on the state of a resource are lacking or are too variable. For example, sediment cores drawn from lakes or estuaries can often be used to obtain a more accurate picture of the state of contamination than can standard sediment samples. Landings of commercial fish species are notoriously variable, but historical trends can identify appropriate baseline population levels as targets for restoration efforts.

Trends analysis in land disturbance have also been used to estimate future cumulative effects based on the causal relationship between land use and resource degradation. Time-series data and aerial photos illustrating trends in land disturbance in Elkhorn Slough, CA, over a 50-year period were used to predict the effect of future residential development (Dickert and Tuttle 1985). In addition, the trends analysis produced a historical trends target that was deemed acceptable for final buildout of the area.

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**Table A-2. Habitat loss by historic period in Commencement Bay, WA
(modified from USACE 1993)**

Historic Period	Habitat Type	Historical Records of Lost Habitat	Total Lost Habitat (includes historical records and photographic evidence)	Acres Remaining
1877 - 1894	mudflat marsh	11 20	0 0	2,074 3,874
1894 - 1907	mudflat marsh	208 41	605 415	1,469 3,459
1907 - 1917	mudflat marsh	51 35	542 64	927 3,395
1917 - 1927	mudflat marsh	48 0	162 72	765 3,320
1927 - 1941	mudflat marsh	143 399	133 1,676	632 1,44
1941 - Present	mudflat marsh	105 1,557	412 1,587	187 57
TOTALS	mudflat marsh	566 1,052	1,54 3,814	

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7

OVERLAY MAPPING AND GIS

Overlay mapping and geographic information systems (GIS) incorporate locational information into cumulative effects analysis. Simple mapping characterizes the spatial aspects of resources, ecosystems, and human communities and helps set the boundaries of the analysis. Overlay mapping can directly evaluate cumulative effects by identifying areas where effects will be the greatest. Mapping and GIS can also address concerns, such as landscape connectivity, that are difficult, if not impossible, to address with other methods. Map overlays *are extremely useful for any form of visual representation*.

The most direct use of overlay mapping for analyzing cumulative effects is "impact-oriented," wherein a composite cumulative effects map is produced by overlaying individual effects from different actions. Examples include the combined effects of both air deposition and water discharge of contaminants to a river, as well as the cumulative effects of multiple land uses in a forested watershed. The more common map overlay approach, however, combines thematic maps of different landscape features to rate areas or resources as to their suitability for development or risk from degradation. In this "resource-oriented" approach, cumulative effects in specific areas can be compared to land suitability determinations (resource or ecosystem thresholds) for those areas. The result is a suitability map that combines development opportunities and environmental and socioeconomic constraints (e.g., both endangered species habitats and public transportation routes) to

disturbance or the areas where disturbance will have the greatest consequences (e.g., those that

identify parcels suited to each activity type (McHarg 1969).

Resource-oriented overlay mapping supports the planning approach to cumulative effects analysis and is often called resource capability analysis. Resource capability analysis can be used to optimize the integration of a site's natural and cultural features with various site design elements (Rubenstein 1987), or to minimize wastefulness in resource utilization (McKenzie 1975). Resource capability analysis uses opportunity, constraint, and suitability maps (Rubenstein 1987). Opportunity maps generally depict conditions related to factors such as soil types or topographic slopes that are suitable for development; constraint maps depict areas that for various reasons, such as the presence of wetlands, floodplains, or cultural resources, are not conducive to development. The land suitability map combines the information in the opportunity and constraints maps to identify those areas best suited for the activities planned.

Suitability ratings can be used to express the responses of resources, ecosystems, and human communities in the absence of more sophisticated quantitative cause-and-effect models (Contant and Wiggins 1993). Where these suitability ratings are based on thresholds above which effects exceed the capacity of the affected resources to sustain themselves, the evaluation is equivalent to carrying capacity analysis. Resource-oriented overlay mapping usually identifies the areas most sensitive to

are most valued or have endured the greatest past losses).

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Overlay maps and land suitability maps have rapidly evolved from handmade transparencies to GIS-based computer overlays (for potential problems see Bailey 1988). In the simplest case, map layers are hand drawn on transparent sheets and then overlain. Each sheet represents a single map layer containing a certain type of information. Within each sheet (or overlay), the importance (or weight) assigned to different data categories is represented by the degree of shading used. The shading seen when all map overlays are stacked atop each other reveals graphically the overall suitability of different areas within the mapped region for the

user-defined purpose. In the effect-oriented approach, darker shading may be used to identify areas subject to the greatest cumulative effects (from multiple actions).

Using a GIS to implement overlay mapping allows the analyst to electronically overlay natural and cultural features and produce composite maps quickly (Johnson et al. 1988). In some cases, GIS maps are derived directly from satellite images using land cover interpretation algorithms. Like the user of the manual transparent map overlay technique, the GIS user can develop weighted functions to assign numeric weights to each map area (or groupings of grid cells) within a map layer. Such weights might be determined by an expert in the field, or based on a statistical classification drawn from field measurements.

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7 EXAMPLES:

Examples of the use of overlay mapping and GIS to analyze cumulative effects include both the effect-oriented approach (e.g., where two or more contaminant sources are mapped over a single resource) and the resource-oriented approach (e.g., where the map overlays are used to characterize land areas in terms of their suitability for development). The former approach is typified by GIS-based groundwater analyses where multiple plumes of contaminated water are overlain on the aquifer of interest to determine the cumulative effects. Many other resources and ecosystems have important geographical characteristics that must be considered in analyzing cumulative effects. For example, overlay mapping can reveal the cumulative fragmentation of a spatially contiguous forest (critical to many migratory songbirds) from activities such as road and building construction. In the Corridor Selection Supplemental Draft EIS for the construction of the Appalachian Corridor H highway near Elkins, West Virginia (West Virginia DOT 1992), GIS map overlays produced estimates of the amount of forest fragmentation, reduction in core forest area, and spatial contact of construction with remote habitat areas.

The resource-oriented overlay mapping approach is commonly used to select the preferred development option (e.g., the right-of-way route that minimizes cumulative effects on resources, ecosystems, and human communities). In his classic *Design With Nature*, Ian McHarg (1969) described the use of map overlays for planning coastal island development, highways, open space in Philadelphia, suburban growth near Baltimore, land use on Staten Island, and regional development around metropolitan Washington, D.C. In the highway development example, he used overlay mapping to determine

a "minimum-social-cost alignment" to replace the originally proposed highway corridor.

Master plans often use resource capability analysis to address the cumulative effects of multiple actions. The resources to be included in the capability analysis depend on the activities being undertaken, and analyses range from comprehensive assessments of all physical, biological, and socioeconomic factors in a regional planning area to limited analyses of the potential for sediment runoff related to the slope, soil, and permeability of a given plot of land. For example, overlays of a site's topographic features (e.g., geology, soils, slope, and vegetation) can be used to designate areas where construction will not contribute to cumulative runoff problems (i.e., soils with low erosion potential). Overlay mapping is also critical to planning conflicting land uses, such as combat training activities and natural resource conservation on military installations. The intersection of impact areas (e.g., aircraft flight corridors, tank maneuvers, large weapon firing areas, ordinance impact areas) and sensitive environments (e.g., wildlife refuges and endangered species habitats) can be determined through overlay mapping as illustrated in Figure A-9 (produced from map archives, Department of the Navy, Naval Air Station Patuxent River, MD, 1996).

Overlay mapping and GIS can also be used to document past cumulative effects and help predict future effects. Walker et al. (1987) used remote sensing data and GIS to evaluate the indirect effects of oil field development in the Prudhoe Bay Oil Field, Alaska. Aerial photographs revealed surface disturbance (flooding

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and thermokarst) extending beyond the areas directly affected by construction. These unanticipated effects on frozen arctic soils and thaw-lake wetlands constitute an important cumulative effects problem for oil field activities. Overlay mapping of the spatial properties of areas (e.g., vegetation, amount of open water, land and surface form types, and soil type) where these indirect effects were more pronounced can be used to predict future cumulative effects and better plan resource extraction in this fragile ecosystem.

The promise of GIS as a tool for solving cumulative effects problems is evidenced by the rapidly increasing applications of GIS to land management of forests (Sample 1994) and wetlands (Lyon and McCarthy 1995). Jerry Franklin (1994) states that GIS may be the most important technology resource managers have acquired in recent memory. He predicts that GIS will be invaluable in (1) inventory and monitoring, (2) management planning, (3) policy setting, (4) research, and (5) consensual decisionmaking. In a much publicized example, the

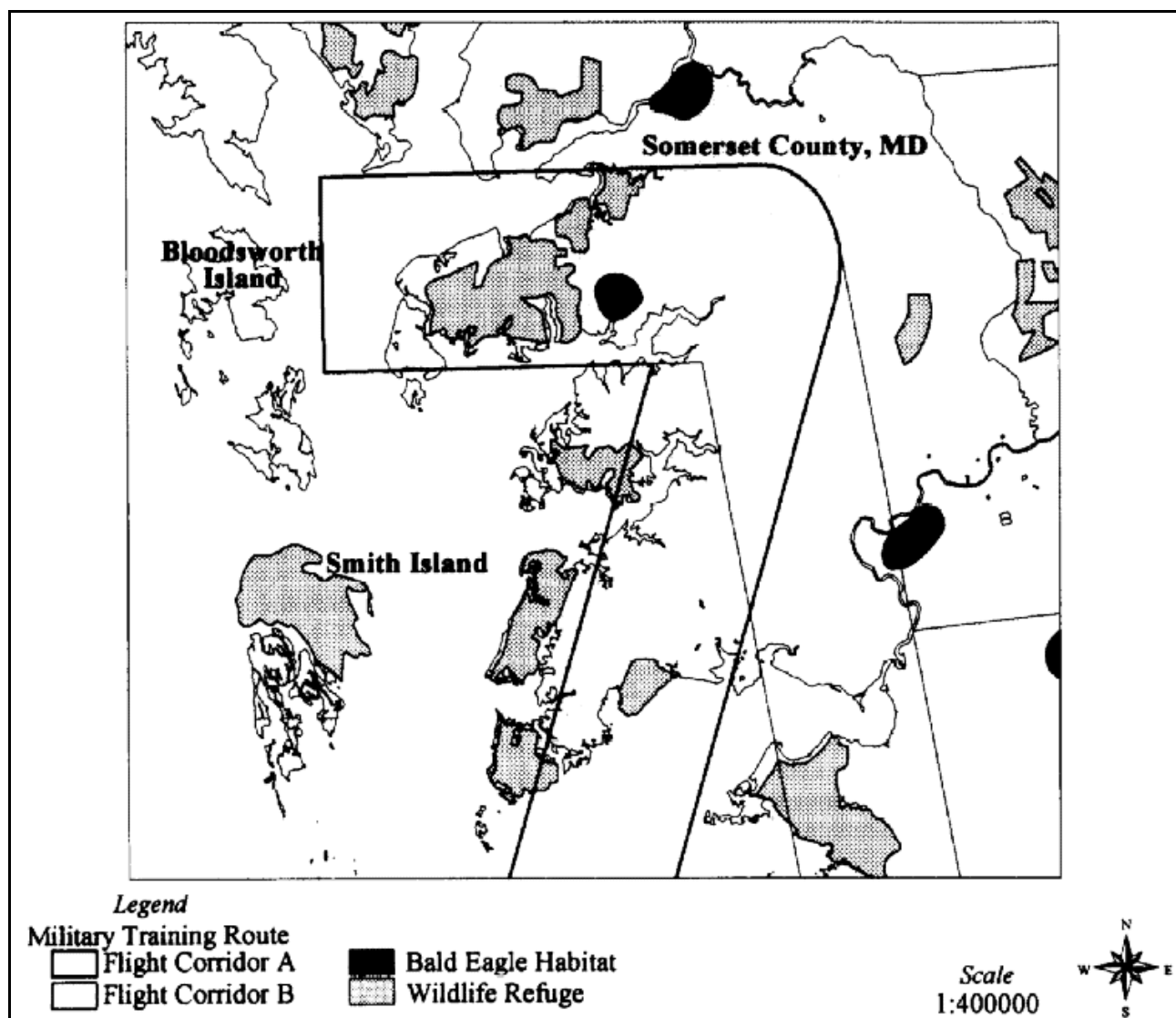


Figure A-9. Hypothetical intersection between aviation flight corridors and environmental resources near a typical U.S. military installation (Department of the Navy 1996)

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resolution of the Pacific Northwest forest controversy would have been impossible without GIS. Only when GIS was combined with remote sensing information was the actual extent (or lack) of old growth forest determined. Perhaps more importantly, various scientific panels were charged with developing and evaluating alternatives for protecting late-successional forest ecosystems and associated species (e.g., northern spotted owl). Only when an effective GIS capability was developed, was it possible to display and modify the alternatives before decision-makers (including Congressional delegations) so that reasonable consensus could be achieved.

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8

CARRYING CAPACITY ANALYSIS

Carrying capacity analysis derives from the fact that inherent limits, or thresholds, exist for many environmental and socioeconomic systems. Carrying capacity in the ecological context *is defined as the threshold of stress below which populations and ecosystem functions can be sustained*. In the social context, the carrying capacity of a region is the sum of human activities that can be maintained while providing the level of services (including ecological services) desired by the populace. When cumulative effects exceed the carrying capacity of a resource, ecosystem, and human community, the consequences are significant.

As a method for evaluating cumulative effects, carrying capacity analysis serves to identify thresholds for the resources and systems of concern (as constraints on development) and provide mechanisms to monitor the incremental use of unused capacity. Carrying capacity analysis begins with the identification of potentially limiting factors (e.g., the supply of water in a desert riparian ecosystem). Mathematical equations are then developed to describe the capacity of the resource or system in terms of numerical limits (thresholds) imposed by each limiting factor. In this way, projects can be systematically evaluated in terms of their effect on the remaining capacity of limiting factors (Contant and Wiggins 1993).

Carrying capacity analysis can be especially useful for assessing cumulative effects in the following situations:

- Infrastructure and public facilities
- Air and water quality
- Wildlife populations
- Recreational use of natural areas
- Land use planning

The determination of carrying capacity is straightforward for public facilities such as water supply systems, sewage treatment systems, and traffic systems. A reservoir can only supply water to a finite number of consumptive users. In the case of air and water quality control programs, statutory limits (or standards) are regulatory thresholds of the carrying capacity of air or water in the region of interest. Cumulative effects can be estimated through physical and mathematical models and then compared with these standards. Unlike engineered systems, thresholds involving subjective human uses must be based on goal-oriented statements of public opinion and can only be obtained through opinion survey information or the scoping process. Such thresholds include the degree of enjoyment obtained from a recreational experience. In natural systems, the carrying capacity of well-studied populations (usually game species) can be adequately modeled, but the capacity of whole ecosystems to withstand and recover from stress (i.e., their resilience) has yet to be modeled precisely and at best is expressed in gross probabilistic terms (i.e., the likelihood of a set of events occurring).

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8 EXAMPLES:

The air and water quality criteria provisions of the Clean Air Act and Clean Water Act, respectively, represent carrying capacity approaches to dealing with cumulative effects (as opposed to best available technology approaches). Under the Clean Air Act Amendments of 1990, states measure the cumulative effect of all sources on the concentration of air pollutants in specified attainment areas using regional models. New stationary sources are not permitted if they are determined to cause, in the aggregate, the concentration of a pollutant of concern to exceed its standard (the presumed carrying capacity of the area). Similarly, total maximum daily loads (TMDLs) are calculated for water bodies receiving point and nonpoint discharges as part of the NPDES permit process to ensure that the cumulative effects on water quality do not exceed the assimilation capacity of the receiving waters. If the cumulative effect remains below standards, capacities are not exceeded, and new proposals can be authorized (Contant and Wiggins 1993).

Wildlife and fisheries managers have been conducting carrying capacity analyses for many years (Smith 1974). Specifically, managers have used the maximum-sustained-yield concept to determine the amount of harvest of fish or game populations that will not result in deterioration of the population (i.e., not exceed the capacity of the population to renew itself). The U.S. Forest Service developed *Management Recommendations for the Northern Goshawk in the Southwestern United States* based on the concern that the goshawk, a forest habitat generalist, may be experiencing declining populations and reproduction associated with tree harvests and other factors affecting the carrying capacity of western forests (Reynolds et al. 1992). These guidelines will be used to develop national forest plans in the Southwestern Region that will

maintain the forest carrying capacity (i.e., specific habitat attributes and important prey species) needed to sustain goshawk populations despite the cumulative effects of human influences and natural perturbations, including loss of an herbaceous and shrubby understory, reduction in the amount of older forests, and increased areas of dense tree regeneration.

Managers of natural areas also employ the carrying capacity concept to prevent parks and other recreation areas from becoming overused.

Techniques used to evaluate the cumulative effects of recreation applications involve use thresholds (i.e., standards) based on social values (e.g., opportunities for solitude) and ecological factors (e.g., presence of rare and endangered species). The recreational carrying capacity concept is explicitly linked to the notion of nondegradation, where current conditions set a baseline or standard for environmental quality. For example, Forest Service researchers have devised the Limits of Acceptable Change process for setting and monitoring recreational carrying capacity in a wilderness area (Stankey et al. 1985). The U.S. Army Corps of Engineers (1993) addressed both the social carrying capacity and the resource carrying capacity of the Fox waterway in Illinois as it developed permitting policy guidelines for the area. Based on a definition of when people feel crowded, the social carrying capacity was determined to be approximately 854 boats and 236 jet skis on the open areas of the waterway. Based on a water quality definition that used a threshold of water clarity needed for vegetation growth, the resource carrying capacity was determined to be 350 cruising boats (i.e., the number that could use the deeper water areas that did not support sensitive vegetation).

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Carrying capacity analysis is a critical part of land use planning for sustainable development. Ideally, knowledge of the carrying capacity of an area provides the basis for developing suitability maps to guide future growth (including proposed federal projects). When applied to human communities, carrying capacity can be defined as "the ability of a natural or man-made system to absorb population growth or physical development without significant degradation

or breakdown" (Schneider et al. 1978). As part of comprehensive planning for Sanibel Island, Florida, land capability analysis was conducted to determine the cumulative effects of development actions on the structure and functions of the ecological zones of the island (Clark 1976). This analysis led to a comprehensive set of management guidelines based on the carrying capacity of these natural systems for sustaining human development. Figure A-10 illustrates the combinations of population numbers and population density that are possible without exceeding the carrying capacity of interior wetlands to assimilate runoff from developed areas.

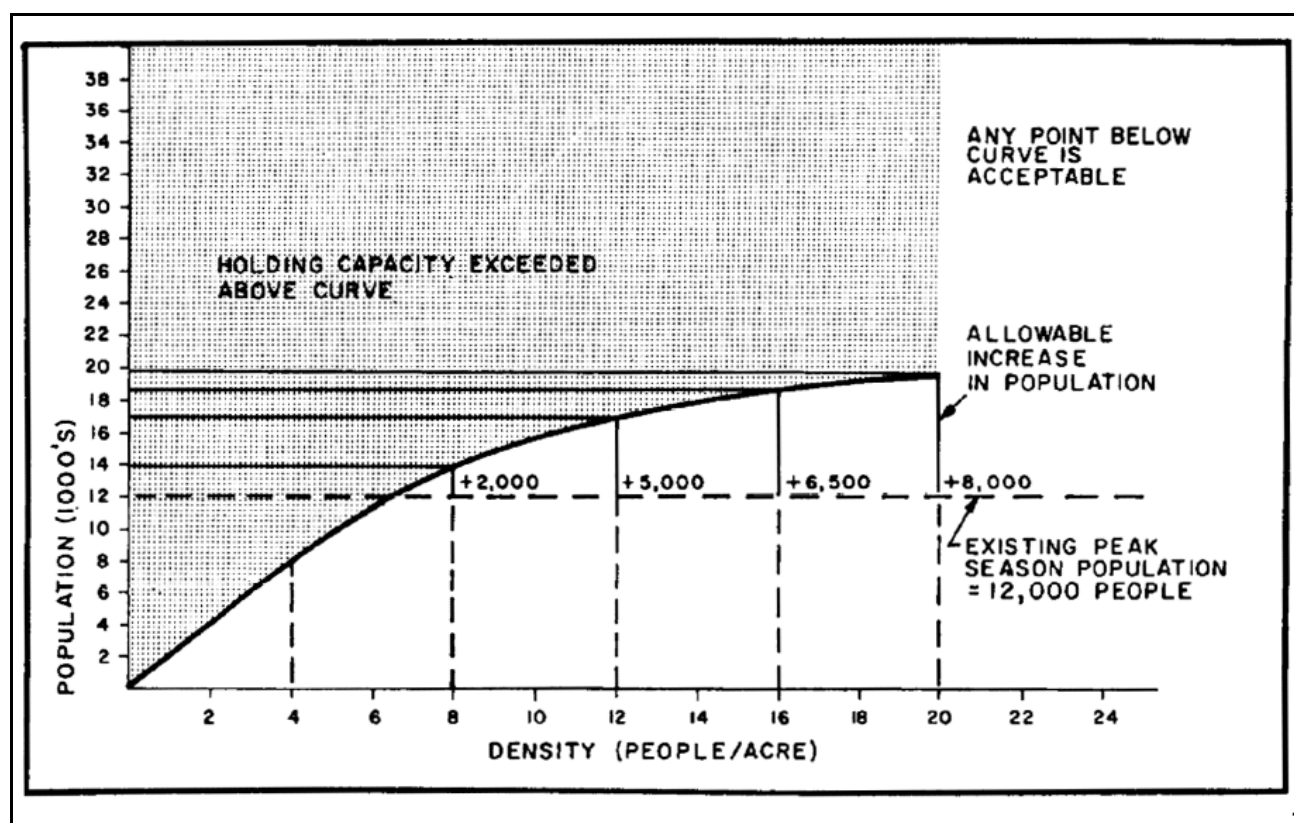


Figure A-10. Sanibel Island, Florida population versus runoff assimilation capacity (Clark 1976)

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9 ECOSYSTEM ANALYSIS

Ecosystem analysis involves considering the full range of ecological resources and their interactions with the environment. This approach can improve cumulative effects analysis by *providing the broad regional perspective and holistic thinking needed to address the following cumulative effects principles*:

- **Focus on the resource or ecosystem.** Ecosystem analysis specifically addresses biodiversity and uses the full range of indicators of ecological conditions ranging from the genetic to species to local ecosystem to regional ecosystem levels.
- **Use natural boundaries.** Ecosystem analysis uses ecological regions, such as watersheds and ecoregions, to encompass ecosystem functioning and landscape-scale phenomena such as habitat fragmentation.
- **Address resource or ecosystem sustainability.** The ecosystem approach to management explicitly addresses the ecological interactions and processes necessary to sustain ecosystem composition, structure, and function (Ad Hoc Committee on Ecosystem Management 1995).

Traditionally, environmental impact assessment has considered air quality, water resources, wildlife, and human communities as separate entities for analysis. This separation of resources has obscured many cumulative effects. Recognition of the interconnectedness of land, water, and human resources has driven many federal and state agencies to undertake eco-

system or watershed approaches to environmental protection. Since 1991, the U.S. EPA (1996) has embraced the watershed approach as the major mechanism for addressing cumulative nonpoint-source pollution. Specific applications include watershed-based TMDLs (U.S. EPA 1994) and the "watershed analysis" approach to addressing cumulative effects and improving resource management on timber land (Washington State Department of Natural Resources 1992; Regional Interagency Executive Committee 1995).

By its nature, biodiversity conservation is a cumulative effects issue. Because it encompasses all the structural and functional components of the biological environment (and its interactions with the physical world), biodiversity is constantly affected by a wide range of stresses. For this reason, the goals of biodiversity and ecosystem protection are usually coincident with those of cumulative effects analysis; therefore, the analyst should employ an ecosystem approach whenever biodiversity is an issue.

Principles of the ecosystem approach are included CEQ's (1993) report, *Incorporating Biodiversity Considerations Into Environmental Impact Analysis Under the National Environmental Policy Act* (see box) and the Interagency Ecosystem Management Task Force's (1995) report, *The Ecosystem Approach: Healthy Ecosystems and Sustainable Economics*. These principles involve three basic concepts: (1) taking a "big picture" or landscape-level view of ecosystems, (2) using a diverse suite of indicators including community-level and ecosystem-level

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indices, and (3) addressing the myriad interactions among ecological components that are needed to sustain ecosystem functioning. Applying the ecosystem approach to cumulative effects analysis entails using biological indicators (e.g., indices of biotic integrity for surface waters; Karr 1991; U.S.

EPA 1990) as integrators of cumulative effects and landscape indices (e.g., patch distribution of wetlands; Preston and Bedford 1988; Leibowitz et al. 1992) as measures of the cumulative diminution of ecosystem functioning. Natural resource agencies may soon be able to provide guidance on assessing and mitigating environmental effects at the ecosystem level (Truett et al. 1994).

PRINCIPLES OF BIODIVERSITY CONSERVATION (CEQ 1993)

1. Take a "big picture" or ecosystem view.
2. Protect communities and ecosystems.
3. Minimize fragmentation.
Promote the natural pattern and connectivity of habitats.
4. Promote native species.
Avoid introducing non-native species.
5. Protect rare and ecologically important species.
6. Protect unique or sensitive environments.
7. Maintain or mimic natural ecosystem processes.
8. Maintain or mimic naturally occurring structural diversity.
9. Protect genetic diversity.
10. Restore ecosystems, communities, and species.
11. Monitor for biodiversity impacts.
Acknowledge uncertainty.
Be flexible.

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9 EXAMPLES:

Constructing precise models of ecosystem structure and function sometimes exceeds the capabilities of NEPA practitioners. Considerable progress, however, has been made in applying the principles of ecosystem analysis to analyzing cumulative effects by extending considerations beyond species to the ecosystem and by looking at landscape-scale processes such as habitat fragmentation.

The most celebrated example where ecosystem analysis was used to extend the analysis of cumulative effects beyond a single species is the *Supplemental Environmental Impact Statement on Management of Habitat for Late-Successional and Old-Growth Forest Related Species Within the Range of the Northern Spotted Owl* (U.S. Forest Service and Bureau of Land Management 1993). Expert panels were convened to determine the likelihood of maintaining viable populations of a comprehensive suite of species and groups of species based on available habitat. Addressing the entire ecosystem involved considering terrestrial forest ecosystems (i.e., amounts of late-successional and old-growth forests and the viability of species ranging from fungi to bats), aquatic ecosystems (habitat conditions, riparian ecosystem processes), and aquatic and riparian dependent organisms (e.g., anadromous salmonids, resident fish species and subspecies, and other aquatic, riparian, and wetland organisms). The U.S. Forest Service (in conjunction with the U.S. Bureau of Land Management and Food and Drug Administration) also incorporated ecosystem analysis into the *Pacific Yew Final Environmental Impact Statement* by defining the role of the Pacific yew in the forest ecosystem (Figure A-11; U.S. Forest Service 1993). The cumulative effects of harvesting Pacific yew

on federal lands in the Pacific northwest for taxol production (for use as a cancer treatment) were analyzed in three different contexts: the Pacific yew itself (including its genetic diversity), the forest ecosystem that supports yew populations, and the relationship of the yew and human communities.

The ecosystem analysis approach implemented by the Forest Ecosystem Assessment Team (FEMAT) in the spotted owl EIS also considered ecosystem processes affected by the cumulative actions on lands owned and managed by states, tribes, corporations, individuals, and other nonfederal agencies. The analysis included an aquatic conservation strategy based on the designation of key watersheds and the use of watershed analysis. The Washington State Department of Natural Resources (1992) recently published a watershed analysis manual including a set of technically rigorous procedures that can be used to determine what processes are active in a watershed, how these processes are distributed in time and space, what the current upland and riparian conditions are, and how all of these factors influence ecosystem services or other beneficial uses. Watershed analysis is being expanded to encompass other aspects of the ecosystem approach to management (Montgomery et al. 1995; Regional Interagency Executive Committee 1995). In the **synoptic landscape approach** to cumulative effects analysis developed by the U.S. EPA Environmental Research Laboratory in Corvallis, OR, the landscape is the unit of analysis (Leibowitz et al. 1992). Synoptic indices are chosen from the following landscape-level measures: function value, functional loss, and replacement potential. Subsequently, landscape indicators are chosen as

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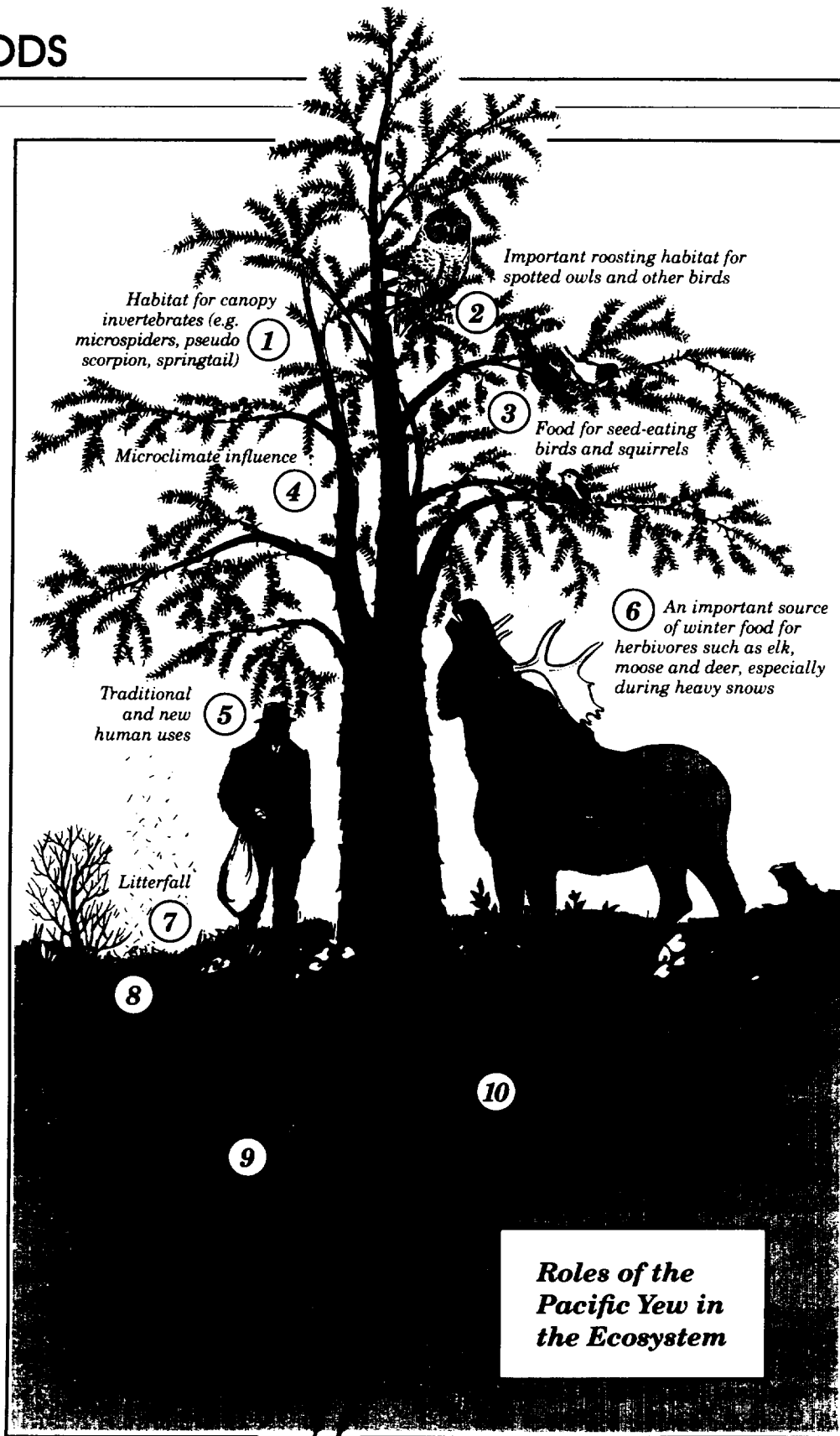


Figure A-11. Roles of the Pacific Yew in the Ecosystem (U.S. Forest Service 1993)

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first-order approximations of the synoptic indices. This approach provides a framework for comparing the cumulative effects of actions on landscape processes such as flood storage and wildlife support.

Habitat fragmentation is one of the most important ecosystem-level processes to address in cumulative effects analysis. Concerns about potential cumulative effects of habitat fragmentation on biodiversity prompted a supplemental information report to the FEIS and Record of Decision (ROD) of the Trail Creek Timber Sale, Beaverhead National Forest, Montana (U.S. Forest Service 1991). The report assessed habitat loss effects, edge effects, patch size effects, insularity effects (on genetics of populations linked by habitat corridors), and effects on rare elements. Specifically, the report evaluated the importance of the area as a biological corridor between the large wildland areas of the Northern Continental Divide, Selway-Bitterroot, and Greater Yellowstone areas. Similar concerns have been raised in other areas (e.g., Klamath National Forest; Pace 1990) and have prompted considerable research into landscape-level indicators such as abundance or density of habitats, habitat proportion, patch size and perimeter-to-area ratio, fractal dimension (amount of edge), and contagion or habitat patchiness (Hunsaker and Carpenter 1990; Noss 1990; O'Neill et al. 1994).

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10

ECONOMIC IMPACT ANALYSIS

Economic impact analysis satisfies the mandate under NEPA to "...fulfill the social, economic and other requirements of present and future generations of Americans" [National Environmental Policy Act, Title I Sec. 101 (a)]. *It is an important component of analyzing cumulative effects, because the economic well-being of a local community depends on many different actions.* The following effects are the minimum that an economic impact analysis should determine:

- change in business activity
- change in employment
- change in income
- changes in population.

The three primary steps in conducting an economic impact analysis are (1) establishing the region of influence, (2) modeling the economic effects, and (3) determining the significance of the effects.

The definition of the geographic region of influence (ROI) is often controversial. Most regional and urban analysts prefer to use a functional area concept for defining study regions (Fox and Kuman 1965). Regions defined in this way explicitly consider the economic linkages between the residential population and the businesses in the geographic area. Specifically, the affected region should include all of the self-sustaining ingredients of region-local businesses, local government, and local population (Chalmers and Anderson 1977). Although no standard methodology exists, the definition of a ROI should consider residence patterns of the affected population,

availability of local shopping opportunities, "journey-to-work" time for employees, and local customs and culture.

Economic models are invaluable for analyzing cumulative effects. The suite of economic models can vary from simple to complex (Richardson 1985; Treyz 1993). As a rule, economic models are sets of mathematical equations that represent the interactions among the integral components of the regional economy; the modeled relationships are based upon economic principals that have a long history of accuracy and use. Data to "drive" the models are critical to performing an impact analysis and acquiring data is often the limiting factor for the analyst. Although they are focused on economic relationships, economic models can incorporate demographics. Ultimately, economic models are used to project effects under each alternative.

Once model effects projections are obtained, additional tools, such as the rational threshold value (RTV) and the forecast significance of impacts (FSI) approaches, can provide timely and cost-effective evaluations of the significance of the effect (Huppertz and Bloomquist 1993). These analytical tools review the historical trends for the defined region and develop measures of historical fluctuations in sales activity, employment, income, and population. This use of time-series data provides the analyst with a historical context in which to evaluate significance. The use of economic impact models in combination with the RTV and FSI techniques has proven successful in addressing cumulative economic impacts.

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10 EXAMPLES:

Three kinds of models are most often used in economic impact analysis: economic base models, input-output models, and econometric models. The underlying assumption of an economic base model is that changes in a regional economy occur as a result of changes in the amounts of goods and services that are sold outside the region. The economic base model is based on the bifurcation of the regional economy into "basic" and "non-basic" sectors. Defined simply, basic sectors produce goods and services that are generally consumed outside the region and non-basic sectors produce goods and services that are consumed within the region. Basic sectors can be identified by surveying local firms and households to determine where they purchase their goods and services or by the "location-quotient" technique (Isserman 1977), which measures the extent to which a sector is more concentrated within the region than within the nation as a whole. The location-quotient assumes this excess production is exported outside the region.

Input-output models (Miller and Blair 1985) explicitly consider the interrelationships between different sectors of a regional economy and how these interactions affect the process of economic changes within the region. Input-output models provide more information on economic transactions by sector within a local economy than economic base models, but they require more data. Regional econometric models (Glickman 1977; Treyz 1993) represent a compromise between economic base and input-output analysis in terms of data requirements and information produced. Econometric models are usually statistically derived and draw upon survey-based data, traditional regression techniques, and other statistical tools. fluctuations in the subject regional economies, respectively. The total aggregate changes in business volume, employment, income, and population (four of the model outputs) are then used

Econometric models use time-series data to show the pattern of effects due to outside influences over a period of years. As a result, regional econometric models are better suited for predictions of long-run effects. Unfortunately, local-time series data are often not available for the region of concern.

The Economic Impact Forecast System (EIFS) is perhaps the most commonly used method for assessing regional economic effects; it is the specified model of choice for all environmental analyses associated with Army Base Realignment and Closure (BRAC). EIFS was developed as a simple model based upon three major criteria: (1) basis in sound theory, (2) acceptance by the scientific community, and (3) availability of data to drive the model. By entering county names to designate the Region of Economic Influence (ROI), Bureau of Economic Analysis (BEA) and other data are readily available for use. After six variables associated with the action [i.e., number of military and civilian employees being transferred, the average salary of both categories, the percent of military personnel living on base, and the anticipated change in local (or total) procurements] are added to the thousands of BEA data elements, EIFS automatically performs the needed trends analysis, multiplier calculations, and other computations. EIFS has provided a consistent methodology for all BRAC studies and has allowed the Army to "rank-order impacts" among alternatives as required by NEPA.

The significance of BRAC actions is determined by adding two evaluative components to EIFS. As described previously, RTV and FSI techniques measure historical and statistical

to assess the significance of regional economic effect. As analysts begin to address the cumulative effects of more and more actions,

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other models that lead directly from available data to conclusions of significance will be needed.

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11 SOCIAL IMPACT ANALYSIS

Social impact analysis fulfills the mandate under CEQ's regulations that the "human environment" in NEPA be "interpreted comprehensively" to include "the natural and physical environment and the relationship of people with the environment" (40 CFR§ 1508.14). The social sciences have *made considerable progress in addressing cumulative effects related to environmental stewardship by focusing on key social impact variables*. The Interorganizational Committee on Guidelines and Principles (1994) has identified five basic categories of social impact variables:

1. Population characteristics such as its size and expected size, ethnic and racial diversity, and the influx and outflux of temporary (e.g., seasonal or leisure) residents.
2. Community and institutional structures including the size, structure, and linkages of local government; the historical and present patterns of employment and industrial diversification; and the size, activity, and interactions of voluntary associations, religious organizations, and interest groups.
3. Political and social resources such as the distribution of power and authority, the identification of interested and affected parties, and the leadership capacity within the community or region.
4. Individual and family changes including factors that influence the daily life of individuals and families (and indigenous and religious subcultures) in the community or region such as attitudes toward the proposed policy, alterations in family and community networks, and perceptions of risk, health, and safety.
5. Community resources such as patterns of natural resource and land use; the availability of housing; and community services including health, police, fire protection, and sanitation facilities.

The key to analyzing the cumulative effects on these social impact variables is incorporating multiple actions into projections of future social conditions. The following general categories describe the range of methods used to predict future social effects:

- linear trend projections (identifying taking an existing trend and projecting the same rate of change into the future);
- population multiplier methods (a specified increase in population implies designated multiples of some other variable);
- scenarios (characterization of hypothetical futures through a process of mathematically or schematically modeling the assumptions about the variables in question);
- expert testimony (experts can be asked to develop scenarios and assess their implications);
- simulation modeling (mathematical formulation of premises and a process of quantitatively weighing variables).

METHODS

11 EXAMPLES:

Social impact analysis differs from other analyses of cumulative effects because it must deal with the subjective perception of effects. Social effects appraisal and social well-being accounts are examples of methods for analyzing subjective social variables.

Social effects appraisal determines the social meaning and significance of the objective changes produced by cumulative actions. The social analyst assesses the social meaning of the changes from the different perspectives of the affected groups. One way to measure the meaning of a change is to tap the knowledge of opinion leaders (formally or informally) within the affected groups to determine the values they assign to each change. For example, an influx of 200 construction workers and their families might be viewed positively by families suffering from a stagnant economy but negatively by retirees looking for a quiet neighborhood. The social analyst needs to acknowledge that while some negative social effects can be remedied materially (perhaps by economic growth), others are qualitative and defy mitigation.

The social well-being account is a display that summarizes findings by cross tabulating levels of analysis, evaluation categories, and effect factors with a social effects evaluation of the present condition and each of the alternatives (including no-action). It provides either a quantitative (numerical) or qualitative rating of each alternative's overall social effect and a description of the rating scale. The Multi-Attribute Tradeoff System (MATs) and other computer programs assist in producing a systematic numerical evaluation of social effects. The result is an overall quantitative ranking for

each alternative, reflecting the alternative's relative social benefit to the affected group.

The Federal Highway Administration (FHWA) frequently deals with social impact issues related to its transportation projects. FHWA (1996) recently prepared a primer for analysts who assess the effects of proposed transportation actions on human communities. FHWA states that community impact studies must include secondary effects and influences from outside developmental pressures to determine the ability of an area to survive removal of housing, businesses, and community services. Also, such studies must describe a community's ability to absorb relocated residents and businesses in terms of social and economic disturbance (e.g., available housing, public services affected, areas zoned for business use). The primer describes nine impact categories to be analyzed, including social and psychological aspects, physical aspects, visual environment, land use, economic conditions, mobility and access, provision of public services, safety, and displacement. Considering these effects naturally includes environmental justice issues. Community impact analysis is analogous to ecosystem analysis in that the human community should be thought of as an integral unit with a characteristic social setting and operation. Decisions about avoiding and mitigating effects should be based on consensus visions of the desired condition of the community. Lastly, if community effects are to receive attention comparable to that given the natural environment, special effort to ensure public involvement must be employed (e.g., using nontraditional and informal approaches).

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METHODS

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METHODS

APPENDIX B

ACKNOWLEDGEMENTS

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Research Article

Realized Population Change for Long-Term Monitoring: California Spotted Owl Case Study

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ABSTRACT The annual rate of population change (λ_t) is a good metric for evaluating population performance because it summarizes survival and recruitment rates and can be used for open populations. Another measure of population performance, realized population change (Δ_t) is an encompassing metric of population trend over a period of time; it is the ratio of population size at an end time period relative to the initial population size. Our first goal was to compare mean λ and Δ_t as summaries of population change over time. Our second goal was to evaluate different methods for estimating these parameters; specifically we wished to compare the value of estimates from fixed effects models, random effects estimates from mixed effects models, and Bayesian Markov chain Monte Carlo (MCMC) methods. Our final goal was to evaluate the use of the posterior distribution of Δ_t as a means for estimating the probability of population decline retrospectively. To meet these goals, we used California spotted owl (*Strix occidentalis occidentalis*) data collected on 3 study areas from 1990 to 2011 as a case study. The estimated MCMC median λ s for 2 of the study areas were 0.986 and 0.993, indicating declining populations, whereas median λ was 1.014 for the third study area, indicating an increasing population. For 2 of the study areas, estimated MCMC median Δ_t s over the 18-year monitoring period were 0.78 and 0.89, suggesting 21% and 11% declines in population size, whereas the third study area was 1.22 suggesting a 22% increase. Results from Δ_t analyses highlight that small differences in mean λ from 1.0 (stationary) can result in large differences in population size over a longer time period; these temporal effects are better depicted by Δ_t . Fixed effects, random effects, and MCMC estimates of mean and median λ and of Δ_t were similar ($\leq 9\%$ relative difference). The estimate of temporal process variance was larger for MCMC than the random effects estimates. Results from a Bayesian approach using MCMC simulations indicated that the probabilities of a $\geq 15\%$ decline over 18 years were 0.69, 0.40, and 0.04 for the 3 study areas, whereas the probabilities the populations were stationary or increasing were 0.07, 0.22, and 0.82. For retrospective analyses of monitored populations, using Bayesian MCMC methods to generate a posterior distribution of Δ_t is a valuable conservation and management tool for robustly estimating probabilities of specified declines of interest. © 2013 The Wildlife Society.

KEY WORDS Bayesian MCMC approach, California, California spotted owl, hierarchical model monitoring, Pradel's temporal symmetry model, random effects estimator, rate of population change, realized population change, *Strix occidentalis occidentalis*.

Long-term monitoring programs are often focused on species of concern, from game to threatened species. Management of these species is often controversial and sociopolitical challenges are often as important as biological

ones. Controversial species require clear, simple, and objective biological metrics to inform the management decision process, particularly for regular and relatively short-term intervals, such as management plans and status updates (e.g., ≤ 5 years). Population size is often used because of its ease of interpretation and because management or conservation goals often include maintaining population levels close to sustainable objectives (Thompson et al. 1998, Williams et al. 2002) or above some minimum threshold, such as the size of a minimum viable population (Soulé 1980). However, population size alone reveals little about the long-term

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sustainability of a population (Lancia et al. 2005). Determining whether the population is increasing, decreasing, or remaining stable is also critical to ensuring future population size objectives (Thompson et al. 1998, White et al. 2002, Williams et al. 2002). The annual rate of population change (λ_t) is a good metric for evaluating population performance because it summarizes survival and recruitment rates and can be used for open populations (Nichols and Hines 2002). The value of λ_t is interpreted as the rate of annual (or other time period of interest) increase or decrease in the population, and is used more frequently for monitoring and management decisions.

Another metric used for evaluating changes in population status is realized population change (Δ_t), which is the change in population over a period of time (Franklin et al. 2004). This quantity is the ratio of population size at some point in time period K , relative to the initial population size N ($\Delta_t = N_K/N$), which reflects the cumulative effect of λ_t for a time period of interest. For example, if λ_t had a geometric mean of 0.97, a population size starting at 100 would decline to approximately 86 over 5 years (a common management time frame) and Δ_t would be 0.86. Specifically, Δ_t incorporates all estimates of λ_t and provides an intuitive number for evaluating population change over periods of time.

In the past, the confidence intervals (CI) for estimates of mean λ and of Δ_t were used to evaluate population decline. That is, if the CI included 1, even if just barely, the conclusion was that there was no evidence for a decline. However, with this methodology, the influence and probability of a Type II error (inability to detect a decline or change) cannot be eliminated from the interpretation of no decline. The key element missing in this approach was the ability to estimate the probability of decline. Using Bayesian Markov chain Monte Carlo (MCMC) methods, a posterior distribution of Δ_t can be used to estimate any probability of decline. The approach has not been widely used, although Gerrodette and Rojas-Bracho (2011) used it to evaluate declines in vaquita (*Phocena sinus*) over a 15-year monitoring period. Indeed, the posterior distribution of Δ_t provides a robust method for detecting and describing retrospective population trajectories, similar to how population viability analysis (PVA) and more generally, projection models, are used to evaluate potential prospective population trajectories.

The inclusion of sampling variation in estimates of λ_t can negatively bias estimates of Δ_t , similar to how it can negatively bias estimates of persistence in PVA models. Bayesian MCMC methods can be used to separate process variation from sampling variation during the estimation of Δ_t . In addition to Bayesian MCMC methods, a random effects estimator, also called a shrinkage or empirical Bayes estimator, is an analytical approach to separate sampling variation from the overall process variance (Efron and Morris 1977, Ver Hoef 1996, Burnham and White 2002). Depending on computing tools available, both approaches can be used for estimating λ_t and Δ_t .

Our first goal was to compare mean λ and Δ_t as summaries of population change over time. Our second goal was to

evaluate different methods for estimating mean λ and Δ_t . Specifically, we wished to compare the value of estimates based on a random effects estimator from a mixed effects model and a Bayesian MCMC approach for evaluating population performance of species with long-term monitoring data. Our final goal was to evaluate a Bayesian approach to generate a posterior distribution of Δ_t as a means to estimate the probability of population decline retrospectively. We use data collected on the California spotted owl (*Strix occidentalis occidentalis*) as a case study. The California spotted owl remains a focal species of conservation concern, and knowledge of population trends is an important component of assessing status and informing forest management planning efforts.

STUDY AREA

We used data from spotted owls on 3 study areas in the Sierra Nevada and southern Cascade Mountains, California, collected from 1990 to 2011 (Fig. 1). Although we did not randomly select the study areas, they spanned the length of the contiguous California spotted owl range in the Sierra Nevada and encompassed all habitat types known to be used by spotted owls in the Sierra Nevada. The Lassen (LAS) study area was in the southern Cascades, but it was included in the Sierra Nevada province by the United States Forest Service for management purposes (U.S. Forest Service 2004). Most of the LAS and Sierra (SIE) study areas were located on public land managed by the United States Forest Service, whereas the Sequoia and Kings Canyon (SKC) study area was in 2 national parks. Franklin et al. (2004) and Blakesley et al. (2010) described in detail the LAS, SIE, and SKC study areas; however, SKC has changed from Blakesley et al. (2010). In 2006, the study area for SKC was reduced; all estimates of λ_t were based on data from this reduced study area. Long-term mark-resight data were available for each study population. The number of marked birds varied each year, but generally ranged between 40 and 90, with 4–14 new birds marked each year (Table 1).

METHODS

Field Surveys

Field methods for the study of spotted owl population dynamics have been well described elsewhere (Forsman 1983; Franklin et al. 1996, 2004; Anthony et al. 2006). In particular, the field methods and protocols used to collect the data are detailed by Franklin et al. (2004). Therefore, we present only a brief summary of the methods used to capture and recapture (by resighting) owls.

We conducted surveys to find and locate California spotted owls from 1 April to 31 August on LAS and from 1 March to 30 September on SIE and SKC. We identified owls by capturing and banding, or by resighting owls previously banded with unique color band combinations. We surveyed spotted owls primarily at night by vocally imitating spotted owl calls or by broadcasting recordings of spotted owl calls. We completely surveyed the core study areas on ≥ 3 occasions throughout each field season. When we detected owls, we



Figure 1. Outline of southern Cascade and Sierra Nevada Mountains, California, showing the location of 3 study areas for California spotted owls, 1990–2011.

conducted walk-in surveys during daylight hours to visually locate owls, identify color bands, or capture unbanded owls.

We identified spotted owls to sex (male, female) by vocalization and behavior, and determined age by plumage characters (Franklin et al. 1996). Owls can be identified to 4 age classes (juvenile [young of the year], 2 subadult ages [1–2 years old; 2–3 years old], and adult [≥ 3 years old]; Moen et al. 1991). We use the term non-juvenile owl to refer to subadult and adult age classes; we used only non-juvenile owls for our analyses.

Rate of Population Change

We used each owl's encounter history to estimate the annual rate of population change in territorial owls (λ_t) using Pradel's temporal symmetry model (Pradel 1996, Nichols and Hines 2002, Franklin et al. 2004) in Program MARK (White and Burnham 1999). We refer to Pradel's temporal

symmetry model as the Pradel model. All 3 study areas had territorial survey areas, in which some areas were not consistently surveyed, and a subset core study area, which was surveyed consistently for estimation of λ_t . In the core areas, coverage was complete, in that each year, we surveyed areas without known owl territories, as well as areas with known owl territories. For population growth rate to represent changes in the number of owls for the Pradel model, the study area size and boundary must remain unchanged through time (Hines and Nichols 2002, Franklin et al. 2004). Consequently, we used data only from the core areas to interpret λ_t as the annual rate of population change.

We used the $(\phi\lambda p)$ structure of the Pradel model, where ϕ is apparent survival (probability that an owl alive in year t survived to the next year $t + 1$ and remained on the study area [i.e., available for recapture or resight]) and p is the resight (by recapture or resight) probability. Based on previous California spotted owl analyses (Franklin et al. 2004, Blakesley et al. 2010), we used a model with fixed effects of sex and year, $\lambda(t)\phi(t)p(s \times t)$, where s = sex and t = year as a categorical time effect. For each study area, we estimated the overdispersion parameter ($\hat{c}$) using the median $\hat{c}$ procedure in Program MARK under the Cormack-Jolly-Seber (CJS) global model $\phi(s \times t)p(s \times t)$. When $\hat{c}$ was >1 , we used $\hat{c}$ to inflate variances of parameter estimates (Burnham and Anderson 2002).

Using the model structure above, $\lambda(t)\phi(t)p(s \times t)$, we estimated the mean rate of population change using a fixed effect model ($\hat{\lambda}$). Using the same model, we also used a mixed model approach to estimate the mean rate of population change ($\tilde{\lambda}$) and its temporal process variation ($\hat{\sigma}^2$), as well as to generate random effects estimates of λ_t ($\tilde{\lambda}_t$; White et al. 2001). The parameters ϕ and p were fixed effects and λ_t was a random effect. To estimate $\tilde{\lambda}$, we used an intercept-only (means) model for λ_t . We did not include the first 2 estimates and last estimate of λ_t to estimate mean λ because the first and last estimates were confounded with estimation of p , and the second estimate has a potential bias from trap response or a learning curve experienced by field crews at the beginning of the studies (Hines and Nichols 2002). We calculated $\hat{\lambda}$, $SE(\hat{\lambda})$, $\tilde{\lambda}$, $SE(\tilde{\lambda})$, and $\hat{\sigma}^2$ on the log scale and used the delta method to estimate variance of the back-transformed geometric means of $\hat{\lambda}$ and $\tilde{\lambda}$ (Franklin et al. 2004). We used the log-scale because the geometric mean generates an unbiased estimate of mean λ over a finite time period, whereas the arithmetic mean generates a biased estimate (Morris and Doak 2002).

Table 1. Descriptions of the 3 study areas in the southern Cascades and Sierra Nevada, California, and sample sizes of California spotted owls.

Study area ^a	Years	Area (km ²)	Avg. total no. marked ^b	Avg. new marked/year ^c
LAS	1990–2011	1,254	88	14
SIE	1990–2011	562	76	8
SKC	1991–2011	182	59	7

^a LAS is Lassen, SIE is Sierra, and SKC is Sequoia Kings Canyon.

^b Average number of marked owls on study area; includes territorial adult and subadult owls.

^c Average number of newly marked owls on study area; includes territorial adult and subadult owls.

Both LAS and SIE had expansion areas, areas in which surveying began several years after the start of the study. If these were not accounted for, new owls found in these areas would enter the Pradel model as new recruits, and result in a positive bias in estimates of λ_t . Therefore, we accounted for these areas by grouping them separately and excluding estimates of λ_t from the year of and year following the expansion, and estimates of p for the year of expansion (see Blakesley et al. 2010, Appendix G, for a detailed explanation of the procedure). One study area, SKC, had a year of missed data collection (2005); we used an unequal time interval to account for this in Program MARK, which resulted in an average survival over the 2-year interval. We did not use the average estimate from these 2 years (2004–2005 and 2005–2006) in any random effects analyses because random effects in Program MARK assumes equal time intervals.

Realized Population Change

We translated fixed effects estimates of $\lambda_t(\hat{\lambda}_t)$ into estimates of realized population change ($\hat{\Delta}_t$) on each study area, which is the proportional change in estimated population size, relative to the initial population size (Franklin et al. 2004). We calculated $\hat{\Delta}_t$ as the product $1 \times \hat{\lambda}_k \times \hat{\lambda}_{k+1} \times \hat{\lambda}_{k+2} \times \dots \times \hat{\lambda}_K$, where k was year of the first estimated λ_t (i.e., the third year because the first 2 estimates of λ_t were confounded or biased) and K was the last (i.e., the second to last estimate because the last estimate was confounded). For each study area, we used the delta method to estimate variance of realized change (on the natural log scale) and the associated back-transformed CIs (Franklin et al. 2004). We also used the random effects estimates of $\lambda_t(\hat{\lambda}_t)$ to estimate realized population change ($\hat{\Delta}_t$). Because the random effects variance estimate is conditionally biased, we based CIs on root mean square error (RMSE; White et al. 2001, Burnham and White 2002), which includes a term for the difference between $\hat{\Delta}_t$ and $\hat{\Delta}_t$ (e.g., $[\hat{\Delta}_t - \hat{\Delta}_t]^2$). To estimate the covariance between random effects estimates, we multiplied the correlations between fixed effects estimates by the RMSE² (i.e., variance) of each estimate.

To estimate probabilities of population declines or increases for each area, we used a bayesian approach via

MCMC sampling implemented in Program MARK to estimate posterior distributions of λ_t ($\lambda_{t\text{MCMC}}$) using the same mixed effects model and years as described above. We used the posterior distributions of $\lambda_{t\text{MCMC}}$ to estimate the posterior distribution of median λ (λ_{MCMC}) and Δ_t ($\Delta_{t\text{MCMC}}$). For all MCMC simulations, we used 4,000 tuning samples, 1,000 burn in samples, and 20,000 realizations. We used vague priors for all parameters included in the model. For estimating median λ_{MCMC} and $\Delta_{t\text{MCMC}}$, we used a hyperprior for μ and σ of λ_t . For μ , we used a normally distributed prior with mean = 0 and standard deviation = 100 and for σ , we used a gamma prior to model its transformation, $1/\sigma^2$, with $\alpha = 1.00001$ and $\beta = 0.000001$. Although we did not use estimates of ϕ and p in the hyperprior to estimate μ and σ of λ_t , we did include them in the model, $\lambda(t)\phi(t)p(s \times t)$, and they required a prior distribution. Because they were logit transformed parameters, we used a normal prior distribution with mean of 0 and a standard deviation of 1.75, which is a vague prior when back transformed to the real scale (2.5th and 97.5th percentiles of approximately 0.02 and 0.98, with a uniform distribution between those percentiles). We determined if the Markov chains converged using the Gelman–Rubin statistic, R-hat (Gelman et al. 2004). For each parameter, we used 10 chains of 1,000 each and used a threshold of R-hat < 1.1 to indicate adequate sampling of the posterior distribution.

RESULTS

We used encounter histories for 323, 317, and 165 individual owls, for LAS, SIE, and SKC respectively, to model rate of population change. Median $\hat{c}$ ranged from 1.09 to 1.18, suggesting some overdispersion but no serious lack of fit. We adjusted all variance estimates by site-specific estimates of c . The MCMC chains for all model parameters converged (R-hat < 1.1).

Estimates of mean $\hat{\lambda}$, $\tilde{\lambda}$, and median λ_{MCMC} were <1.0 for LAS and SIE, which suggested declining populations (Table 2). Estimates of median λ_{MCMC} were very close to $\hat{\lambda}$ and $\tilde{\lambda}$, although estimates of σ were $\geq 2.9 \times$ greater for MCMC than for the random effects estimate (Table 2).

Table 2. Estimates of mean annual rate of population change ($\bar{\lambda}$) and its temporal process standard deviation ($\hat{\sigma}$). Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, for 1990–2011. Random effect estimates are based on mixed effects models using a means model for time-specific estimates of rate of population change (λ ; random effect) with fixed effects for time-specific apparent survival (ϕ) and resight probability (p), and Markov chain Monte Carlo (MCMC) estimates are based on a Bayesian approach to generate posterior distributions of annual rate of population change (λ_t) that is implemented in Program MARK.

Study area	Estimator ^a	$\bar{\lambda}$ ^b	SE	95% CI		$\hat{\sigma}$	95% CI	
LAS	FE	0.985	0.017	0.950	1.022			
	RE	0.987	0.011	0.967	1.008	0.018	0.013	0.026
	MCMC ^c	0.986		0.880	1.072	0.052	0.012	0.212
SIE	FE	0.993	0.017	0.959	1.027			
	RE	0.990	0.009	0.973	1.008	0.000	0.000	0.052
	MCMC	0.993		0.925	1.058	0.037	0.011	0.134
SKC	FE	1.016	0.021	0.976	1.057			
	RE	1.010	0.014	0.982	1.038	0.018	0.000	0.101
	MCMC	1.014		0.907	1.170	0.058	0.015	0.217

^a FE are fixed effects estimates, RE are random effects estimates from a mixed effects model, and MCMC are estimates from 20,000 simulations.

^b This estimate does not include the first 2 estimates and last estimate of λ_t because they were confounded or potentially biased.

^c MCMC estimates are the median and 2.5 and 97.5 percentiles from the posterior distribution, based on 20,000 simulations.

For LAS and SKC, the annual pattern of λ_t was the same between the fixed effects, random effects, and MCMC estimates, although values of $\tilde{\lambda}_t$ and $\lambda_{t \text{ MCMC}}$ were closer to their estimated means compared to $\hat{\lambda}_t$ (Fig. 2). On average, the variance was greater for fixed effects estimates (Fig. 2a) than for random effects estimates from the mixed model (Fig. 2b). However, because we used RMSE for the random effects estimates, the variance for several estimates of $\tilde{\lambda}_t$ was greater than for the fixed effects $\hat{\lambda}_t$ (most noticeably, SIE 1992 and 1997 and SKC 1992, 2001, and 2002). The MCMC estimates of median $\lambda_{t \text{ MCMC}}$ had smaller credible intervals than fixed effects CIs (Fig. 2a,c), and although some credible intervals were larger than the random effects CIs, they were more consistent (Fig. 2b,c).

The consecutive estimates of Δ_t reflected the temporal variation in λ_t , with $\tilde{\Delta}_t$ (Fig. 3b) not necessarily having less variance than $\hat{\Delta}_t$ (Fig. 3a and Table 3). Credible intervals of estimates of median $\Delta_{t \text{ MCMC}}$ (Fig. 3c) started out smaller than CIs of $\hat{\Delta}_t$ (Fig. 3a), but grew to be approximately the same size by the end of the monitoring period. Over the 18-year study period, the different estimators of Δ_t indicated population declines of 21–22% for LAS and 11–16% for SIE,

and an increase of 16–27% for SKC, although CIs overlapped 1.0 for all estimators and study areas (Fig. 3 and Table 3). We found small but variable differences in magnitude between the estimators of Δ_t (1–9% absolute difference; Table 3). The size of standard errors for Δ_t were also variable with no particular pattern between the estimators (Table 3).

From the Bayesian approach, posterior distributions of $\Delta_{t \text{ MCMC}}$ showed the 3 populations had different population trajectories (Fig. 4). The probability that any population declined by $\geq 30\%$ was low, varying from 0.24 for LAS to $<0.01\%$ for SKC (Table 4). The probability of a minor decline was more substantial; we calculated a 0.69 and 0.40 probability LAS and SIE declined by $\geq 15\%$ (Table 4). The populations had variable probabilities of remaining stationary or increasing as well; SKC had a relatively high probability (0.82), whereas LAS and SIE had lower probabilities (0.07 and 0.22; Table 4).

DISCUSSION

For long-term monitoring data, Δ_t is an insightful metric for portraying the cumulative dynamics of a population across

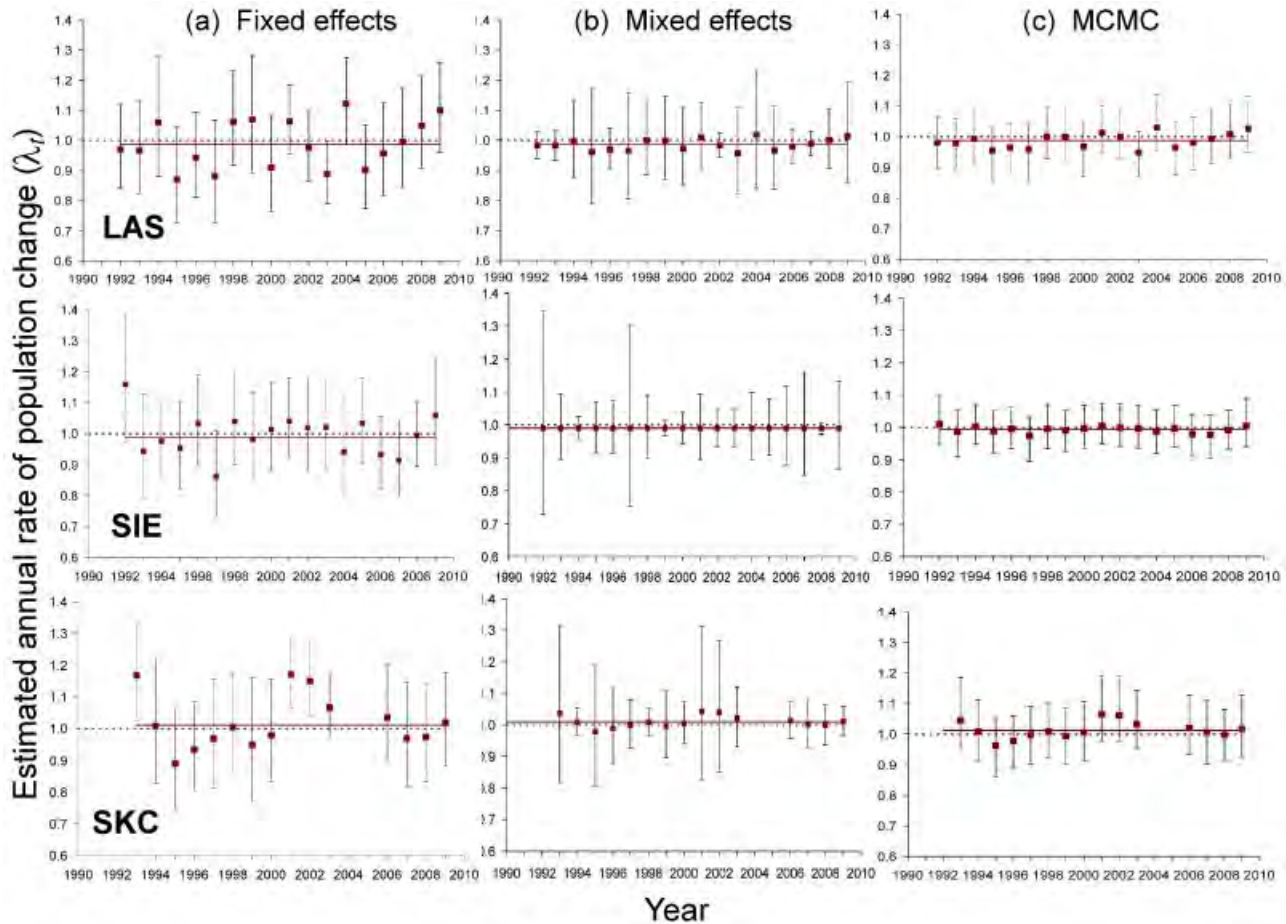


Figure 2. Estimates of annual rate of population change (λ_t) and 95% confidence intervals based on (a) fixed effects estimates, (b) random effects estimates from a mixed effects model, and (c) a Bayesian Markov chain Monte Carlo (MCMC) approach for California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, 1992–2010. We excluded the first 2 and last estimates because of confounding or potential bias. Solid lines indicate the best estimates of mean λ from a mixed effects model for each study area. We used the root means squared error for 95% confidence intervals for random effects estimates, and show the median and 2.5 and 97.5 percentiles for MCMC methods.

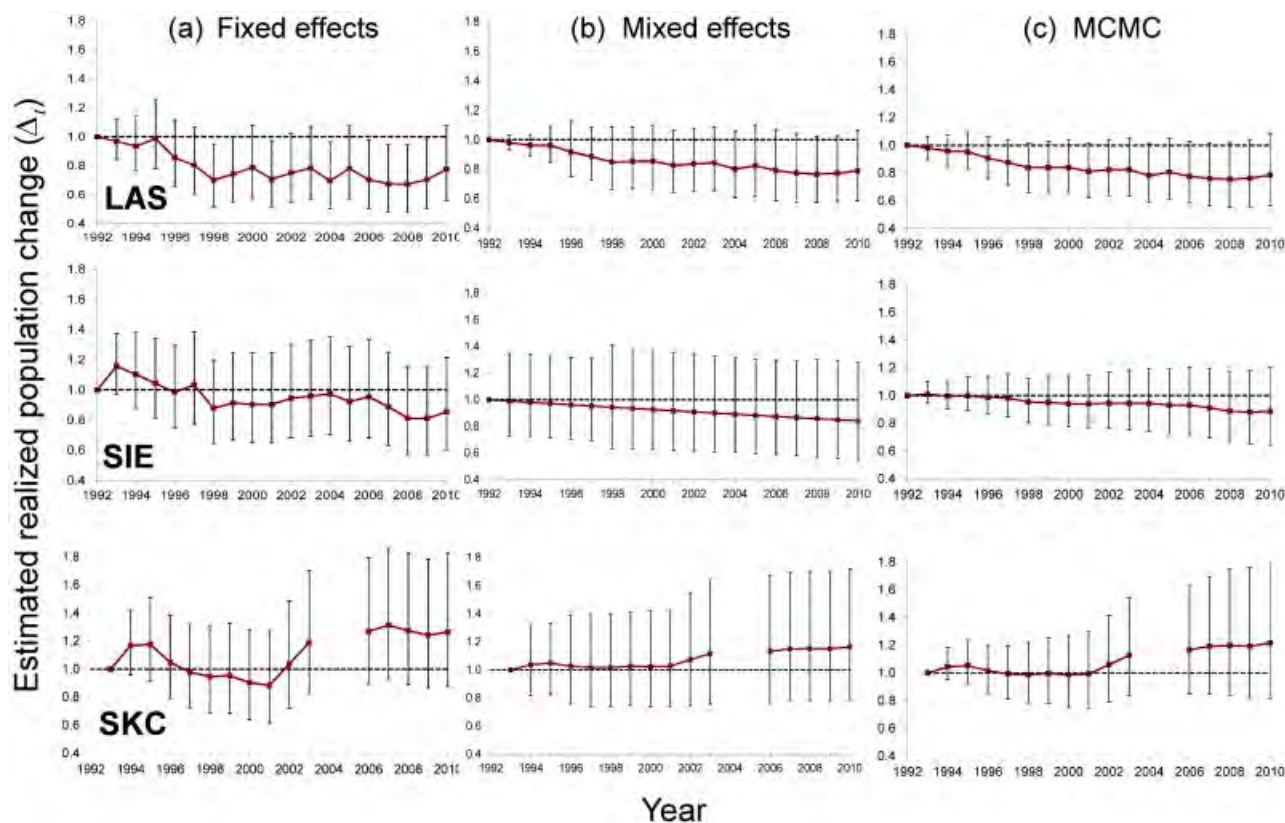


Figure 3. Estimates of realized population change (Δ_t) and 95% confidence intervals based on (a) fixed effects estimates, (b) random effects estimates from a mixed effects model, and (c) a Bayesian Markov chain Monte Carlo (MCMC) approach. Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, 1992–2010. We excluded the first 2 and last estimates because of confounding or potential bias. We used the root means squared error for 95% confidence intervals for random effects estimates, and show the median and 2.5 and 97.5 percentiles for MCMC methods. Realized population change is the proportion of the initial population size remaining each year.

medium and long time scales, such as 5–20 years. Further, if a Bayesian approach is used to estimate Δ_t , uncertainty is portrayed more completely through the posterior distribution, and the probability of decline can be calculated. For the California spotted owl, values of Δ_t are more immediately interpretable than $\bar{\lambda}$ because interpreting differences in $\bar{\lambda}$ from 1.0 (stationary) depends on the time period, and summarizing how much a population will change over a given time period can be difficult. For example, estimated median $\Delta_{t, \text{MCMC}}$ was 0.78 for LAS, indicating that the population likely declined by 22% over the 18-year monitoring period. This is more directly interpretable than stating that estimated median λ_{MCMC} was 0.986 over the 18-year period. Although $\bar{\lambda}$ is an important metric of population performance, we conclude that Δ_t is generally more interpretable, particularly for depicting population changes over longer time periods.

Because estimates of $\bar{\lambda}$ and Δ_t can be biased by sampling variation, we recommend using a hierarchical Bayesian MCMC or a random effects approach to estimate these parameters. Both these approaches remove sampling variation and generally have improved precision as a result of reduced mean square error, and equal or improved coverage when compared to fixed effects estimators (Burnham et al. 1987, Link 1999, Burnham and White 2002). However, in this study, we found random effects estimates

for Δ did not necessarily have improved precision. Although the average variance of the random effects point estimates of λ_t was less, 17–25% of the random effects estimates had variances that were 1.3–3.2 $\times$ larger than their fixed effects counterparts. These large variances occurred when fixed effects estimates of λ_t were far from the random effects estimate; for example see SIE in 1992 and 1997 (Fig. 2). Because we added variances and covariances to estimates of Δ_t on the natural log scale, the few large variances propagated larger variances for subsequent estimates of Δ_t and, compared to their fixed effects counterparts, resulted in larger CIs for estimates of Δ_t for SIE and little reduction of the CIs for SKC.

We also found that the credible intervals on estimated median $\Delta_{t, \text{MCMC}}$ increased through the monitoring period, such that by the end of the 18 years they were similar to fixed effects CIs. This was not initially intuitive because the credible intervals for estimated median $\lambda_{t, \text{MCMC}}$ were smaller than the CIs of the fixed effects $\hat{\lambda}_t$. However, for these data we found relatively high proportions of negative covariances between fixed effects estimates that reduced the overall additive variance of subsequent estimates of Δ_t . Thus, the data and type of estimator (e.g., when the estimates of interest are the result of additive or multiplicative combinations) will determine whether random effects estimates or estimates from Bayesian MCMC methods

Table 3. Estimates of overall realized population change (Δ_t) for 3 estimators, which are based on estimates of annual rate of population change (λ_t). Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, for 1990–2011. Overall realized population change is the proportion of the initial population size remaining at the end of the time period.

Study area	Estimator ^a	Δ_t^b	SE	95% CI		CV (%)
LAS	FE	0.78	0.13	0.56	1.08	17
	RE	0.79	0.12	0.59	1.06	15
	MCMC ^c	0.78		0.57	1.08	
SIE	FE	0.85	0.15	0.60	1.21	18
	RE	0.84	0.18	0.55	1.28	22
	MCMC	0.89		0.65	1.20	
SKC	FE	1.27	0.24	0.88	1.83	19
	RE	1.16	0.23	0.79	1.72	20
	MCMC	1.22		0.82	1.84	

^a FE are fixed effects estimates, RE are random effects estimates from a mixed effects model, and MCMC are estimates from 20,000 simulations.

^b This estimate does not include the first 2 estimates and last estimate of λ_t because they were confounded or potentially biased.

^c MCMC estimates are the median and 2.5 and 97.5 percentiles from the posterior distribution, based on 20,000 simulations.

will show improved precision compared to fixed effects estimates.

However, for estimating and removing process variation, a Bayesian hierarchical MCMC approach is generally preferable to the random effects estimator for a more practical reason. For the random effects estimator, a minimum of 9,

and preferably 15, estimates are required (Efron and Morris 1977, Burnham and White 2002). Thus, the random effects method may be daunting in terms of required effort, or even impossible for many studies that lack sufficient spatial replication or temporal longevity. In addition, the variation in length of CI for random effects estimates (Fig. 2b compared to c) may not be readily interpretable and, therefore, may be less desirable.

Finally, we found that estimates of σ for mean λ were $\geq 2.9\times$ larger from the Bayesian MCMC approach compared to random effects estimates (Table 2). This is presumably because inference is exact and MCMC incorporates all uncertainty in the modeled system (Royle and Dorazio 2008, Higgins et al. 2009, Kéry 2010), thus providing a more realistic estimate of the variance of mean λ and Δ . In contrast, random effects estimates are based on maximum likelihood and are approximations with asymptotic properties, which means $\hat{\sigma}^2$ may be biased low for small sample sizes (Gelman and Hill 2007). In addition, unbiased estimates of σ^2 may be harder to achieve when σ^2 is small or sampling variation is relatively large (Burnham and White 2002). For the California spotted owl case study, the sampling variation was likely large relative to σ^2 , resulting in estimates that were biased low or estimated as 0.

The biggest advantage of using a Bayesian approach and the posterior distribution of Δ_{MCMC} is that probability of decline can be estimated for a retrospective analysis, similar to how projection models or PVAs are used for a prospective analysis. In the past, evaluating whether the population declined typically relied on hypothesis tests with a null hypothesis of no decline. If the null hypothesis was not rejected, a retrospective power analysis was recommended to address the probability of accepting a false null or to determine the smallest detectable effect size, given study sample sizes (Taylor and Gerrodette 1993, Steidl et al. 1997, Loughheed et al. 1999). More recently, research has shown that retrospective power analyses are not appropriate to make inference about a non-significant result (Hoenig and Heisey 2001, Lenth 2001, Dixon and Pechmann 2005). Even if retrospective power was a valid approach, it still does not answer the real question of interest, what is the probability the population declined?

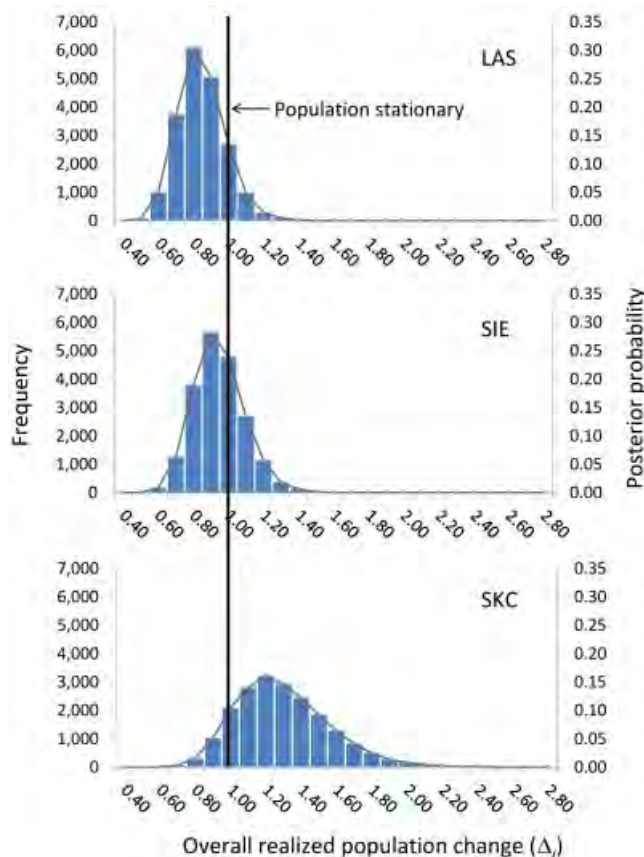


Figure 4. Estimated posterior distributions of overall realized population change (Δ_t) based on posterior distributions of λ_t from 20,000 Markov chain Monte Carlo (MCMC) simulations. Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, 1992–2010. We excluded the first 2 and last estimates because of confounding or potential bias. Overall realized population change is the proportion of the initial population size remaining at the end of the monitoring time period.

Table 4. Estimates of the probability of a population declining or increasing a given percentage or greater over a 17-year (SKC) or 18-year (LAS and SIE) monitoring period. Data are from California spotted owls on 3 study areas (Lassen [LAS], Sierra [SIE], and Sequoia Kings Canyon [SKC]) in the southern Cascades and Sierra Nevada, California, for 1990–2011. Probabilities are based on a posterior distribution of overall realized population change (Δ_t MCMC), which is the proportion of the initial population size remaining at the end of the monitoring time period.

Study area	Overall decline in population							
	$\geq 50\%$	$\geq 30\%$	$\geq 25\%$	$\geq 20\%$	$\geq 15\%$	$\geq 10\%$	$\geq 5\%$	$> 0\%$
LAS	0.00	0.24	0.39	0.54	0.69	0.80	0.88	0.93
SIE	0.00	0.07	0.15	0.26	0.40	0.54	0.67	0.78
SKC	0.00	0.00	0.01	0.02	0.04	0.07	0.12	0.18

Study area	Overall increase in population							
	$\geq 0\%$	$\geq 5\%$	$\geq 10\%$	$\geq 15\%$	$\geq 20\%$	$\geq 25\%$	$\geq 30\%$	$\geq 50\%$
LAS	0.07	0.04	0.02	0.01	0.01	0.00	0.00	0.00
SIE	0.22	0.14	0.08	0.05	0.03	0.01	0.01	0.00
SKC	0.82	0.76	0.68	0.60	0.52	0.45	0.38	0.10

Hypothesis testing is a less informative evaluation compared to using a Bayesian approach to generate a posterior distribution of Δ_t . If the hypothesis is rejected, or if the 95% CI of estimated $\bar{\lambda}$ or Δ_t covers 1.0, even if barely, we have no way of evaluating the probability of a decline or lack thereof. The posterior distribution of Δ_t has broader application beyond use with Pradel model estimates of λ_t ; it can be used for changes in density, abundance, or any population parameter of interest. For example, Gerrodette (2011) used data on the vaquita to examine the usefulness of frequentist versus other methods of hypothesis support for determining the change in abundance over an 11-year period. In a frequentist test for difference in abundance (i.e., overall change), $P = 0.38$, which did not mean abundance was equal, but rather that the data were not inconsistent with this hypothesis. However, although Gerrodette (2011) found a non-significant P -value when testing whether abundance had changed, Bayesian methods suggested a high probability of decline (0.88).

In our study, all CIs of estimates of $\bar{\lambda}$ and Δ_t covered 1. However, the probability of a decline varied widely between the 3 study sites, with LAS having a substantial probability of $\geq 10\%$ decline (0.80), whereas SKC only had a 0.07 probability of the same decline. The problem of having a large probability of decline, even when the null hypothesis of no decline is not rejected, is especially important for small populations. Smaller populations can drop, undetected by a null hypothesis approach, to low levels where the probability of extinction increases to unacceptably high levels due to demographic variability and stochastic environmental events (White 2000, Lande 2001, Morris and Doak 2002). The undetected decline is a problem faced by ecologists studying sensitive populations. For example, even with 12–19 years of northern spotted owl (*Strix occidentalis caurina*) monitoring data collected on 13 study areas, Anthony et al. (2006) found that although 12 of 13 areas had estimates of $\bar{\lambda}$ that were < 1 , they could only conclude that populations were declining on 4 areas based on whether confidence intervals overlapped 1. Further, using Δ_t , Anthony et al. (2006) were only able to detect a change in population for 6 of the 12 areas with estimated $\bar{\lambda} < 1$. Clearly, using a Bayesian approach to

generate the posterior distribution of Δ_t MCMC is a powerful tool for estimating probability of change and provides a more refined measure of risk to monitored populations, which is particularly significant when monitoring results affect the legal status of a species and have broad management ramifications.

Although measures of central tendency, such as mean or median λ and Δ_t , have the discussed advantages, they also have limitations. If a population is growing ($\bar{\lambda} > 1$), managers cannot tell whether the growth is from internal recruitment or immigration. Likewise, if a population is declining, managers cannot determine whether the declines are due to deaths within the population or emigration. Thus, additional information on specific vital rates is necessary to understand what is driving λ and ultimately, the mechanisms driving population dynamics. Although $\bar{\lambda}$ and Δ_t are important metrics, they may not suffice for a full assessment of a population's health. Ultimately, the choice of appropriate monitoring parameters should be based on management and conservation objectives and information needs, given available resources.

MANAGEMENT IMPLICATIONS

Managers and regulators charged with formulating conservation strategies for focal wildlife species require robust information to support decisions that are often ecologically complex and socially and politically controversial. Realized population change is a useful metric for assessing population trends of focal species. Further, using Bayesian MCMC methods to generate a posterior distribution of Δ_t is a valuable tool for robustly estimating risk, or probability of declines, for retrospective analyses of monitored populations. In addition, compared to a random effects estimator, Bayesian MCMC methods also provide a more broadly applicable approach for estimating mean or median λ and σ because they do not have the restriction of requiring ≥ 10 estimates. Finally, Bayesian MCMC methods are also preferable for point estimates of λ_t because they are exact for the data and, with sampling variation removed, their credible intervals are smaller than CIs for likelihood estimates. The Bayesian approach to generate a posterior distribution of Δ_t ,

in particular, provides biologists, managers, and regulators with more insightful information on the probability of population changes that can better inform conservation assessments and strategies.

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California Spotted Owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape

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RESEARCH ARTICLE

California Spotted Owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape

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ABSTRACT

Fire is a dynamic ecosystem process of mixed-conifer forests of the Sierra Nevada, but there is limited scientific information addressing wildlife habitat use in burned landscapes. Recent studies have presented contradictory information regarding the effects of stand-replacing wildfires on Spotted Owls (*Strix occidentalis*) and their habitat. While fire promotes heterogeneous forest landscapes shown to be favored by owls, high severity fire may create large canopy gaps that can fragment the closed-canopy habitat preferred by Spotted Owls. We used radio-telemetry to determine whether foraging California Spotted Owls (*S. o. occidentalis*) in Yosemite National Park, California, USA, showed selection for particular fire severity patch types within their home ranges. Our results suggested that Spotted Owls exhibited strong habitat selection within their home ranges for locations near the roost and edge habitats, and weak selection for lower fire severity patch types. Although owls selected high contrast edges with greater relative probabilities than low contrast edges, we did not detect a statistical difference between these probabilities. Protecting forests from stand-replacing fires via mechanical thinning or prescribed fire is a priority for management agencies, and our results suggest that fires of low to moderate severity can create habitat conditions within California Spotted Owls' home ranges that are favored for foraging.

Keywords: California Spotted Owl, fire severity, habitat selection, Yosemite National Park

Patrones de uso de hábitat de *Strix occidentalis occidentalis* en un paisaje con incendios

RESUMEN

Los incendios son procesos dinámicos de los ecosistemas de bosques mixtos de coníferas de la Sierra Nevada, pero la información científica que evalúa el uso de hábitat de la fauna en paisajes quemados es limitada. Estudios recientes presentan información contradictoria con respecto a los efectos de los incendios forestales que reemplazan rodales de bosque sobre poblaciones de *Strix occidentalis* y su hábitat. Mientras que los incendios promueven paisajes de bosque heterogéneos que son preferidos por estos búhos, los incendios de alta severidad pueden crear grandes claros en el dosel que pueden fragmentar el hábitat de dosel cerrado preferido por *S. occidentalis*. Usamos telemetría de radio para determinar si los *S. o. occidentalis* del parque nacional Yosemite exhiben selección por un tipo particular de severidad en los incendios en su ámbito hogareño mientras forrajea. Nuestros resultados sugieren que *S. o. occidentalis* presentó selección de hábitat en su ámbito hogareño para sitios cerca de los nidos y hábitats de borde, y selección débil por áreas con incendios menos severos. Aunque los individuos seleccionaron bordes de alto contraste con mayores probabilidades relativas que los bordes de bajo contraste, no detectamos una diferencia estadística en estas probabilidades. La protección de los bosques contra los incendios forestales usando podas o incendios controlados es una prioridad para las agencias de manejo y nuestros resultados sugieren que los incendios de intensidad baja a moderada pueden crear condiciones de hábitat preferidas para el forrajeo en los ámbitos hogareños de *S. occidentalis*.

Palabras clave: parque nacional Yosemite, selección de hábitat, severidad de los incendios forestales, *Strix occidentalis*

INTRODUCTION

In the multilayered, structurally complex, and large tree–dominated forests (hereafter, ‘old forests’) occupied by the California Spotted Owl (*Strix occidentalis occidentalis*),

fire is critical for maintaining forest structure and function (Collins et al. 2011). Currently, California Spotted Owl populations are declining due to habitat loss and fragmentation (Tempel et al. 2014). The role of stand-replacing fires is complex and research has produced

conflicting results, with some studies suggesting that large stand-replacing fires may pose a new threat to Spotted Owl habitat (Spies et al. 2010, Tempel et al. 2014, Jones et al. 2016) and others indicating limited negative effects on the owls (Bond et al. 2009, 2016, Lee and Bond 2015a). Fire has an essential role in forests inhabited by Spotted Owls, yet that role is changing as the spatial extent and behavior of fire increases and intensifies, respectively, due to a warming climate (Stephens et al. 2013) and decades of fire suppression (Collins et al. 2011). Therefore, it is critical for land managers to understand the effects of fire on California Spotted Owl habitat selection, especially if they want to develop a conservation strategy for a changing forest.

Patterns of fire severity (magnitude of change in vegetation, often measured as tree basal area removed by fire) affect important characteristics of owl nesting and roosting habitat, such as canopy closure and cover, forest structure, and persistence of large trees (Collins et al. 2011, Roberts et al. 2011). However, because the foraging habitat of owls has greater structural variability than their nesting and roosting habitats (Bias and Gutiérrez 1992, Call et al. 1992), the influence of fire severity on owl foraging habitat is complex. Foraging sites are typically moderately dense forest stands ($\geq 40\%$ canopy closure) close to nests and small streams, with trees greater than 15 cm diameter at breast height, large hardwoods (Call et al. 1992, Irwin et al. 2007, Williams et al. 2011), and higher woody debris and greater snag presence than expected by chance (Gutiérrez et al. 1992). Foraging habitats often contain more variable characteristics than nesting and roosting habitats, such as different forest types or gaps in the canopy where shrubs may be abundant, due to the distribution and range of habitat needs of primary owl prey, which include woodrats (*Neotoma* spp.), northern flying squirrels (*Glaucomys sabrinus*), and mice (*Peromyscus* spp.; Call et al. 1992).

Diversity in vegetation and fuels composition and structure, weather, and topography results in a mosaic of postfire forest patches burned at varying fire severities, including interspersed areas untouched or measurably unchanged by fire (Miller and Urban 1999, Collins et al. 2007). This postfire spatial habitat complexity can increase a foraging owl's access to different types of habitat and number of habitat edges, including high and low contrast edges (Miller and Urban 1999, Franklin et al. 2000, Collins et al. 2007). Research examining how different edge types affect owl foraging habitat quality is limited, but some studies have revealed that Northern Spotted Owls (*S. o. caurina*) avoid high contrast edges (sharply defined edge between 2 different habitat patches, e.g., a patch burned at low fire severity adjacent to a patch burned at high severity) and prefer low contrast edges (blended edges between different habitat types, e.g., a habitat patch unchanged postfire adjacent to patch burned at low fire

severity), depending on the spatial scale used to examine habitat selection (Glenn et al. 2004, Clark 2007, Comfort et al. 2016). Therefore, by creating a patchwork of stands of different ages, fire may enhance foraging opportunities for Spotted Owls by increasing the number or amount of edges present in the landscape (Franklin et al. 2000). However, others have argued that patch edges fragment habitat, decrease owl survival (Blakesley et al. 2005), and increase owl home range size (Schilling et al. 2013), although differences in primary prey species may contribute to these differences.

We examined California Spotted Owl habitat use patterns in a landscape with a range of fire severities, patch edge types, and fire ages in Yosemite National Park (hereafter, Yosemite), California, USA. The forests in Yosemite, unlike surrounding private timberlands and areas administered by the U.S. Forest Service (USFS), have not been managed and harvested for timber, which allows the examination of fire effects without the confounding influence of plantations or logging. Learning how sensitive species, such as the California Spotted Owl, respond to fire is critical for implementing future management plans. Specifically, we wanted to know how owl foraging patterns may be influenced by (1) fire severity, (2) fire-created edges, and (3) other factors such as topography or distance to a stream or nest or roost site. We hypothesized that fire severity would be important to owl habitat use because of changes in forest structure and canopy cover (Shaffer and Laudenslayer 2006, Beaty and Taylor 2007). Further, we postulated that fire-created edges would influence owl habitat use (Clark 2007, Comfort et al. 2016). We also speculated that abiotic factors, such as slope, aspect, and distance to streams and nests or roosts, would influence owl foraging habitat use, based on earlier work (Clark 2007, Irwin et al. 2012). By providing insight into owl use of fire severity patch type patterns, this study may help to inform future fuels reduction efforts and prescribed burning programs in similarly managed public lands (i.e. National Parks).

METHODS

Study Area

Yosemite spans 302,688 hectares (ha) in the central Sierra Nevada of California. We surveyed California Spotted Owls in the 87,200 ha of lower montane forest dominated by California black oak (*Quercus kelloggii*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*; Figure 1). Monthly average temperatures for the Yosemite Valley range from -3°C to 32°C , and precipitation, which mostly occurs as snow at high elevations, varies from 0.8 cm to 15.7 cm (<http://www.nps.gov/yose/planyourvisit/climate.htm>). A Mediterranean

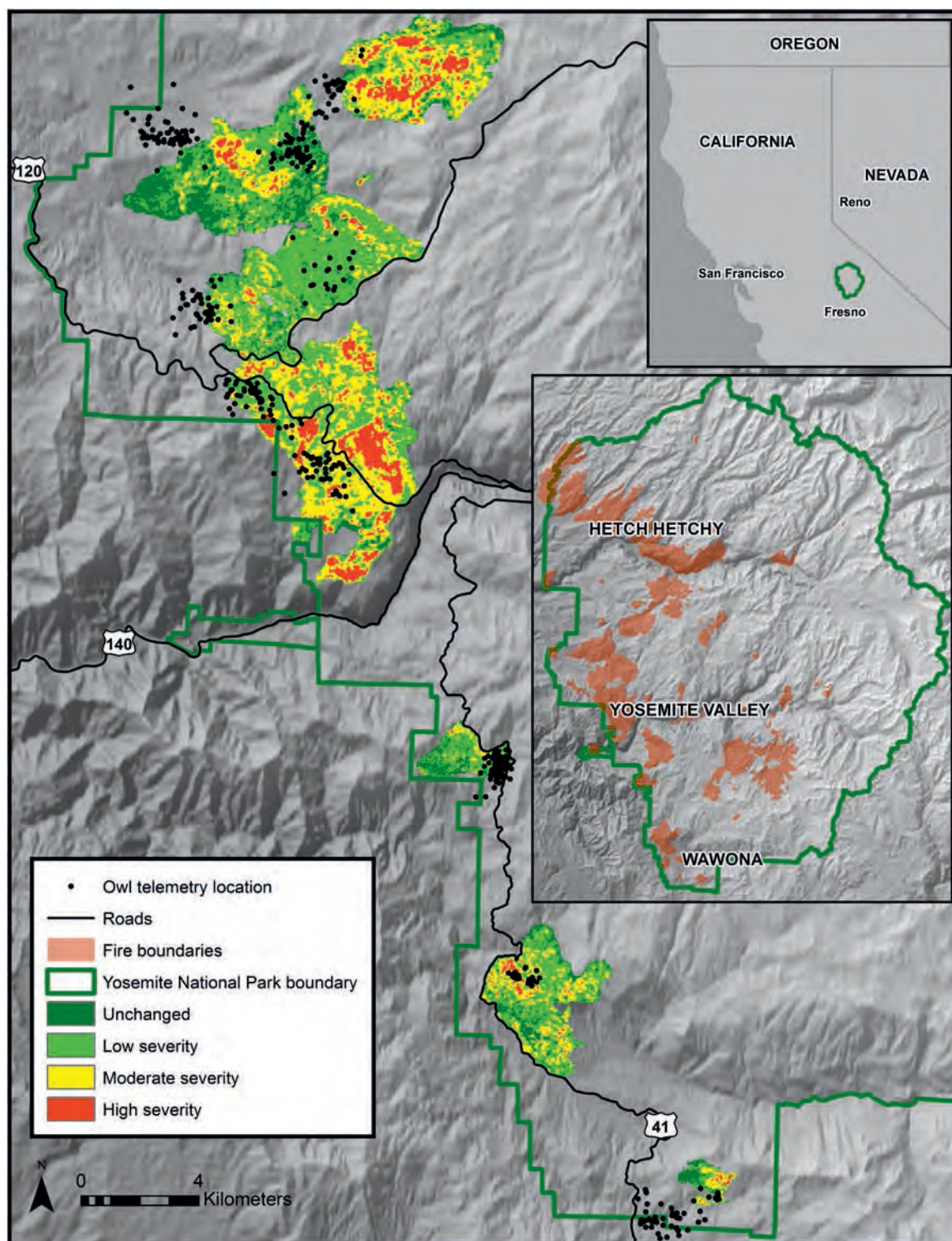


FIGURE 1. Study area used to examine California Spotted Owl foraging habitat use patterns within California, USA, and Yosemite National Park, 2010–2012. Inset map of Yosemite National Park shows all fires that have burned in Yosemite since 1997. Large map shows fire severity patterns for specific fires near owl locations.

climate of cool, wet winters and warm, dry summers characterizes Yosemite's climate.

Field Methods

We located owls following established protocols (Forsman 1983) at previously known nest or roost sites (Roberts et al. 2011). We selected 10 sites based on (1) the occurrence of a recent (since 1997) wildfire or prescribed fire, (2) the presence of a known owl pair, and (3) site accessibility (the crew needed to be able to rapidly hike or drive to the telemetry stations at night). We conducted all fieldwork from June through September, 2010–2012, so the extremely large 'Rim Fire' that burned portions of Yosemite in 2013 did not form part of this analysis. We attached a backpack-mounted radio-transmitter (AVM Instrument Company, Colfax, California, USA) to captured owls following established procedures (Forsman 1983, Bull and Henjum 1990, Guetterman et al. 1991). Because Glenn et al. (2004) showed that Spotted Owl mates do not forage independently, we only radio-tagged one member of a pair in a given year.

We performed nocturnal telemetry surveys from 30 min after sundown to 30 min before sunrise to determine foraging locations. We used Communications Specialists receivers (model R-1000; Communications Specialists, Orange, California, USA) and 3-element Yagi antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA) to track all radio-tagged owls. We triangulated owl foraging locations with compass bearings from georeferenced monitoring stations and collected one foraging location per owl each night to avoid pseudoreplication (Guetterman et al. 1991). To ensure that we sampled each owl at different times throughout the sampling period, we randomly assigned telemetry survey start times to each owl.

Home Range Analysis

We used the arithmetic mean estimator in Program LOAS (Location of a Signal) 4.0b (Ecological Software Solutions, Hegymagas, Hungary, <http://www.ecostats.com/web/LOAS>) to generate owl point locations from our triangulated compass bearings recorded from the georeferenced telemetry stations. To reduce location signal bias, we only used location polygons ≤ 5 ha (this excluded only 4% of our locations).

To assess the accuracy of our telemetry locations, we followed the same techniques as have been used in other owl telemetry studies (Glenn et al. 2004, Bond et al. 2009, Wiens 2012). We triangulated to stationary owls at diurnal roosts visually located by an independent observer. We also placed transmitters in locations unknown to technicians. A naïve technician then performed triangulation to estimate the location of the hidden transmitter. We calculated telemetry bias as the

linear distance between locations estimated by triangulation and actual locations.

We plotted owl locations in ArcGIS 10.0 (ESRI, Redlands, California, USA), and created a buffered owl location using the median error distance as our radius (Figure 2). From these telemetry locations, we calculated a home range for each owl with ArcGIS and Geospatial Modelling Environment (GME 0.6.0.0; Beyer 2012) using 100% minimum convex polygons (MCP) including the error buffer. We then calculated home range size by summing the area contained within the MCP. In order to conform to a normal distribution, we log-transformed the home range sizes and used the geometric mean, which provides a better measure of the middle of a dataset than the arithmetic mean (Sheskin 2003).

Habitat Selection Analysis

We applied logistic regression to compare used habitat (owl telemetry locations) with available habitat and to estimate a resource selection function (Manly et al. 2002) at the within-home-range scale (i.e. third order selection; Johnson 1980). Because we could not ensure that our sample of owls was truly random across the broader landscape, we did not attempt to examine the selection of home ranges within a larger study area (i.e. second order selection). We defined available habitat within the MCP, rather than within a fixed kernel home range estimate, because MCPs may more accurately represent available area (Gillies et al. 2006, Kauhala and Auttila 2009, Comfort et al. 2016). Depending on the particular habitat variable, we used the point center location or the entire telemetry circle (point location with error buffer) in our estimations (see below).

We randomly generated ~ 3 times as many available locations as used locations within each owl's home range in ArcGIS to minimize rates of contamination and overlap. Contamination refers to having both used and unused units in the pool of available units (Johnson et al. 2006), and overlap occurs when a random (available) sample falls in the same location as a used location. We buffered available locations with a radius of our median error distance to account for the same spatial error as the used locations, and estimated the same habitat variables for both used and available locations. For the final candidate model set, we fit generalized linear mixed-effects models (GLMM) allowing for both fixed and random effects. We used the `glmer` function in the `lme4` package (Bates et al. 2015) in R (R Core Team 2015) to fit all models and considered owl ID as a random effect. Therefore, we fit a model with a varying-intercept group effect using the variable 'owl ID,' which allowed used and available locations to be compared at the level of each individual owl. We considered all other habitat variables as fixed effects (see below).

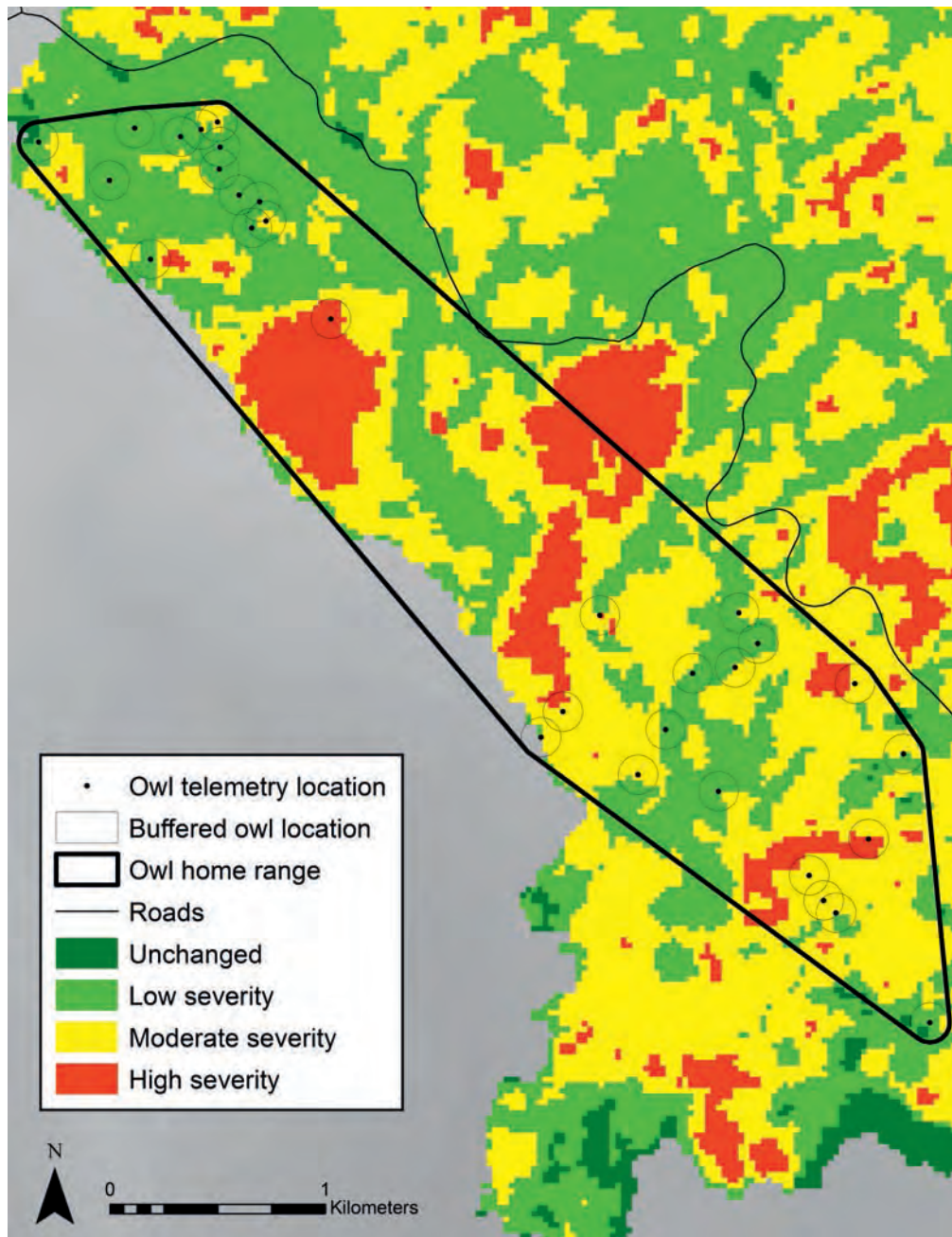


FIGURE 2. An example of one California Spotted Owl home range showing fire severity patterns within a home range in Yosemite National Park, California, USA, 2012. Black dots represent owl telemetry locations and circles show the buffered owl location with a 92-m radius to represent telemetry error.

Habitat Variables

We calculated all predictor variables using ArcGIS and GME and used fire severity maps generated by Yosemite fire specialists to describe the extent and boundaries of fires in each owl's home range. To quantify fire severity, we used the relative differenced Normalized Burn Ratio (RdNBR), which measures the amount of spectral (reflectance) change in vegetation after fire (Miller and

Thode 2007). Miller and Thode (2007) created relative thresholds to classify all RdNBR values into 4 fire severity patch types: no detectable change (hereafter, unchanged); low; moderate; and high. Following van Wagtendonk and Lutz (2007), we reclassified these types with integer values of 2, 3, 4, and 5, respectively, to aid in the calculation of a total fire severity index (FSI) for each buffered owl location. Reclassification with integer values allowed every

combination of fire severity patch composition within each buffered owl location to have its own unique value.

We overlaid the used and available locations onto the fire severity maps to determine fire severity composition at each location (Figure 1). We calculated the proportional area of each fire severity patch type within the buffered owl location using ArcGIS and GME and then multiplied the area of each patch type by its corresponding RdNBR integer value. We calculated a total FSI for each foraging location by summing all of these values (Roberts et al. 2008). Our FSI ranged continuously from 2 (i.e. a buffered owl location that was entirely unchanged) to 5 (i.e. an area completely burned at high severity). Values between these extremes corresponded to buffered owl locations burned at moderate severity or, since some buffered owl locations contained multiple fire severity types, burned at a combination of higher and lower fire severities. This FSI summation within a buffered location thus collapsed heterogeneity within a buffered location to a single value, but we feel that this appropriately acknowledged the uncertainty of the owl's actual location within the buffered location circle and resulted in a conservative analysis (i.e. owls less likely to show strong selection for high or low FSI values). We believe that simply using the centroid of the error polygons as the owl's assumed location, common in some studies, fails to reflect the imprecision typical in radio-telemetry studies. Nonetheless, we did not want to ignore heterogeneity of habitats within an estimated location, so we also included edge effects in our analysis.

We classified all used and available locations as an edge (no edge, low contrast edge, or high contrast edge) if they contained more than one fire severity category. Edge locations that contained patches burned at high fire severity were considered high contrast edges, and edge locations without patches burned at high fire severity were categorized as low contrast edges (Clark 2007).

Our abiotic covariates included horizontal distance to roost (m); horizontal distance to stream (m); slope (degrees); elevation (m); and aspect (north, northeast, east, southeast, south, southwest, west, and northwest) as a categorical variable. Employing the point location, or the center of the error-buffered owl location, we generated all abiotic covariates in ArcGIS using a 10-m digital elevation model for the study area.

Because slope, elevation, and distance to roost were on different scales (e.g., degrees vs. hundreds of m), we rescaled these variables to make coefficients more comparable by subtracting the mean of each variable from an individual value and dividing the difference by the standard deviation. Logistic regression does not require that predictor or response variables be normally distributed (Johnson 1998), and, to avoid multicollinearity, we confirmed that all correlation coefficients between variables in candidate model sets were <0.2 .

Model Development and Selection

Based on previous Spotted Owl research, we developed a priori candidate models incorporating 3 sets of covariates: (1) fire, (2) edge, and (3) abiotic, and proceeded through model development in stages (Olson et al. 2004, Irwin et al. 2012). Applying an information-theoretic approach based on Akaike's Information Criterion (AIC) to evaluate candidate models, we used second-order AIC (AIC_c) to account for small sample sizes and ranked models according to Akaike weights (w_i ; Anderson 2008). The model with the lowest AIC_c value and the greatest Akaike weight represented the best fit to the data, and we considered models with ΔAIC_c (difference in AIC_c value between the candidate model and the best-fit model) <2 as plausible alternative models (Anderson 2008).

We hypothesized that topographical characteristics (slope, aspect, and site elevation) would be important because of differing forest structure and composition associated with these characteristics. Topography can affect forest structure, microclimate, and fire behavior, with higher canopy cover, cooler microclimates, and lower fire severity and frequency at northern aspects, and more open canopies, warmer microclimates, and higher fire severity and frequency at southwestern aspects (Lydersen and North 2012). Further, forest structure and composition can influence owl prey abundance (Coppeto et al. 2006, Roberts et al. 2008, 2015). To determine whether owls were selecting intermediate elevations or slopes, we incorporated quadratic forms for these variables.

We postulated that distance to the roost site would be influential because Spotted Owls are central-place foragers and have high site fidelity to roost locations (Carey and Peeler 1995). We speculated that distance to a perennial stream would affect owl foraging because riparian areas are important for primary prey species such as the northern flying squirrel (Meyer et al. 2007). Because the relationship with distance may be nonlinear, we incorporated quadratic terms for all distance covariates.

We hypothesized that fire severity would be pivotal to owl habitat use because of corresponding changes in forest structure (Shaffer and Laudenslayer 2006, Beaty and Taylor 2007). We postulated that edge would be important because it has been found to affect life history traits (Franklin et al. 2000, Tempel et al. 2014); therefore, the final candidate model set included edge type as a predictor.

We translated the above hypotheses into a final candidate model set in various combinations along with the best models from the abiotic predictor variable model sets. We created a 95% confidence set of models by including models for which Akaike weights summed to 0.95. We applied model averaging to the entire candidate model set, not just the 95% confidence set, to calculate logistic regression coefficients for all predictor variables using R package AICcmodavg (Mazerolle 2016). We

TABLE 1. Fire severity proportions, patch sizes for patches used more than once by California Spotted Owls, and mean patch sizes available in Yosemite National Park, California, USA, 2010–2012.

Fire severity patch type ^a	Percentage contained in owl home range (mean $\pm$ SE)	Patch size (ha) used by owls (mean $\pm$ SE)	Patch size (ha) used by owls (range)	Patch size (ha) intersecting home range (mean $\pm$ SE)
Unburned	42 $\pm$ 8	**	**	**
Unchanged	6 $\pm$ 2	4.4 $\pm$ 17.9	0.1–118.4	2.2 $\pm$ 0.7
Low	26 $\pm$ 4	99.7 $\pm$ 391.1	0.1–2,035.5	30.5 $\pm$ 13.7
Moderate	21 $\pm$ 4	56.2 $\pm$ 159.3	0.1–696.9	10.6 $\pm$ 4.7
High	6 $\pm$ 1	6.5 $\pm$ 10.5	0.1–36.0	2.9 $\pm$ 0.8

^a Unburned = area untouched by fire outside the fire perimeter; Unchanged = no detected change in vegetation, relative differenced Normalized Burn Ratio (RdNBR) threshold <42 ; Low = surface fuels consumed with little change to overstory structure, RdNBR threshold ≥ 42 and <220 ; Moderate = understory vegetation, midstory shrubs, and small trees consumed and $\sim 0.5\%$ canopy trees killed, RdNBR threshold ≥ 220 and <566 ; High = nearly all mature plants killed ($\sim 75\%$ of canopy trees), RdNBR threshold ≥ 566 .

** Unburned mean and range of patch sizes were not calculated because unburned areas consisted of large, contiguous patches of forest.

evaluated logistic regression coefficients for the model-averaged estimates by calculating 95% confidence intervals to determine the strength of estimates. We used odds ratios to examine the change in the relative probability of selection for every 1 unit change in the covariate (Manly et al. 2002). Odds ratios >1 indicate increased likelihood of owl use with each unit increase of the predictor variable. Odds ratios <1 indicate a decreased likelihood of owl use with each unit increase of the predictor variable. Use-availability designs are unable to estimate the true probability of selection (Johnson et al. 2006), therefore we refer to our findings as relative probability. We evaluated the full model using both marginal and conditional R^2_{GLMM} (Nakagawa and Schielzeth 2013). Marginal R^2 accounts for the variance explained by fixed factors, while conditional R^2 accounts for the variance explained by fixed and random factors. For all statistical analyses, including AIC_c estimations and evaluations, we used R (R Core Team 2015).

RESULTS

From June through September, 2010–2012, we captured 13 owls (8 females and 5 males) from 8 unique territories within Yosemite. We monitored the same territories for multiple years, but captured a different member of the pair each year, except in one situation in which we caught the same female in 2010 and 2012. We therefore had 14 sets of used and available location data to consider as random effects. We calculated 480 ($\bar{x}$ = 35 per owl) owl foraging locations (used points) and generated 1,431 random (available) points for the logistic regression analysis. Based on the 18 distance error samples that we collected across all 8 of our sampled territories, our median error distance was 92 m, which we used as the error buffer for our analyses.

Home Range Analysis

Home range size ranged from 65 ha to 1,136 ha for male owls and 90 ha to 2,983 ha for female owls, averaging 302 ha (95% CI: 119–787 ha) and 451 ha (95% CI: 175–1,293 ha), respectively. There was no statistically significant difference in log-transformed home range size between males and females ($F_{1,13} = 0.5$, $P = 0.5$); therefore, we pooled the data for the analyses and the mean pooled home range size was 391 ha. Mean home range size also did not differ between years using MCP estimates ($F_{1,13} = 0.2$, $P = 0.7$).

In our study area, nearly 75% of most owl home ranges burned in one or more fires that occurred between 1997 and 2009. However, 2 owl home ranges contained $<5\%$ burned area, although both of these territories were immediately adjacent to large burns. Overall, the proportion of the home range in each fire severity category declined with increasing severity, and the average size of patches used more than once by owls varied depending on fire severity, with the largest used patches burned at low to moderate severities (Table 1).

Habitat Selection Analysis

Across all owl locations, the mean ($\pm$ 1 SE) FSI was 2.8 ± 0.8 and distance to roost was $1,310 \pm 1,518$ m. The mean slope and elevation of all owl locations were $12.1 \pm 5.9^\circ$ and $1,692 \pm 161$ m, respectively.

We collected data for 3 yr and treated year as a categorical variable, blocking this factor to account for any variability across years and including it as an interaction term to examine whether the effect of a predictor differed across years. Because models with the year of data collection and its interaction with predictor variables showed little evidence of support from the data, we dropped year from our candidate models and combined data for all years in subsequent analyses.

TABLE 2. Models within the 95% confidence set that best explained California Spotted Owl habitat use patterns in Yosemite National Park, California, USA, 2010–2012. K is the number of model parameters, $-2\text{Log}_e(\mathcal{L})$ is the $\log_e$ (likelihood), ΔAIC_c is the difference from the top model in Akaike's Information Criterion corrected for small sample size, and w_i is the Akaike model weight. Models highlighted in bold are within $2 \Delta\text{AIC}_c$ of top model.

Model ^a	K	$-2\text{Log}_e(\mathcal{L})$	ΔAIC_c	w_i
DistRoost + DistRoost² + FSI + EdgeType	7	2133.95	0.00 ^b	0.27
Slope + Elev + DistRoost + DistRoost² + FSI + EdgeType	9	2130.59	0.69	0.19
Slope + DistRoost + DistRoost²	5	2138.91	0.94	0.17
Slope + Elev + DistRoost + DistRoost ²	6	2138.26	2.31	0.09
DistRoost + DistRoost ²	4	2142.53	2.55	0.08
Slope + Elev + DistRoost + DistRoost ² + EdgeType	8	2135.88	3.95	0.04
Elev + DistRoost + DistRoost ²	5	2141.96	3.99	0.04
DistRoost + DistRoost ² + FSI	5	2142.01	4.13	0.03
Slope + Elev + DistRoost + DistRoost ² + FSI	7	2138.15	4.21	0.03

^a DistRoost = distance to roost, i.e. distance (m) from center of buffered owl location for used and available points to roost; DistRoost² = quadratic term for distance to roost; FSI = fire severity index, i.e. index value for fire severity proportions within buffered owl location for used and available points, with values ranging from 2 (low) to 5 (high); EdgeType = 3 values of edge type: high contrast edge, low contrast edge, and no edge. High contrast edges contained high severity fire, while low contrast edges did not contain high severity fire; Slope = slope (degrees) at center of buffered owl location for used and available points; Elev = elevation (m) at center of buffered owl location for used and available points.

^b $\text{AIC}_c = 2148.00$.

Our analysis of topographic variables indicated that slope and elevation were the most important factors to consider in the final candidate model set. Because slope was strongly significant and the 95% confidence interval did not overlap zero, we placed more emphasis on including it in the final candidate models. Aspect and a quadratic effect of slope had poor support and we excluded them from subsequent analyses (Anderson 2008).

We determined that the model with the quadratic form of distance to roost (distance + distance²) had the lowest AIC_c value, and no other models that included distance to stream or other forms of distance to roost were within $2 \Delta\text{AIC}_c$ of this top model. Therefore, we incorporated only this nonlinear effect of distance to roost in the final candidate set of models.

After selecting the best models from the abiotic variables candidate model sets, the models with the strongest support included a combination of quadratic distance to roost, FSI, edge type (high contrast, low contrast, and no edge), slope, and elevation. The top model contained the fixed effects of quadratic distance to roost, fire severity index, and edge type (Table 2). All models in the 95% model set had substantially higher support than the null model, which had <1% of model weight (Table 2). The null model includes the intercept only, and if it is ranked highly indicates that predictor variables explain little about owl habitat use patterns. The marginal and conditional R^2_{GLMM} for the full model were both 0.02, indicating that little additional variance was explained by the random effect of individual owl ID.

Two models were within $2 \Delta\text{AIC}_c$ units of the top model and together all 3 carried 63% of the Akaike weight (Table 2). Because no model had a substantial amount of weight

(i.e. >0.75), we model-averaged all models in the set and report odds ratios from this averaged model (Table 3). Confidence intervals for the odds ratio estimates did not overlap 1 for distance to roost predictors, low contrast edge, and no edge, while those for fire severity index, slope, and elevation included or slightly overlapped 1 (Table 3). However, in estimates from the top model only, the 95% confidence interval for the odds ratio for FSI did not overlap 1 (Table 3).

Distance to roost had the highest relative variable importance (0.97), followed by FSI (0.55), edge type (0.54), slope (0.54), and elevation (0.40), when Akaike weights were summed across all models. Further, all models that did not contain the distance to roost variable had 0% of the Akaike model weight and thus were not included in the 95% confidence set of models. Confidence intervals did not overlap 1 and the odds of use were highest closest to the roost, with a slight increase again at distances far from the roost (Figure 3). The relative probability of use was highest for high contrast edge, followed by low contrast edge, and then no edge sites (Figure 4). The odds of owls using the high contrast edge type were 2.78 times greater than odds for the low contrast edge type and 3.5 times greater than for the no edge type. However, 95% confidence intervals for use of all 3 categories of edge type overlapped. The odds of nonuse increased by 1.25 for each 1 unit increase in FSI (odds ratio = 0.80), however the 95% confidence interval included 1 (Table 3), indicating less confidence in the estimate. The 95% confidence intervals for the odds ratios for slope and elevation overlapped 1, however the relative probability of use increased in areas with gradual slopes and higher elevations. Post hoc, we conducted an analysis that included an interaction term between FSI and

TABLE 3. Estimates, standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits for odds ratios from model-averaged model of California Spotted Owl habitat use patterns in Yosemite National Park, California, USA, 2010–2012. Estimates from the top models (Table 2) are included for comparison.

Predictor variable	Estimate	SE	95% LCL	95% UCL	Top model estimate	Second-best model estimate
High contrast edge	0.51	0.32	−0.11	1.14	0.91	0.89
Distance to roost	0.84 ^a	0.08	0.68	0.99	0.84 ^a	0.86
Distance to roost ²	1.12 ^a	0.04	1.04	1.21	1.13 ^a	1.12
Fire severity index	0.80	0.10	0.61	1.00	0.77 ^a	0.79 ^a
Low contrast edge	0.36 ^a	0.18	0.01	0.72	0.40	0.38 ^a
No edge	0.28 ^a	0.12	0.04	0.51	0.22 ^a	0.23 ^a
Slope	0.91	0.05	0.81	1.01	N/A	0.92
Elevation	1.05	0.06	0.93	1.17	N/A	1.06

^a 95% CI does not overlap 1.

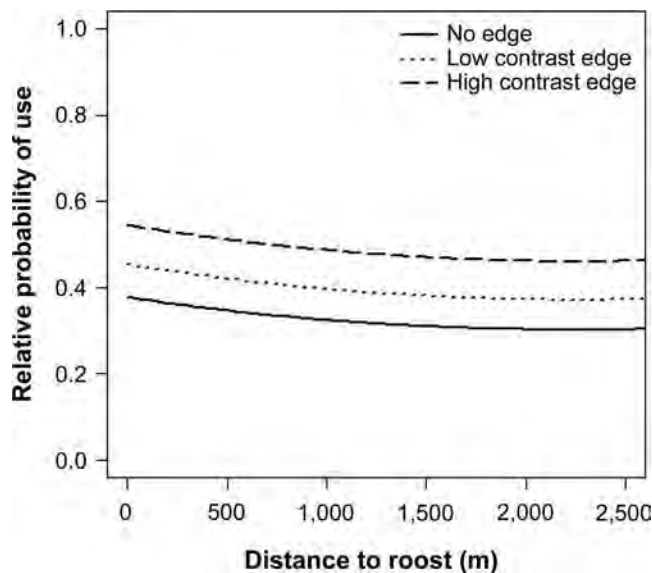
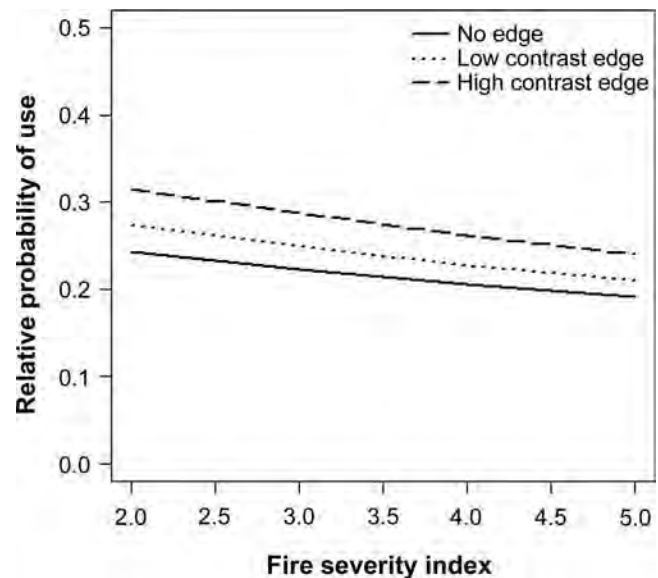
edge type in the top model, with no change to model interpretation.

DISCUSSION

Overall, California Spotted Owls in our study area selected foraging sites close to their roosts and avoided areas containing no habitat edges created by fire (Tables 2 and 3). The top model also suggested that owls showed an avoidance of areas with a high FSI (Figure 4), although the 95% confidence interval for the model-averaged estimate included 1 (Table 3). Model selection indicated strong support for the variables in the top models.

Our study joins several others that have documented that distance to the roost or nest is important for foraging habitat selection by Spotted Owls (Glenn et al. 2004, Irwin

et al. 2007, 2012, Wiens 2012, Bond et al. 2016). Spotted Owls have high site fidelity to nest sites and tend to roost near the eventual nest site, which is typically used for many years (Forsman et al. 1984). Furthermore, Spotted Owls are central-place foragers and often remain near the nest site in the nonbreeding season, so nest and roost locations may play a significant role in owl foraging habitat selection throughout the year (Forsman et al. 1984, Carey and Peeler 1995). Rosenberg and McKelvey (1999) argued that not including distance to the nest or roost in habitat selection models might bias selection for habitat characteristics near the central place, perhaps resulting in a false suggestion that it is the habitat type that the owls are selecting rather than merely its adjacency to the nest. In our study, support was strongest for a nonlinear effect of distance to the roost, with a slight flattening at intermediate distances from the

**FIGURE 3.** Modeled relative probability of California Spotted Owl habitat use as a function of distance to roost and edge type in Yosemite National Park, California, USA, 2010–2012.**FIGURE 4.** Modeled relative probability of California Spotted Owl habitat use as a function of fire severity index and edge type in Yosemite National Park, California, USA, 2010–2012.

roost and a slight increase at distances far from the roost (Figure 3). This nonlinear effect suggests that, while owls show a preference for areas in close proximity to the roost, they will also actively use more distant foraging sites, perhaps where there may be greater access to high contrast edges and/or higher prey availability.

Our results suggest that owls show a higher relative probability of selection for fire-created edge habitats than contiguous habitats. Collectively, recent research has revealed that Northern and California spotted owl survival and reproductive rates are higher in areas with a mosaic of vegetation types and edges (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Keane 2014), which may explain owl use of habitat edges associated with fire. In our study system, fire, rather than logging, was the main cause of forest change, and we found that selection was strongest for high contrast edges. In the Klamath Mountains of southern Oregon and northern California, Comfort et al. (2016) found that Northern Spotted Owls foraged in edges and, at large spatial scales (12.9–207.0 ha), appeared to select diffuse or low contrast edges created by fire, whereas at smaller spatial scales (3.2 ha), owls selected hard edges. However, Schilling et al. (2013) associated larger Spotted Owl home ranges with habitat fragmentation from increased edges in southwestern Oregon, where most edges were artifacts of past logging. A recent study that investigated foraging habitat selection in burned forests in southern California found no evidence of edge selection (Bond et al. 2016). The disparity in these results suggests that there may be a threshold level of habitat patch edges, where some edge habitat can have neutral to positive effects, but too many edges may lead to negative effects on owl habitat quality. Although not a focus of our analysis, it appears that owls used small patches burned at high severity, but used a much larger size range of patches burned at low and moderate severity, which implies that owls may have more flexibility in the latter burned patch types (Table 1). Further, it appears that burned patches used more than once by owls may be larger than the average available burned patch size (Table 1), suggesting that patch size could influence selection of burned habitat and warrants future investigation. The complexities of these results from different studies suggest that, to find a balance between high-quality edge habitat and potentially detrimental fragmentation, more research addressing Spotted Owl use of habitat edges is necessary, especially in burned landscapes.

Our analyses showed that California Spotted Owls in our study area also had a weak negative relationship with FSI (Figure 4). This negative relationship with FSI suggests that, while owls in Yosemite frequently used edges created by high severity fire, they may have avoided the interiors of large patches burned at high fire severity, a result similar to that from research on California Spotted Owls in megafires

(Jones et al. 2016) and Northern Spotted Owls (Comfort et al. 2016). Therefore, perhaps small proportions of patches burned at high fire severity embedded in a larger matrix of areas burned at low and moderate fire severities may be beneficial for owl foraging habitat by creating high contrast edges.

Frequent low and moderate severity fires, characteristic of the mixed-conifer zones of the Sierra Nevada, have shaped these forests for millennia (Collins et al. 2011, Thode et al. 2011). Therefore, the native forest inhabitants, such as the California Spotted Owl, have evolved with the fire regime of these forests and should be adapted to fire that burns within the natural range of variation for this habitat type. Low severity fires typically result in minimal overall tree mortality and can maintain the closed canopy conditions favored by California Spotted Owls (Blakesley et al. 2005, Roberts et al. 2011). In fire-suppressed (unburned) forests, California Spotted Owls forage in mature forest with an abundance of large trees, multiple canopy layers, and 40–70% overstory canopy cover (Williams et al. 2011). Forests where fire is allowed to burn within the natural range of variation (at low and moderate severities), such as in Yosemite, typically retain all of these characteristics (Thode et al. 2011) and may explain the Spotted Owl foraging patterns that we observed in this study.

The effect of fire on California Spotted Owl habitat selection is complex and incompletely understood, with some studies finding contradictory results. For example, Bond et al. (2009) used radio-telemetry to examine the foraging habitat selection of California Spotted Owls in Sequoia National Forest, California, USA, and found that owls selected patches burned at high fire severity for foraging, perhaps due to a higher density of snags and increased shrub cover that provided refuge for their prey. In Bond et al.'s (2009) study, all owl territories experienced a fire with severity patterns that were not representative of the natural range of variation typical for those habitats (Meyer 2015). Our study encompassed a larger area and more than a dozen fires that burned with a considerable range of variation, yet still within the natural range of variation for the area. Bond et al. (2009) collected habitat use data during a single year, 4 yr after a single fire, while our study included many fires that burned 2–15 yr before data collection. Overall, fire severity proportions also differed between the 2 study areas because, on average, only 5% of owl home ranges in Yosemite contained patches burned by high severity fires, while foraging ranges in the study area of Bond et al. (2009) contained 13% high severity fire areas. The unburned forest matrix differed between the 2 study areas as well. The Sequoia National Forest, where the Bond et al. (2009) study occurred, had a history of timber harvest and much more aggressive fire suppression programs, whereas our study area in Yosemite

experienced minimal harvesting from the 1900s to the 1930s and, since 1970, managers have implemented prescribed fires and allowed many wildfires to burn unsuppressed (van Wagtenonk 2007, Lutz et al. 2009). Also, we used MCP to estimate available area, while Bond et al. (2009) used capture radius, which may have led to different estimated proportions of areas burned at high fire severity (Bond et al. 2016). Furthermore, Yosemite's complex fire history may have confounded the effects of any one fire, since past fires often drive the location and behavior of future fires. This makes it difficult to isolate the importance of repeated burning in owl foraging habitat selection without having a much larger sample size of owl foraging locations.

Other recent work has also suggested that Spotted Owls are not negatively affected by stand-replacing high severity fires. For example, Lee et al. (2012) examined colonization probabilities and concluded that fires that burned up to 32% of the total affected area at high severity had no effect on extinction or colonization probabilities of California Spotted Owls in burned forests of the Sierra Nevada. A further demonstration of uncertainty surrounding owl response to fire comes from Lee and Bond (2015a), who found high occupancy rates (modeled burned site occupancy probability for pairs = 0.87) 1 yr following a large fire in the Sierra Nevada. However, this occupancy probability may have been high because only historically occupied sites were monitored, compared with another study that randomly selected sites in burned and unburned forest to calculate occupancy rates (modeled burned site occupancy probability for pairs = 0.46; Roberts et al. 2011). Likewise, California Spotted Owls in southern California with <50 ha of severely burned habitat within core areas had extinction probabilities similar to those in unburned sites, but extinction probability increased if severely burned habitat exceeded 50 ha (Lee et al. 2013). Another consideration is that owl site occupancy is influenced by the previous year's reproductive state, making it difficult to separate the effects of disturbance vs. reproductive status (Lee and Bond 2015b).

Although we discovered that distance to roost, patch edge metrics, and fire severity patterns explained California Spotted Owl foraging habitat selection, we recommend that our top models be interpreted with caution, since it is likely that there are other factors that affect Spotted Owl foraging that we did not measure, such as prey availability. The tests that we used to evaluate our models assume that we measured all of the effects that may influence Spotted Owl foraging, which this study never intended to do; therefore, the low variability explained by the 'best' model is not unexpected. Incorporating owl ID as a random effect did not explain any of the variance in the model, meaning that the probability of use was not influenced by individual owls, a

result also seen in 2 other studies (Gillies et al. 2006, Williams 2008). Future research investigating microscale habitat characteristics associated with foraging locations or prey abundance and movement could help to shed more light on owl habitat use patterns. Our low model evaluation values indicate that other variables that we did not measure may be more important to patterns of Spotted Owl foraging habitat selection.

Conclusion

Protecting old forests in the Sierra Nevada from stand-replacing fires via mechanical thinning or prescribed fire is a priority for management agencies (Roloff et al. 2012, Kane et al. 2015). Researchers have concluded that active management, such as prescribed fire and silvicultural treatments, that promotes a matrix of tree age classes can reduce fire threat, promote forest resiliency, and decrease owl habitat loss to stand-replacing fire (Irwin et al. 2004, Roloff et al. 2012, Winford et al. 2015). For example, the Rim Fire, one of the largest fires in California's history, burned 5 of our study sites and 2 owl nest trees, demonstrating the need to incorporate fire as a management tool to avoid large stand-replacing fires. However, it is important to balance the benefits of fire for hazard reduction with the potential impacts of fire on sensitive wildlife, since long-term gains may result in short-term habitat loss for California Spotted Owls (Tempel et al. 2014, 2015, Jones et al. 2016). Our study found that edge type and fire severity index were important for explaining owl habitat selection, which suggests that maintaining closed canopy forest within owl home ranges that includes variably sized patches burned at low and moderate fire severity and small patches (<36 ha) burned at high severity may be beneficial for owls. Our results also suggest that sustaining forests burned in a mosaic of lower fire severities in different years interspersed with large unburned patches may help to preserve California Spotted Owls in Yosemite National Park.

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Data deposits: Our data will be deposited through the National Park Service Research Permit and Reporting System on the Integrated Resource Management Applications Portal.

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RESEARCH ARTICLE

Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes

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Abstract

Context Climate and land-use change have led to disturbance regimes in many ecosystems without a historical analog, leading to uncertainty about how species adapted to past conditions will respond to novel post-disturbance landscapes.

Objectives We examined habitat selection by spotted owls in a post-fire landscape. We tested whether selection or avoidance of severely burned areas could be explained by patch size or configuration, and whether variation in selection among individuals could be explained by differences in habitat availability.

Methods We applied mixed-effects models to GPS data from 20 spotted owls in the Sierra Nevada, California, USA, with individual owls occupying home ranges spanning a broad range of post-fire conditions after the 2014 King Fire.

Results Individual spotted owls whose home ranges experienced less severe fire (< 5% of home range severely burned) tended to select severely burned forest, but owls avoided severely burned forest when more of their home range was affected (~ 5–40%). Owls also tended to select severe fire patches that were smaller in size and more complex in shape, and rarely traveled > 100-m into severe fire patches. Spotted owls avoided areas that had experienced post-fire salvage logging but the interpretation of this effect was nuanced. Owls also avoided areas that were classified as open and/or young forest prior to the fire.

Conclusions Our results support the hypothesis that spotted owls are adapted to historical fire regimes characterized by small severe fire patches in this region. Shifts in disturbance regimes that produce novel landscape patterns characterized by large, homogeneous patches of high-severity fire may negatively affect this species.

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Keywords California spotted owl · Disturbance · Functional response · Individual variation · Resource selection · Salvage logging · *Strix occidentalis* · Wildfire

Introduction

Disturbance regimes create and maintain the characteristic vegetation patterns and dynamics to which animals are adapted in ecological systems (Lytle 2001; Betts et al. 2019). Climate and human land use change have led to modern disturbance regimes in many ecosystems that do not have a historical analog (Seidl et al. 2016), giving rise to novel post-disturbance landscape mosaics and altered regeneration pathways (Johnstone et al. 2016). Landscapes experiencing novel disturbance regimes are often characterized by changes in vegetation composition, patch size, and configuration that are expected to change selection pressures, which can affect the behavior and fitness of individual organisms (Karr and Freemark 1985). Responses to changing disturbance regimes vary among taxa (Elmqvist et al. 2003), but are likely to depend on the species' degree of habitat specialization as well as the extent to which these novel disturbances affect resources that limit individuals and populations (e.g., nesting or denning sites, primary prey/food) (Clavero et al. 2011). Therefore, the way in which individuals and populations select or avoid conditions in novel post-disturbance landscapes may offer insights into the ability of species to persist in landscapes experiencing changing disturbance regimes.

Wildfire is an important disturbance regime that is changing worldwide (Turner 2010; Seidl et al. 2017), and is considered to be a significant evolutionary force (Bond and Keeley 2005; Pausas and Parr 2018; Foster et al. 2020). The dry forests of western North America appear to be experiencing changes from a historically frequent-fire regime that consisted of predominately lower-severity fire with a relatively small component of high-severity fire by comparison (Stephens and Collins 2004; Steel et al. 2015; Safford and Stevens 2017), to one where fires have become larger and more severe (Steel et al. 2015; Abatzoglou and Williams 2016; Westerling 2016). More frequent 'megafires' in western dry forests are generally thought to be the consequence of a century of fire suppression, which increased landscape fuels (Stephens et al. 2014; Collins et al. 2017a), and anthropogenic climate change, which produced conditions enhancing fire risk (Diffenbaugh et al. 2015). As a consequence, the patch structure in post-fire landscapes is increasingly characterized by homogeneous large patches of

severely burned areas (Collins et al. 2017b; Stevens et al. 2017). Decreased heterogeneity in post-fire conditions (i.e., more homogeneously severe burned areas) may influence the behavior and space use of species that have evolved to exploit more heterogeneous environments and ultimately reduce individual fitness and population abundance.

Forest-dependent species inhabiting dry forests in western North America evolved under a frequent-fire regime that created diverse mosaics of post-fire conditions and thus have developed life history strategies to accommodate the structural and landscape heterogeneity created by fire. One of the more well-known of these species is the spotted owl (*Strix occidentalis*), an older-forest associated raptor that inhabits dry forests in portions of its geographical range that has been the focus of forest management conflict in the western United States for several decades (Simberloff 1987; Redpath et al. 2013; Gutiérrez et al. 2015). Recently, this conflict has shifted from "owls versus jobs" to "owls versus forest restoration"—a seemingly intractable conflict between efforts to increase resilience of seasonal dry forests and the conservation of spotted owl habitat (Peery et al. 2019; Stephens et al. 2019). A key feature of the current conflict involves the potential effects of large, severe wildfires on spotted owls. If such fires render forests unusable by spotted owls and thereby adversely affect owl populations, then fuels reduction activities (e.g., mechanical removal of small and medium trees, prescribed fire, and managed fire) might benefit this species by reducing severe fire impacts, if fuels reduction activities have minimal negative effects to owls (Peery et al. 2017). However, there is considerable disagreement in the literature regarding these tradeoffs and this has led to uncertainty about how to manage forests (Ganey et al. 2017; Lee 2018).

Uncertainties about how spotted owls respond to severe fire may be resolved, in part, by (i) distinguishing between the mean, population-level response and variation in responses by individual owls that experience a range of post-fire conditions, and (ii) explicitly incorporating the role of the spatial configuration of severe fire (e.g., patch size and shape), which has not been the focus of previous studies (Ganey et al. 2017). Resource selection functions (RSFs) offer an analytical method for characterizing selection or avoidance of resources (hereafter 'habitat'; i.e., cover types) that are available to individuals or populations

(Manly et al. 2002). It is often assumed when using RSFs that individuals will select (or avoid) habitats in the same way (i.e., habitat selection is a constant function of habitat availability; Mysterud and Ims 1998). However, the strength of habitat selection or avoidance can vary strongly in both direction and magnitude among individuals within a population, so accounting for individual variation in selection patterns is important for statistically rigorous testing of population-level selection (Duchesne et al. 2010). Individual-specific habitat selection may vary as a function of habitat availability, a phenomenon known as a “functional response” in habitat selection (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Matthiopoulos et al. 2011; Aarts et al. 2013). Testing for functional responses may give insights into how individuals respond across a gradient of habitat conditions—including novel landscape conditions and configurations—and allow explicit testing of hypotheses about the effects of increasing novelty caused by either climate change or human impacts on habitat selection.

We used mixed-effects RSFs to examine both individual- and population-level habitat selection (Muff et al. 2020) in GPS-tagged California spotted owls (*S. o. occidentalis*) occupying home ranges containing a wide range of high-severity fire effects following a recent California megafire (2014 King Fire; Jones et al. 2016). We examined the potential effects of fire characteristics (fire severity, pyrodiversity, and severe fire patch size and configuration) on owls while controlling for potential confounding factors (pre-fire forest cover), post-fire salvage logging, and the central-place foraging behavior exhibited by spotted owls (Carey and Peeler 1995; Rosenberg and McKelvey 1999). Because spotted owls have presumably adapted to frequent-fire regimes dominated by lower-severity effects (Ganey et al. 2017; Rockweit et al. 2017), we predicted that individual owls would avoid severely burned forests when these areas comprised a large portion of the home range or occurred in large patches. We also predicted that spotted owls would select burned areas with greater pyrodiversity, which would be expected to create structural and landscape heterogeneity preferred by owls (Gutiérrez et al. 1995; Franklin et al. 2000). In addition, we tested for the potential effects of salvage logging in burned forests on habitat use because previous studies have found that spotted owls

tend to avoid foraging in logged, post-fire landscapes (Comfort et al. 2016). We tested whether spotted owls exhibited functional responses to novel habitat conditions by assessing support for interaction terms within the RSF.

Methods

Study area

The study was conducted in the central Sierra Nevada, California, USA, as part of a longer-term spotted owl demographic study on the Eldorado and Tahoe national forests (Tempel et al. 2016; Jones et al. 2018). The study area was ~ 50,000-ha in size and consisted of mixed-use publicly-owned lands (~ 54%) managed by the U.S. Forest Service and privately-owned lands (~ 46%) managed primarily for timber resources. Elevations ranged from 590 to 2200 m, the climate was Mediterranean with warm, dry summers and cool, wet winters, and the dominant vegetation type was Sierran mixed-conifer montane forest. The elevational range, climate, and species composition of these forests historically resulted in frequent fires (mean return interval = 11 years; range = 5–50 years) of generally lower severity (5–15% area burned at high-severity), with some inclusion of smaller (< 10–100 ha) patches of high-severity fire (Stephens and Collins 2004; Safford and Stevens 2017).

In September and October 2014, the King Fire burned ~ 40,000 ha of primarily forested land in the central Sierra Nevada (Jones et al. 2016). Approximately half (~ 20,000 ha) of the King Fire burned at high-severity (> 75% canopy mortality), including very large contiguous patches, making the King Fire one of the largest and most uniformly severe fires in recent California history (Stevens et al. 2017). Areas along the fire boundary and in the southern portion of the King Fire experienced greater “mixed-severity” fire effects, characterized by a mosaic of low, moderate, and high-severity fire. Post-fire salvage logging occurred in portions of the burned area (Fig. 1) and the majority of salvage-logged areas (89%) occurred on private lands.

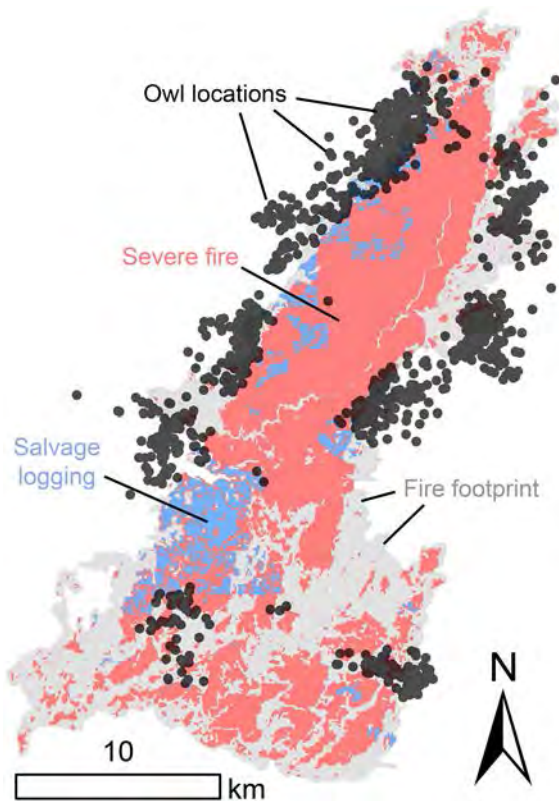


Fig. 1 King fire study area, showing the extent of the fire, severe fire, salvage logging, and locations used by owls

Global positioning system (GPS) data

In 2015–2017, we captured adult spotted owls occupying forests within and near the King Fire perimeter (Fig. 1) and fitted them with 7–10 g backpack-mounted dual GPS/VHF units (hereafter “GPS tags”) (Biotrack Ltd., Wareham, UK). We exhaustively searched the study area to locate owls during daytime and nocturnal walk-in surveys, and once located we captured owls using snare poles, hand-grabs, or bal-chatri traps. All relevant state and federal permits were obtained prior to capture and handling. In 2015, 2016, and 2017, we deployed 12, 10, and 4 GPS tags, respectively (total $n = 26$). There were no owls available for GPS tagging within the large, severely burned patch in the center of the study area (Fig. 1) because owl territories in that patch went extinct immediately after the fire (Jones et al. 2016) and were not re-colonized during the course of the study (G.M. Jones, unpublished data). Three individual spotted owls with GPS tags dispersed before data could be

retrieved (two in 2015, one in 2016), so our final sample size was 23. Of the 23 owls sampled, three individuals were sampled in consecutive years, which we accounted for by specifying a random effect for individual owl. GPS tags were deployed each year in May and early June and recorded 100–150 locations during nocturnal hours (1–3 per night; mean = 1.33/night/owl), and were retrieved in July and August. When multiple locations were recorded in a single night, they were pre-programmed to be separated by at least two hours to reduce spatial autocorrelation. GPS tags had a median location error of approximately ± 20 -m when data were filtered to include only those points recorded with ≥ 5 satellites and a dilution of precision (DOP) ≤ 3 (HA Kramer, unpublished data), so we used only these data in analyses.

Habitat selection analysis

We analyzed our data using mixed-effects RSFs (logistic regression) with intercepts and slopes that varied by individual (Duchesne et al. 2010; Muff et al. 2020). Including coefficients that vary by individual enables explicit modeling of functional responses (Mysterud and Ims 1998) and reduces biases in estimated population-level (fixed) effects (Duchesne et al. 2010; Harrison et al. 2018). Available points were assigned weight $W = 1000$ to facilitate approximate convergence to the inhomogeneous Poisson process likelihood, and we fixed the variance term for individual-specific intercepts to a large value ($\sigma^2 = 1000$) to avoid shrinkage toward zero (Muff et al. 2020). Available area for each individual owl was defined as a circle with radius equal to the furthest Euclidean GPS distance from the activity center (minimum radius = 1654.8 m; maximum = 5165.5 m; mean = 3437.6 m), where the activity center was the geometric mean of annual daytime nest and roost locations obtained from walk-in surveys. We generated 10 times as many available points as used points for each owl (Hooten et al. 2017). Available points were distributed uniformly with respect to distance to the activity center (i.e., all distances had equivalent point densities).

There were three types of inferences we were interested in drawing from mixed-effects RSF models. First, we were interested in understanding how spotted owl habitat selection was explained by a suite of environmental predictor variables including pre-fire

forest conditions, fire conditions including whether or not areas burned at high-severity and the diversity of fire effects (pyrodiversity), and post-fire management (salvage logging). Second, we were interested in whether spotted owl use (or non-use) of areas that burned at high-severity could be explained by spatial characteristics of those areas, such as severe fire patch size and configuration. Finally, we wanted to examine whether there was evidence for functional responses in habitat selection. With respect to severe fire effects, these inferences can be viewed as a set of three sequential or hierarchical questions: do owls select or avoid severely burned areas; is that selection (or avoidance) mediated by spatial characteristics of severely burned areas; are these patterns driven by variation in the availability of severe fire within individual home ranges? We therefore examined these questions in three stages, constructing models in each stage that allowed us to test the underlying hypothesis related to each question in sequence.

In the first stage, we fitted a single model containing covariate effects for distance to activity center, pre-fire forest cover (sparse/open forest and young forest), and disturbance-related covariates (severe fire,

pyrodiversity, and post-fire salvage logging) (Table 1). Each covariate effect was specified as having a fixed component (population-level coefficient that was constant across individuals) and a random component (coefficient varying by individual) following Muff et al. (2020). The model intercept varied by individual owl. We expected distance to activity center and pre-fire forest cover covariates to be important in explaining space use patterns in spotted owls, but they were not the central focus of this analysis; we included them to control for their potential effects. Distance to activity center was the Euclidean distance (m) between a given GPS location and the individual's geographic activity center. Including distance to activity center as a model covariate in RSFs of central place foragers reduces the potential for a positive bias of selection for habitat types near the central place as well as a negative bias for habitat types more distant from the central place (Rosenberg and McKelvey 1999). Preliminary analyses supported the use of a quadratic (distance + distance²) form, which we used in all subsequent models. Pre-fire sparse/open forest cover was defined as 30 × 30-m pixels with < 40% canopy cover in the year prior to the King Fire (2014)

Table 1 Model covariates for habitat selection function (RSF) analysis including the variable description, group, type and range of values

Variable	Description	Group	Type	Range of used values
Distance to activity center	The Euclidean distance between a point and the annual activity center	–	Continuous	0–5165 m
Pre-fire sparse/open forest	Areas with < 40% canopy cover prior to the King Fire	Pre-fire	Categorical	0 or 1
Pre-fire young forest	Areas with > 40% canopy cover but smaller (< 25 cm QMD) average tree size	Pre-fire	Categorical	0 or 1
Severe fire	Areas that experienced > 75% canopy mortality following the King Fire and were <i>not</i> salvage-logged	Disturbance	Categorical	0 or 1
Pyrodiversity	Shannon Diversity Index of burn severity classes	Disturbance	Continuous	0–1.38 unitless
Salvage logging	Areas that experienced post-fire management that removed standing and downed trees	Disturbance	Categorical	0 or 1
Patch size	The area of a contiguous grouping of severely burned forest	Patch-based	Continuous	0–88.2 km ²
Patch complexity	The perimeter-to-area ratio of a severe fire patch	Patch-based	Continuous	0–0.066 m/m ²
Permeation distance	The distance traveled into a severely burned patch	Patch-based	Continuous	0–356.3 m

All continuous variables were scaled to a range of 0–1 for model fitting

as determined using the VEGCLASS variable classes 1 and 2 in the Gradient Nearest Neighbor (GNN) forest structure dataset for our study area (LEMMA Lab, Oregon State University, Corvallis, OR; lemma-forestry.oregonstate.edu) (Ohmann and Gregory 2002). Pre-fire young forest was also calculated using the VEGCLASS category of the GNN dataset (classes 3, 5, and 8), defined as 30×30 -m pixels with $> 40\%$ canopy cover but with smaller trees (quadratic mean diameter < 25 cm). Including pre-fire sparse/open/young forest vegetation covariates controlled for potential bias toward avoidance of these forest types, independent of the post-fire vegetation patterns created by the King Fire. We assigned the pre-fire sparse/open or young forest class to used/available points when these cover types were the majority class within a 100-m buffer around a given point location.

Disturbance covariates were severe fire, pyrodiversity, and post-fire salvage logging (Table 1). We defined severe fire as areas that experienced $> 75\%$ overstory mortality resulting from the King Fire. We used the 75% overstory mortality threshold to define high-severity because it increases our capacity to compare our results to previous studies (Bond et al. 2009, 2016; Eyes et al. 2017), while acknowledging that more notable ecological effects may correspond with a higher (e.g. 90%) threshold (Miller and Quayle 2015; Jones 2019). We treated this covariate as a categorical effect, such that $x_{ij} = 1$ if the GPS location for individual $i = 1, \dots, I$ at location $j = 1, \dots, J_i$ occurred in severely burned forest and $x_{ij} = 0$ otherwise. If a point fell within a severely burned area that was also salvage-logged (see below), we set the categorical effect for severe fire to $x_{ij} = 0$ and the effect for salvage logging to $x_{ij} = 1$. Thus, within our model the ‘severe fire’ effect can be interpreted as the selection coefficient for ‘unlogged snag forest’. We obtained burn severity data from the Monitoring Trends in Burn Severity (MTBS) project (www.mtbs.gov). We did not investigate potential selection patterns related to forests that burned at low- and moderate-severity because (i) we wanted to limit the number of candidate variables to reflect key hypotheses of interest and (ii) previous work has shown that either they do not affect spotted owls or owls generally use these types of burned forest in proportion to their availability during nocturnal hours (Bond et al. 2009, 2016; Jones et al. 2016; Eyes et al.

2017). Thus, low and moderate burn severities, as well as unburned forests, were effectively grouped together in the reference class of our models. However, we did more explicitly consider low and moderate fire severity in the context of pyrodiversity, which was defined as the Shannon Diversity Index of unburned or unchanged (under 5% site area burned), low severity (up to 25% overstory mortality), moderate severity (25–75% overstory mortality), and high-severity (over 75% overstory mortality) classes within a 100-m buffer of point locations. Based on Google Earth aerial imagery, we determined that the majority of salvage operations that occurred within owl home ranges were completed in late 2014 and early 2015 prior to the initiation of this study (2015), so we hand-digitized areas that had been post-fire salvage logged from the National Agriculture Imagery Program (NAIP) aerial imagery from July 2016. We delineated polygons containing visible heavy disturbance (including areas where logging roads had been created, presumably in preparation for salvage logging) in areas that burned in the King Fire, and that had forest present before the fire. While our delineation of salvage logging was limited to areas visibly discernable on NAIP imagery, territory-scale estimates of salvage were highly correlated ($r = 0.88$) with estimates obtained from timber companies conducting salvage operations within our study area (HA Kramer, unpublished data). We erased pre-fire sparse/open forest (GNN) and areas classified as unburned or outside the fire perimeter so that the salvage layer only included areas that were forested pre-fire and disturbed by dense road networks or logging post-fire. Approximately 80% of salvage logging occurred in areas that experienced high-severity fire.

In the second stage, we explored whether severe fire patch characteristics affected spotted owl habitat selection: patch size, patch complexity, and permeation distance (distance an owl traveled into a severely burned patch) (Table 1). We did so adding covariate effects for each of the above variables to the stage one model, and likewise allowed coefficients to vary by individual owl. Stage two variables were moderately- to highly-collinear with each other and therefore were not included in the same model; thus stage two consisted of three separate RSF models. Patch size was the total area (m^2) of a severe fire patch delineated with the four-neighbor rule (Turner et al. 2001). Patch complexity was calculated as the perimeter-to-area ratio of a severe fire patch. Permeation distance was

the minimum Euclidean distance (m) from a used or available point occurring within a severe fire patch to the patch edge (all points outside of severe fire patches were assigned $x = 0$). We transformed stage two variables using the natural logarithm ($\ln$).

In the third stage, we tested for evidence of functional responses by including an interaction term between habitat availability at the level of the individual owl (the mean covariate value in an individual's home range for available points) and the corresponding habitat covariate (*sensu* Matthiopoulos et al. 2011; Aarts et al. 2013). For example, to test for a functional response related to high-severity fire, we included: (i) a covariate for whether a used/available point occurred in severely burned forest (0/1; Table 1), (ii) a covariate that represented the proportion of an owl's home range that burned severely (i.e., this covariate had a constant value for each individual), and (iii) an interaction between these two covariates. If the interaction term (slope) was statistically different from zero, we interpreted this as evidence in support of a functional response in habitat selection. We transformed habitat availability using the natural logarithm because functional responses are assumed to be non-linear (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Beyer et al. 2010). We conducted tests for functional responses among disturbance and patch-level covariates when individual coefficients (i.e. random slope variance) improved model fit according to likelihood ratio tests (see below) from stages one and two to minimize the potential for spurious inferences. We note that while using the mean habitat value within an individual's home range is commonplace in the literature when computing functional response (Gillies et al. 2006; Hebblewhite and Merrill 2008; Aarts et al. 2013), the underlying assumption is that the average value sufficiently describes availability. Such an assumption could mask differences among individuals if the average availability does not reflect the encounter rate of different habitats across the landscape (Beyer et al. 2010).

We made inferences about the statistical importance of fixed effects from their direction (positive/negative), effect size (magnitude), and uncertainty (95% confidence intervals), but avoided interpreting the "significance" of estimates using arbitrary p-value thresholds when possible (Amrhein et al. 2019). We determined whether the variance terms for the random slopes improved model fit (test of $H_0: \sigma^2 = 0$) by

performing likelihood ratio tests (LRT) using restricted maximum likelihood (REML) estimation, correcting for the 'testing on the boundary' problem using $p = 0.5 \times (\chi_1^2 + \chi_2^2)$ (Zuur et al. 2009). All mixed-effects models were fitted using REML (Zuur et al. 2009). We rescaled all continuous covariates to range from 0 to 1. We used the R packages glmmTMB v. 0.2.3 to fit models. All analyses were conducted in program R version 3.6.0.

Results

Variables describing the central place foraging behavior of owls, pre-fire forest cover, and disturbance effects were all associated with spotted owl habitat selection. Population-level (fixed) effects from the stage one model indicated overall selection for areas closer to the activity center ($\beta_{\text{distance}} = 1.6$, 95% confidence interval $[-0.19, 3.43]$; $\beta_{\text{distance}}^2 = -8.25 [-11.44, -5.06]$). The model also indicated avoidance of pre-fire sparse/open forest ($\beta_{\text{sparse/open}} = -1.00 [-1.41, -0.59]$), young forest ($\beta_{\text{young}} = -0.32 [-0.63, -0.001]$), and salvage-logged areas ($\beta_{\text{salvage}} = -1.07 [-1.88, -0.26]$) (Fig. 2a). The estimated coefficient for pyrodiversity was in the hypothesized direction (positive) but slightly overlapped zero ($\beta_{\text{pyrodiversity}} = 0.49 [-0.12, 1.09]$) (Fig. 2a). Similarly, the coefficient for the effect of severe fire (binary effect disregarding patch characteristics) was in the hypothesized direction (negative) but with confidence intervals that overlapped zero ($\beta_{\text{severe}} = -0.35 [-1.07, 0.37]$) (Fig. 2a). While estimated coefficients for pyrodiversity and severe fire overlapped zero when considered at the population-level (i.e., effect fixed across individuals), individual-specific coefficients showed a high degree of variability (Fig. 2b) that improved model fit (likelihood ratio tests; $p < 0.001$). Thus, while the mean effect of pyrodiversity at the population level was 0.49, the deviation from that effect varied significantly across individuals with an estimated variance of $\sigma^2 = 1.92$ (individual coefficients ranged from -1.2 to 2.9) (Fig. 2b). Likewise, while the mean effect of severe fire at the population-level was -0.35 , individual-specific deviations from that effect were considerable ($\sigma^2 = 2.49$; individual coefficients ranged from -3.4 to 2.8) (Fig. 2b).

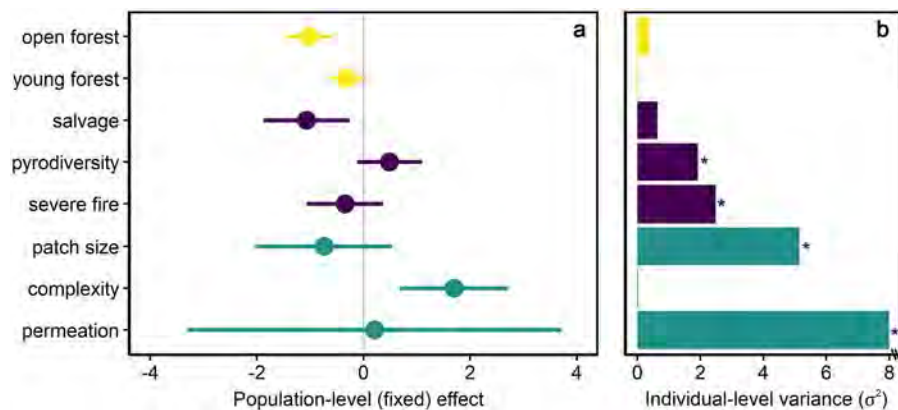


Fig. 2 Coefficient estimates from mixed-effects habitat selection functions. **a** Mean fixed-effects coefficients and their associated 95% confidence intervals. **b** The variance estimates for the individual slope coefficients (random effects), with effects that improved model fit (using likelihood ratio tests) indicated with an asterisk (*). the x-axis of b is truncated to a

Selection/avoidance of severely-burned areas by spotted owls appeared to be mediated by spatial characteristics of severe fire patches (stage two). Population-level (fixed) effects for patch size was negative ($\beta_{\text{patchSize}} = -0.74 [-2.01, 0.54]$) indicating spotted owls selected smaller patches of severely-burned forest, but the 95% confidence interval overlapped zero (Fig. 2a). Spotted owls selected severe fire patches with greater spatial complexity (higher perimeter-area ratio; $\beta_{\text{complexity}} = 1.70 [0.69, 2.71]$) (Fig. 2a). The population-level effect of permeation distance was slightly positive ($\beta_{\text{permeation}} = 0.21 [-3.30, 3.72]$) but confidence intervals widely overlapped zero (Fig. 2a). While their population-level coefficient estimates overlapped zero, both patch size and permeation distance showed significant variation among individuals; individual-specific coefficients improved model fit (likelihood ratio tests; $p < 0.001$). While the mean effect of severe fire patch size at the population level was -0.74 , the deviation from that effect varied significantly across individuals with an estimated variance of $\sigma^2 = 5.15$ (individual coefficients ranged from -4.22 to 5.4) (Fig. 2b). Likewise, while the mean effect of permeation distance (distance traveled into severe fire patch) at the population-level was 0.21 , individual-specific deviations from that effect were considerable ($\sigma^2 = 8.0$; individual coefficients ranged from -5.3 to 28) (Fig. 2b).

smaller range (0–8) for visualization, but note that the variance term for permeation distance was 58.9 . Colors correspond with different covariate groups (see Table 1); yellow = pre-fire forest cover, dark blue = disturbance variables, turquoise = severe fire patch variables. (Color figure online)

The large variation in habitat selection coefficients among individual owls for severe fire (stage one), severe fire patch size (stage two), and permeation distance (stage two) was partially explained by differences in individual-level habitat availability, indicating an apparent functional response (FR). Habitat $\times$ availability interaction coefficients and 95% confidence intervals for these three variables did not overlap zero in stage three models testing for functional responses. Moreover, functional response curves identified thresholds in habitat availability at which point predicted individual coefficients changed sign from positive to negative (the point at which the fitted curve crosses zero; Fig. 3a–c). Individual spotted owls tended to select severely burned forest only when it represented a small proportion of their home range (< 0.05), but avoided severely burned forest when it was more prevalent ($\beta_{\text{severe-FR}} = -0.76 [-1.33, -0.19]$) (Fig. 3a). Individual owls tended to select larger patches of severe fire when the area-weighted average patch size in their home range was smaller than ~ 115 ha, but selected smaller patches of severe fire when their home ranges were characterized by larger patches ($\beta_{\text{patch-FR}} = -9.39 [-13.78, -5.00]$) (Fig. 3b). Owls also avoided making deep forays into severe fire patches when the average permeation distance in their home range exceeded 47 m, corresponding with larger patches on average ($\beta_{\text{permeation-FR}} = -28.17 [-43.67, -12.68]$) (Fig. 3c). Figure 4 provides examples of spotted owls

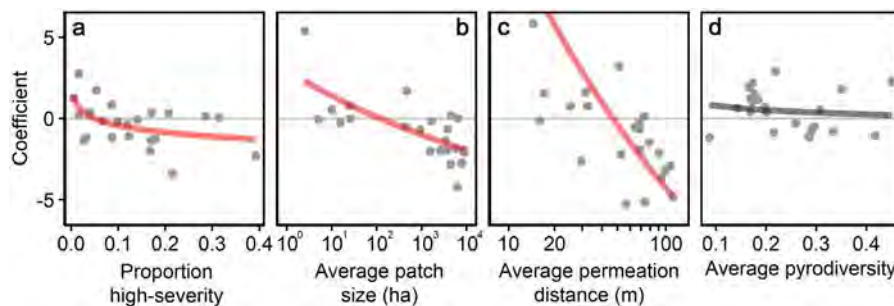


Fig. 3 Functional responses in habitat selection. **a** Severe fire, **b** patch size, **c** permeation distance, **d** pyrodiversity. The y-axes represent slope coefficient estimates for individual owls, and the x-axis represents average covariate conditions within an individual owl's home range (**b**, **c** represent area-weighted

means for patch-based covariates). Functional responses with 95% confidence intervals that did not overlap zero are depicted in red (**a–c**). Note that the y-axis is truncated in panel **c** for better visualization; there is one additional data point located at $x = 11.1$, $y = 27.98$. (Color figure online)

selecting smaller patches of severe fire (Fig. 4a, b), avoiding larger patches of severe fire (Fig. 4b, c), and using a large severe fire patch (unlogged snag forest) but only making short forays into it (Fig. 4c). There was no evidence for a functional response in habitat selection for pyrodiversity ($\beta_{\text{permeation-FR}} = -0.48$ [$-2.15, 1.20$]) (Fig. 3d).

Discussion

There is a natural hierarchical response by species that can be estimated following disturbance: a primary response and a secondary response. The *primary response* is whether an individual either survives or is able to remain (i.e., occupy) in the affected area following a disturbance event. The *secondary response* is conditional on the primary response (i.e., continued occupancy) and may represent shifts in movement, foraging, or reproductive behavior by persisting individuals that are induced by the disturbance. Key uncertainties exist regarding both primary and secondary responses by spotted owls to fire. With respect to primary responses, the 2014 King Fire displaced a significant portion of the population that experienced extensive severe fire and at least one apparent direct mortality (Jones et al. 2016), but other researchers reported no negative effects in a different population of owls that experienced a large, severe fire (Lee and Bond 2015, but see Berigan et al. 2019). With respect to secondary responses, different studies have revealed that GPS- or VHF-tagged owls avoided (Jones et al. 2016; Eyes et al. 2017), preferentially selected (Bond et al. 2009), or used severely burned

forests in proportion to their availability (Bond et al. 2016) when foraging. The analytical approaches used in these studies were similar, raising the question of why owls apparently responded in different ways. We posit one of the reasons may be that these studies have lacked an explicit landscape perspective (i.e., role of spatial patterns of severe fire), which precluded the ability to disentangle different factors that might have led to these conflicting results. While previous work has advanced our understanding of the importance of edges between fire severity classes as a predictor of spotted owl habitat selection (Bond et al. 2009, 2016; Eyes et al. 2017) and the role of these edges across scales (Comfort et al. 2016), they did not explicitly consider the role of severe fire patch size, configuration, permeation distance, or how responses may be conditional on individual variation in habitat availability (i.e., functional response).

Owl response to high-severity fire

Landscape structure and composition following fires appear to affect habitat selection by spotted owls in a more nuanced way than previously reported. Although severe fire was not clearly avoided nor selected at the population level, individuals showed avoidance of severely burned forests (i.e., expected individual coefficients became negative) when $> 5\%$ of their home range burned at high-severity (Fig. 3a). Thus, for those owls not displaced or killed, severe fire appeared to be, on average, benign or beneficial below this threshold, yet appeared to affect owl movements above this threshold. Therefore, spotted owls continued to occupy home ranges in the short term when

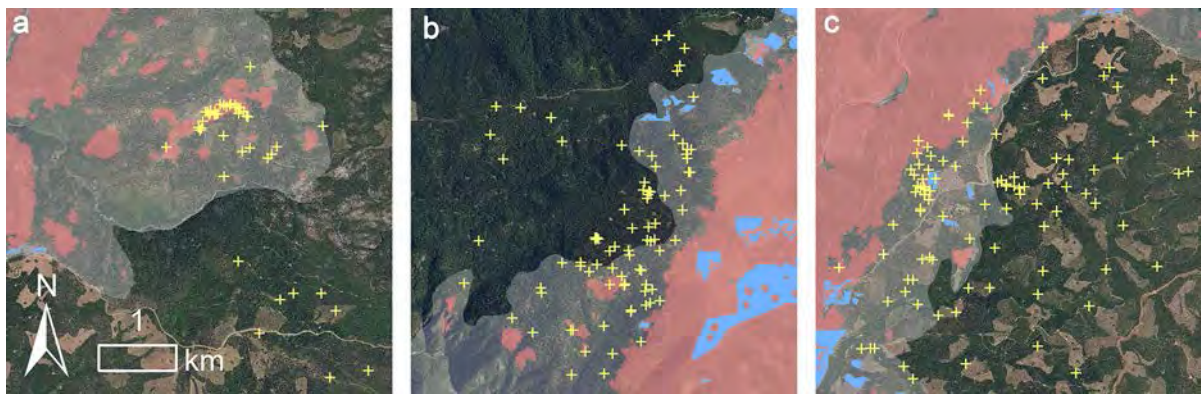


Fig. 4 Examples of owl locations that show selection preferences across different availabilities of severe fire and patch sizes. **a** Selection for a small patch of severe fire; **b**, **c** avoidance of a large patch of severe fire; **c** also shows short (< 100 m)

forays into a large severe fire patch. The fire area is shown in semitransparent white, high-severity fire with no salvage logging in red, salvage logging in blue, and owl locations as yellow “+” signs. (Color figure online)

their home ranges were burned by up to 40% severe fire (the maximum extent experienced by GPS-tagged owls in this study), perhaps via behavioral plasticity including the shifting of foraging sites. However, previous work has shown that habitat loss related to severe fire occurring over > 50% of an owl territory led to territory abandonment and mortality (Jones et al. 2016). These thresholds could serve as benchmarks for understanding severe fire effects on spotted owls when detailed site occupancy and tagging information are not available, but we hypothesize that wildfires with different severe fire spatial patterns may result in different responses by owls than we report here. We observed similar functional responses for severe fire patch size and permeation distance; owls avoided using larger patches of severe fire and avoided making deeper forays into severely burned areas when their home ranges were characterized by a larger severe fire component. Had we used a more traditional analysis that did not account for individual variation and spatial configuration, and simply made inference about population-level effects, we would likely have concluded that owls use severely burned forests in proportion to its availability (i.e., the model from stage one). Instead, we gained a more nuanced understanding that patch size and the spatial extent and configuration of severely burned forests within individual spotted owl home ranges strongly mediated the effect of severe fire.

The specific thresholds at which we observed that spotted owls began to avoid severely burned forest appear to align closely with the best available

estimates of historical severe fire extent and patch sizes within dry mixed-conifer forests (Safford and Stevens 2017). Specifically, fires that historically burned in yellow pine mixed-conifer forests in the Sierra Nevada contained 5–15% severe fire effects (Safford and Stevens 2017); our study suggested owls tended to avoid severely burned forest when more than 5% of their home range was affected. Moreover, historical severe fire patch sizes in yellow pine mixed-conifer forests in the Sierra Nevada typically ranged from 10 to 100 ha in size (Safford and Stevens 2017); we showed that spotted owls tended to avoid larger severe fire patches when the average patch size in their home range exceeded ~ 115 ha in size. In addition, the spatial complexity of severe fire patches has been decreasing in recent decades (Stevens et al. 2017); we showed that owls select more complex severe fire patches. We suggest these results provide evidence that owls are responding to severe fire in a way that reflects adaptation to historical fire regimes under which this species evolved. Our work suggests that increasingly novel fire conditions within this system—i.e., more severe fire characterized by patches that are larger and less complex—will negatively affect spotted owls.

There are several possible reasons why spotted owls avoided large patches of unlogged, severely burned forest. First, severe fire in the King Fire likely altered spotted owls’ prey communities either (i) indirectly by eliminating the understory and coarse woody debris important for key small mammal prey species such as woodrats (*Neotoma* spp.; Roberts 2017) in the

short term, or (ii) directly through fire-related mortality. Although some dense brush cover regenerated within many severely burned patches 1–2 years post-fire that could potentially provide prey habitat, owls appeared to avoid large, severely burned patches throughout the three-year study, suggesting prey populations had not yet recovered. Second, perching structures in large tracts of severely burned forest may not provide adequate concealment for this “sit and wait” predator relative to forests with live trees and foliage structure (Gutiérrez et al. 1995; Ganey et al. 2017). Third, and related to the second reason, large fires create extensive open areas that provide habitat for avian predators of spotted owls such as great-horned owls (*Bubo virginianus*; Gutiérrez et al. 1995), which increases predation risk (Johnson 1992). Discriminating among these hypotheses will be challenging and require both small mammal and predator sampling. There is a fourth explanation for why spotted owls avoided large tracts of severely burned forest: severely burned forest contains a limiting resource (e.g., food) that is preferentially selected when it is scarce, but is relatively less important (and its use/availability ratio decreases) when it is abundant (Beyer et al. 2010; Aarts et al. 2013). Given our three above hypothesized mechanisms for avoidance of large severely burned areas we think this is relatively unlikely because rather than containing abundant resources, large severe fire patches appear to contain fewer food resources and more risks to owls.

Owl response to salvage logging

Salvage logging is a management practice that removes fire-killed or fire-affected trees with the primary intention of recouping economic value and reducing safety hazards in multi-use forests (Lindenmayer and Noss 2006). Salvage logging can affect post-fire forest conditions and ecosystem processes by altering post-fire biological communities (Thorn et al. 2018), increasing fire risk by leaving behind fine and coarse woody fuels (Donato et al. 2006), and reducing natural vegetative recovery (Lindenmayer et al. 2008). However, salvage logging is also being used as a tool for improving post-fire reforestation success in dry forest types of the western US (North et al. 2019) that face an increased risk of natural regeneration failure and conversion to non-forest ecosystems following large, high-severity fires (Welch et al. 2016; Shive

et al. 2018; Wood and Jones 2019). Thus, there is strong practical interest among land managers to understand ways to reduce negative effects of salvage logging on species and communities of conservation concern, particularly the spotted owl (Peery et al. 2017).

Our results suggest that spotted owls tended to avoid areas that experienced salvage logging. However, interpreting the significant negative statistical effect of salvage was challenged by several considerations. First, 95% confidence intervals for the population-level severe fire effect (i.e., unlogged snag forest) overlapped the 95% confidence intervals for the salvage effect (Fig. 2)—suggesting that salvage and severe fire effects at the population level may have been similar. Second, salvage logging was often embedded within the very large patch of severely burned forest in the northern part of the King Fire that owls strongly avoided (e.g., Figs. 1, 4b, c) such that owls may have been predisposed to avoiding some salvage-logged areas. Third, salvage-logged areas were relatively rare within owl home ranges (average 3.4% of owl home range) compared to severely burned areas (14.5%), and rare cover types are subject to false negative error (Frair et al. 2010).

Nevertheless, our study may provide some important insights into the relative effects of salvage logging and severe fire on spotted owl habitat selection. While the population-level (fixed) effect of salvage logging was negative and numerically more negative than population-level effect of severe fire, the variance among individual-level effects for salvage logging was narrow ($\sigma^2 = 0.64$) and not statistically different from zero, compared to the significant variance among individual-level effects for severe fire ($\sigma^2 = 2.49$). These variances resulted in a narrow range of individual coefficients (ranging from -1.6 to -0.2) for salvage logging, compared to a wider range for severe fire individual coefficients (ranging from -3.4 to 2.8) (Fig. 5). Thus, it appears that individual owls with relatively large high-severity burned areas within their home range tended to avoid these areas more strongly than any owls avoided salvage-logged areas (Fig. 3a). Conversely, owls with smaller areas of high-severity burned areas in their home ranges tended to select severely burned areas but still tended to avoid salvaged areas, notwithstanding the considerations discussed above.

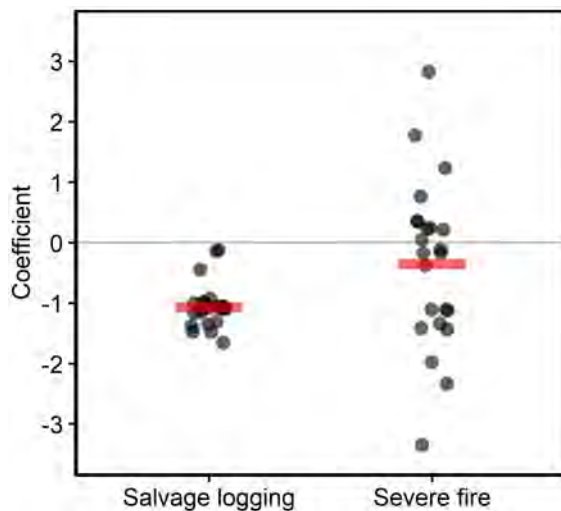


Fig. 5 Comparison of the population-level (red line) and individual-level (black dots) coefficients for salvage logging and severe fire (unlogged snag forest). (Color figure online)

Despite these uncertainties, our findings also have novel implications for post-fire forest management as it relates to species conservation. Specifically, the owls' tendency to avoid large, but not necessarily small patches of severely burned forest and also avoid traversing into interior portions of larger patches (Figs. 3, 4) suggests that salvage logging within interior portions of larger patches may be less likely to affect spotted owls than salvage logging within small patches of severely burned forest. For example, of all spotted owl GPS locations, only 0.6% occurred further than 100 m into a severe fire patch. Stillman et al. (2019) showed that black-backed woodpeckers (*Picoides arcticus*), another focal management species in post-fire landscapes in the Sierra Nevada, tended to use areas of severely burned forest that were closer to patch edges and rarely traveled further than > 500-m into severe fire patches. Thus, salvage operations within the interior of large patches of severely burned patches may be less likely to impact both of these focal species. However, most (89%) of salvage logging within the King Fire perimeter occurred on private lands that often involved higher proportions of harvesting than is typical on national forests (i.e., patches of unlogged snag forest were often left intact within salvage-logged areas on national forests). This limited the inferences we could make about the effects of salvage logging on public lands. Nevertheless, retaining perch sites and snags, and/or creating

habitats that promote the preferred prey species of spotted owls in areas that are salvage-logged (e.g., slash piles for woodrats; Innes et al. 2007), might encourage use of these areas by owls in the future.

Implications for dry forest restoration

The tendency of spotted owls to avoid large areas within their home ranges that burned at high-severity has implications for the management of seasonal dry forests within the range of this species. Our findings of avoidance by spotted owls of forests extensively modified by severe fire suggests that the reduction of large, severe fires ("megafires"; Stephens et al. 2014) such as the King Fire by restoring frequent fire regimes characterized by small patches of severe fire is likely to benefit both spotted owl populations and increase forest resilience. This comes with the caveat also supported by our results that salvage logging be judiciously applied particularly in areas where fires burn heterogeneously within occupied spotted owl home ranges, because owls tend to use smaller patches of severely burned forests and forage along edges of larger patches. Our study (i) supports the general premise that species conservation and forest ecosystem restoration objectives in the Sierra Nevada can be compatible (Scheller et al. 2011; Tempel et al. 2015; Jones et al. 2016; Jones 2019) and (ii) could help reconcile a conservation conflict pitting those promoting restoration of seasonal dry forests in parts of western North America against those interested in preserving old-growth trees and habitat for spotted owls (Redpath et al. 2013; Gutiérrez et al. 2017).

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Megafire causes persistent loss of an old-forest species

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Abstract

Climate change and a long legacy of fire suppression are leading to an increased prevalence of ‘mega-disturbances’ such as drought and wildfire in terrestrial ecosystems. Evidence for the immediate effects of these novel disturbances on wildlife is accumulating, but little information exists on longer term impacts to species and ecosystems. We studied the occurrence dynamics of an iconic old-forest species, the spotted owl (*Strix occidentalis*), on a long-term study area in the Sierra Nevada, CA, USA from 1989 to 2020 to evaluate their multi-scale population response following a 2014 megafire (the ‘King’ Fire) that affected a portion of our study area. We found that extensive severe fire within spotted owl sites resulted in both immediate site abandonment and prolonged lack of re-colonization by owls six years post-fire. Sites that experienced high pyrodiversity – a mosaic of burn severities – were more likely to persist after the fire, but this effect was only apparent at finer spatial scales. A potentially confounding factor, post-fire salvage logging, did not explain variability in the probability of either owls persisting at sites or sites becoming re-colonized; effects could be attributed only to severe fire extent and pyrodiversity. Our study demonstrates the prolonged effects of severe fire on the occupancy of this forest-dependent species, suggesting that forest restoration that reduces megafires could benefit spotted owls. Our work emphasizes that long-term monitoring can offer surprising learning opportunities and provide unparalleled value for understanding and addressing emerging environmental concerns.

Introduction

Disturbance regimes are changing across global forest ecosystems because of past land use (e.g., fire suppression) and climate change (Seidl et al., 2017). A new era of mega-disturbances catalyzed by a changing climate may lead to large-scale transformation of ecosystems as we know them (Millar & Stephenson, 2015; Westerling et al., 2011). Large-scale droughts and ‘megafires’ not only threaten the persistence of forest ecosystems, they also threaten the species that inhabit them and the services those ecosystems provide to people (Hurteau et al., 2014; Wood & Jones, 2019). Consequently, in some forest ecosystems, forest managers and policymakers are faced with either the challenges of managing these vital forests for restoration and persistence or allowing their transition to novel non-forest ecosystems (Rissman et al., 2018) with resulting implications for biodiversity and ecosystem services.

Recent extreme global fire years (e.g., 2019–2020) have hastened efforts to quantify potential impacts of megafires on biodiversity. For example, the 2019–2020 Australia bushfires likely resulted in significant (>30%) habitat loss to 70 taxa

including 21 already threatened with extinction (Ward et al., 2020). An analysis of the 2019 Amazon fires suggested that most species experienced habitat losses across 20–30% of their range (Mortara et al., 2020). Rapidly changing fire regimes, especially when considered alongside synergies from other pressures (e.g., land-use change, invasive species) threaten the habitat and persistence of at least 4400 taxa globally (Kelly et al., 2020). Forest-dependent taxa, in particular, can experience rapid habitat loss following severe, stand-replacing fires (e.g., bats: Ancillotto et al., 2020; Bosso et al., 2018), but less is understood about longer term dynamics. The emergence of the era of megafires has led scientists and managers to consider what can be done to avoid repeat events of large-scale loss of habitat (Wintle, Legge, & Woinarski, 2020).

Can proactive land management prevent or mitigate large-scale fire events that threaten biodiversity? The answer likely varies across ecosystem types (Halofsky et al., 2018; Krawchuk & Moritz, 2011). In seasonally dry forest ecosystems, notably those in western North America, wildfires are now burning larger, longer and at higher severity than they did historically (Singleton et al., 2018; Steel, Safford, & Viers,

2015; Westerling, 2016). In these forests, large-scale restoration approaches such as prescribed fire, managed wildfire and tree thinning have been proposed to enhance ecosystem resilience to wildfire and drought (Stephens *et al.*, 2020). Abundant empirical observations now demonstrate that these restoration activities alter fire behavior in dry forests by reducing tree densities and fuel loads (Tubbesing *et al.*, 2019), reduce drought-related tree mortality (Bradford & Bell, 2016) and promote structural variability that is expected to increase forest resilience to disturbance (Koontz *et al.*, 2020).

Yet large-scale restoration may also result in short-term negative effects to sensitive wildlife populations by removing or altering key habitat elements (e.g., complex understory and horizontal canopy cover). Recent research has sought to understand trade-offs between these potential short-term negative effects of restoration and longer term benefits of mitigating habitat loss from large, stand-replacing fires (e.g., Scheller *et al.*, 2011; Tempel *et al.*, 2015). Whether short-term negative effects of forest restoration are outweighed by longer term benefits of reducing habitat loss to mega-disturbances hinges on the degree to which restoration alters habitat as well as the magnitude of megafire effects on wildlife. So, for example, if large, severe fires are clearly detrimental to sensitive wildlife populations, then the potential short-term impacts of forest restoration to these species' habitats are likely to be outweighed by longer term benefits – assuming some retention of key elements of the species' habitat can be maintained to support landscape scale occupancy while benefits accrue (e.g., Jones *et al.* 2018). The potential benefits of restoration further increase if habitat loss from large, severe fires is persistent (i.e., will not regenerate for long time periods).

We studied the empirical short- and longer term effects of a large megafire on a declining population of spotted owls (*Strix occidentalis*) that has been monitored annually since the late 1980s. The King Fire, which burned 97 717 acres of predominately forested land in the central Sierra Nevada, CA, USA in September and October 2014, impacted approximately one half of our study area while leaving the remaining portion unburned (Fig. 1). This event, therefore, allowed the use of a natural Before–After Control–Impact experimental design to examine the effects of this fire on our study population. Whereas we have previously reported the immediate impact of the fire on owls (Jones *et al.*, 2016), here we sought to characterize the population response to the King Fire over a 6-year post-fire period. As a result, this study answers a criticism of such short-term studies that owls and other old-forest species may simply return after a brief displacement by a fire event. In addition, we (i) conducted our population analysis at multiple spatial scales to assess whether and to what extent fire effects are scale-dependent (McGarigal *et al.*, 2016; Wan, Cushman, & Ganey, 2020), (ii) included survey data from additional spotted owl territories in our study area to strengthen inferences about fire effects, (iii) applied a novel data filtering approach of detection/non-detection data to improve biological meaning of effects (Berigan *et al.*, 2019) and (iv) explored the potential role of pyrodiversity (variation in burn severity) in

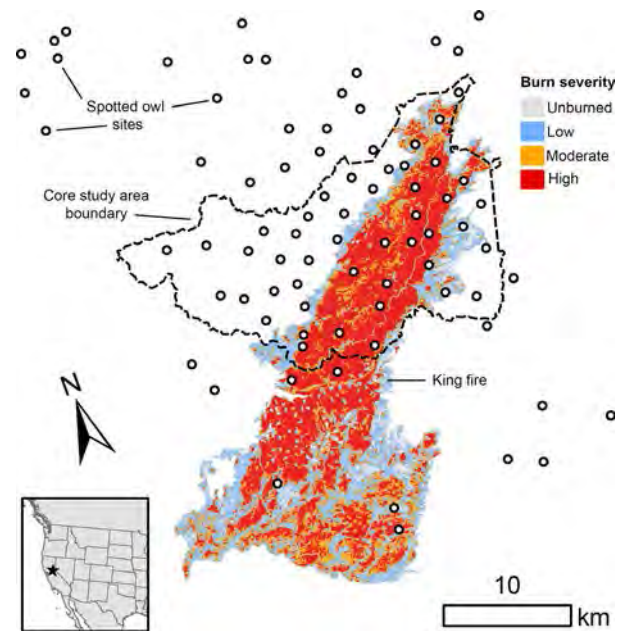


Figure 1 Study area map showing the distribution of spotted owl sites in relation to the 2014 King Fire. The Before–After Control–Impact natural experiment was made possible because a portion of sites was unburned (those outside the King Fire) while other sites experienced a gradient of burn severity. The core study area is outlined with a dashed line; sites outside this boundary were “satellite” territories that were added after initiation of the study (see Methods) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

mediating population response to fire (Jones and Tingley, in press).

We hypothesized that because spotted owls evolved in a frequent, low-severity fire regime, they are poorly adapted to persist in novel conditions after a large, severe fire (Jones *et al.*, 2020). We developed two predictions that would indicate support for this hypothesis. We predicted that (i) post-fire persistence and colonization rates would decrease in areas with extensive severe fire via loss of larger trees that provide suitable nest sites (e.g., Jones *et al.*, 2016) and (ii) post-fire persistence and colonization would increase in areas with higher pyrodiversity, which may more closely reflect historical post-fire conditions, as well as maintain nest structures and produce diverse prey habitat and hunting cover (e.g., Hobart *et al.*, 2021). We also hypothesized that post-fire owl dynamics were driven by the fire itself, rather than post-fire management. Therefore, we predicted that variation in post-fire persistence and colonization would be associated with high-severity fire and pyrodiversity, rather than post-fire salvage logging.

Materials and methods

Study area and data collection

Our study area encompassed ~800 km² of the Eldorado and Tahoe National Forests in the central Sierra Nevada,

California, USA. The study area consisted primarily (~63%) of public land managed by the USDA Forest Service, but contained inholdings of private land (~37%). Elevation on the study area ranged between 300 and 2500 m. Summers were hot and dry, and most precipitation fell as rain or snow during the winter and early spring (Franklin *et al.*, 2004). The primary vegetation type was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*) and Douglas-fir (*Pseudotsuga menziesii*). Common understory species were California black oak (*Quercus kelloggii*), tanoak (*Notholithocarpus densiflorus*), canyon live oak (*Q. chrysolepis*) and bigleaf maple (*Acer macrophyllum*). At higher elevations, vegetation transitioned to red fir (*A. magnifica*) and lodgepole pine (*P. contorta*). Barred owls (*S. varia*) were not present on our study area until the last decade but have remained extremely rare once they invaded this area (Keane, 2017). Thus, we remain confident that our inferences about the effects of severe fire on spotted owls were not influenced by the presence of barred owls.

In the midst of a significant multi-year drought (Asner *et al.*, 2015), the King Fire burned across ~39 545 ha (97 717 acres) of predominately forested land in the central Sierra Nevada in September and October of 2014 (Coen, Stavros, & Fites-Kaufman, 2018). Nearly half of the total area burned experienced stand-replacing fire (>75% canopy mortality), making the King Fire one of the most uniformly severe and homogenous megafires in recent California history (Stevens *et al.*, 2017). The King Fire burned ~44% of our core study area and affected 34 of 83 owl sites (at the 1500-m scale; Table 1), most of which have been consistently monitored since the early 1990s (Fig. 1). Of the portion of our study area that burned, most (64%) of that area burned at high severity (Jones *et al.*, 2016). Because the King Fire affected a contiguous portion of our study area and we had over two decades of pre-fire monitoring data (see below), we were afforded an opportunity to study the effects of fire on spotted owls within a natural Before–After Control–Impact (BACI) experimental design framework (Popescu *et al.*, 2012). Since 2014, California has experienced numerous fires that have matched or exceeded the size and severity of the King Fire (e.g., 2020 Creek Fire and 2020 North Complex). Thus, understanding King Fire effects may foreshadow potential effects of more recent megafires on spotted owls.

We conducted spotted owl surveys annually across the study area from 1989 to 2020. We conducted detection/non-detection surveys from April through August each year, which corresponds with the breeding season for spotted owls. Our study area consisted of a core area that was completely surveyed annually, and additional “satellite” survey areas, approximating the size of a spotted owl home range, surrounding the core area that were added over time to increase sample sizes for demographic analyses. Most satellite survey areas were added to annual survey efforts in 1996 and 1997, and thus have been consistently surveyed for close to 25 years. Several additional satellite survey areas were added to annual surveys in 2005 and 2006. Sampling protocols at satellite survey areas were identical to those conducted in the core area and different only in their start year. The original analyses presented in Jones *et al.* (2016) used owl data only from the core area, but here we expand the analysis to include these satellite survey areas as well (Fig. 1), which includes several additional unburned sites, sites burned by the King Fire and sites burned by other smaller fires earlier in the study period. For the purposes of this analysis, we considered fire effects attributable to the King Fire only, and thus our estimates of fire effects may be conservative because potential variation explained by other fires on the study area was absorbed into other controlling variables in the statistical model (see below). Three smaller fires (2001 Star Fire, 2006 Ralston Fire, 2013 American Fire) occurred on the study area since the year 2000 and resulted in predominately low-severity effects. The 2001 Star Fire likely resulted in reduced post-fire colonization rates at 1–2 territories that experienced moderate amounts of high-severity fire (Tempel *et al.*, 2014). The 2006 Ralston and 2013 American Fires burned ~5 owl territories, but only one territory occurred adjacent to a larger severely burned patch.

We surveyed for spotted owl presence by imitating owl vocalizations at designated survey stations or while walking along routes through historical owl territories or between survey stations (Franklin *et al.*, 1996). When owls were detected through a response vocalization, we determined the sex of the owl by the call pitch, because females have a higher pitched call than males (Forsman, Meslow, & Wight, 1984). Owl surveys were primarily conducted at night, and when owls were detected at night, we conducted follow-up crepuscular and daytime surveys to locate roost and nest locations, assess reproductive status and to capture and band

Table 1 Summary of model covariates for burned sites as calculated across the four selected spatial scales of analysis: nest site scale (300 m), protected activity center (PAC) scale (700 m), territory scale (1100 m) and home-range scale (1500 m)

Variable	Spatial scale			
	Nest site 300 m	PAC 700 m	Territory 1100 m	Home range 1500 m
Sites affected by King Fire (<i>n</i>)	27	29	32	34
Proportion burned at high severity	0.53 (0.44)	0.49 (0.39)	0.41 (0.35)	0.38 (0.33)
Pyrodiversity	0.56 (0.47)	0.71 (0.41)	0.77 (0.39)	0.81 (0.37)
Proportion salvage logged	0.03 (0.10)	0.06 (0.10)	0.07 (0.10)	0.08 (0.10)

Values represent covariate means with standard deviation in parentheses evaluated at *n* burned sites.

unmarked owls (Franklin *et al.*, 1996). Recent work has shown that including detections from nocturnal surveys when colored leg bands (used to identify individuals) were not able to be observed likely results in an overestimation of territorial occupancy owing to wide-ranging, extraterritorial movements by owls (Berigan *et al.*, 2019). Therefore, in this present analysis, we included in our detection history only detections recorded during daytime and twilight, or otherwise detections of individuals within their ‘home’ territories as determined by resighting of uniquely colored leg bands.

Statistical analysis

We used a Bayesian formulation of a dynamic occupancy model (MacKenzie *et al.*, 2003; Royle & Kéry, 2007; Siegel *et al.*, 2019) to assess patterns and correlates of site occupancy on our study area. The model contained parameters for initial occupancy ($\psi_{i,1}$), colonization ($\gamma_{i,t}$), persistence ($\phi_{i,t}$, which is the complement of extinction, $\epsilon_{i,t}$) and detection probability ($p_{i,j,t}$). The primary sampling periods (t) were breeding seasons (i.e., April–August) and the secondary sampling periods (j) were 2-week periods within each breeding season (April 1–15, April 16–30, May 1–15, etc.). Sometimes, multiple surveys within a given site (i) were conducted within a secondary sampling period, in which case a “1” was assigned if owls were detected in any survey during that period, and “0” otherwise. We considered sites where at least one owl was detected during diurnal hours in at least 2 survey years to constitute a bona fide owl territory. Previous research reported one-half the average nearest-neighbor distance between territory centers on our study area to be 1128 m, resulting in ~400-ha circular territories, which approximates an area predicted to be defended by owls (Berigan *et al.*, 2019; Jones *et al.*, 2018; Tempel *et al.*, 2014, 2016).

We calculated a suite of covariates to model the potential effects of the King Fire on local colonization and persistence dynamics of spotted owl territories. We used four spatial scales (varying radii extending from a mapped activity center) to approximate ecologically and/or administratively relevant scales for spotted owls: nest site scale (300 m), protected activity center (PAC) scale (700 m), territory scale (1100 m) and home-range scale (1500 m) (Berigan, Gutiérrez, & Tempel, 2012; Peery *et al.*, 2017; Tempel *et al.*, 2014). We took a multi-scale approach to examine whether and to what extent fire effects were scale dependent (Jackson & Fahrig, 2015; McGarigal *et al.*, 2016; Wan, Cushman, & Ganey, 2020). At each scale, we calculated (i) the proportion of the area that experienced stand-replacing fire (>75% canopy mortality), (ii) the variation in burn severity classes, or pyrodiversity and (iii) the proportion of the area that experienced post-fire salvage logging (Table 1). Fire boundary and severity data were obtained from the Monitoring Trends in Burn Severity project (<http://www.mtbs.gov>). Pyrodiversity was calculated as the Shannon diversity index of five burn categories: unburned (outside fire perimeter), burned but unchanged canopy structure (within fire perimeter), low severity (<25% canopy mortality), moderate severity (25–75% canopy mortality) and high severity (>75%

canopy mortality) (Kramer *et al.*, 2021). Salvage logging was inferred from annual post-fire imagery from the National Agricultural Imagery Program (NAIP) and spatial layers were hand-digitized by one of the authors (HAK) and verified by a second author (WJB). Only areas that had forest cover prior to the fire were considered in salvage digitization; we ensured pre-fire clear-cuts and other non-forested areas were not included in our salvage estimation. Hand-digitized layers were combined with layers indicating that post-fire salvage had occurred in the USDA Forest Service’s Forest Activity Tracking System (FACTS) database.

We constructed a model to describe territory occupancy dynamics and the King Fire’s effects to the spotted owl population. We modeled detection probability p as a logit-linear function of the following covariates:

$$\text{logit}(p_{i,t}) = a_0 + a_1 \text{repro}_{i,t} + a_t$$

where a_0 was the intercept, a_1 was the effect of reproductive status on detection probability where $\text{repro}_{i,t}$ took the value of 0 for non-reproductive territories and 1 for territories that produced young observed on the nest, and a_t was a random year effect to control for unmodeled temporal heterogeneity in p .

We modeled initial occupancy during the first year of our study (1989) at each territory $\psi_{i,1}$ using the following logit-linear function:

$$\text{logit}(\psi_{i,1}) = b_0 + b_1 kf_i$$

where kf_i was an indicator variable for territories that intersected with the King Fire footprint. The kf_i covariate helped control for background differences in occupancy rates at owl sites that were affected by the King Fire and those that were not. For the subsequent years ($t > 1$), we modeled annual occupancy as a process dependent on the true occupancy status ($z_{i,t}$) and affected by the probability that a vacant territory would become colonized ($\gamma_{i,t}$) or that an occupied territory would persist ($\phi_{i,t}$):

$$\psi_{i,t} = \gamma_{i,t-1}(1 - z_{i,t-1}) + \phi_{i,t-1}z_{i,t-1}$$

where colonization and persistence patterns were altered through the effects of site- and time-varying covariates constructed to detect pre- and post-fire effects on site occupancy

$$\text{logit}(\gamma_{i,t-1}) = c_0 + c_1 kf_i + c_2 \text{after}_t + c_3 kf_i \text{after}_t + c_4 kf_i \text{after}_t pSev_i + c_5 kf_i \text{after}_t \text{pyro}_i + c_6 kf_i \text{after}_t pSalvage_{i,t} + c_7 \text{year}_t$$

and

$$\text{logit}(\phi_{i,t-1}) = d_0 + d_1 kf_i + d_2 \text{after}_t + d_3 kf_i \text{after}_t + d_4 kf_i \text{after}_t pSev_i + d_5 kf_i \text{after}_t \text{pyro}_i + d_6 kf_i \text{after}_t pSalvage_{i,t} + d_7 \text{year}_t$$

where kf_i was an indicator variable for fire-affected territories as described above, after_t was an indicator variable for post-fire survey years, $pSev_i$ was a continuous variable representing the proportion of the territory that was affected by stand-replacing fire, pyro_i was a continuous variable describing pyrodiversity and $pSalvage_{i,t}$ was a time-varying site covariate

describing the cumulative proportion of the owl site that had experienced post-fire salvage logging. We modeled salvage logging as a time-varying covariate because most salvage logging within owl sites occurred immediately after the fire (in 2015), but some additional logging occurred in subsequent years. The terms $c.year_t$ and $d.year_t$ were annual, normally distributed random effects that allowed annual unmodeled heterogeneity in colonization and extinction parameters.

We fit the above model at each of the four covariate scales (300, 700, 1100 and 1500 m) to the data using JAGS (Plummer, 2003) in the R statistical programming environment. All coefficients were assigned uninformative Gaussian priors with $\mu = 0$ and $\sigma = 2$ as recommended by Northrup & Gerber (2018). Although on the logit scale this prior appears informative, it is approximately flat when back-transformed to the probability scale (Northrup & Gerber, 2018). We ran three chains of 10 000 iterations, an adaptation phase of 1500 and a thin rate of 10 yielding 3000 posterior samples for each parameter across all chains. We assessed convergence using the Gelman–Rubin statistic (all values <1.1). We made inference about parameters by examining the direction and magnitude of mean effects, the extent to which posterior distributions overlapped zero, computation of odds ratios following Jones & Peery (2019), and by graphical visualization of derived annual rates of occupancy, colonization and persistence.

Results

Following the King Fire, spotted owl sites were less likely to persist when they experienced more stand-replacing fire ($>75\%$ canopy mortality) across all spatial scales examined (Fig. 2a). The strongest effect of severe fire on persistence was found at the 1100 m (territory) scale, where the mean odds of persistence decreased by 7.8% for every 10-ha increase in severely burned area (logit coefficient $d_4 = -3.12$, 95% Bayesian credible interval $[-5.05, -1.23]$). In contrast, the effect of pyrodiversity on spotted owl site persistence was scale-dependent (Fig. 2a). At the nest area (300 m) and PAC (700 m) scales, increased pyrodiversity led to increased persistence probability ($d_5 = 1.30$ $[-0.35, 2.94]$ and $d_5 = 1.19$ $[-0.25, 2.73]$), respectively (posterior densities were 93 and 94% positive; Table S1 in Appendix). Whereas at the territory (1100 m) and home-range (1500 m) scales, the pyrodiversity effect weakened and the CRIs widely overlapped zero. Salvage logging had no effect on persistence probability; posterior means were near zero and credible intervals widely overlapped zero across all scales (Fig. 2a). Thus, we considered salvage logging to be an uninformative parameter for spotted owl site persistence.

Like site persistence, more extensive severe fire reduced the probability of site colonization at all spatial scales examined (Fig. 2b). The effect of severe fire was strongest at the territory (1100 m) scale, where the mean odds of colonization decreased by 8.3% for every 10-ha increase in severely burned area ($c_4 = -3.28$ $[-5.26, -1.52]$). Unlike site persistence, pyrodiversity did not appear to influence site colonization probability, regardless of spatial scale (Fig. 2b). Neither

pyrodiversity nor salvage logging had any apparent effects on site colonization probability; posterior means were near zero and credible intervals widely overlapped zero (Fig. 2b). Posterior distributions for all model coefficients for persistence and colonization sub-models, as well as detection and initial occupancy, are available in the Table S1 in Appendix.

Derived estimates of annual occupancy showed a gradual decline in occupancy over a 25-year pre-fire period for all owl sites, followed by the largest single-year occupancy decline over the study period (-0.08 ; declining from 0.54 to 0.46) in the year following the King Fire. However, when sites were grouped by broad classes of exposure to severe fire at the home-range (1500 m) scale (unburned, $<50\%$ high-severity, $>50\%$ high-severity), a distinctive “hockey stick” post-fire trajectory for the most severely burned sites was apparent (Fig. 3). The probability that sites that experienced $>50\%$ severe fire (at the 1500-m scale) remained occupied dropped sharply from 0.62 in the year prior to the fire (2014) to 0.23 following the fire (2015). Then in 2016, the probability of site occupancy for this severely burned group dropped to 0.039 and remained near zero through the remainder of the study period. Sites that burned less severely ($<50\%$ high severity) experienced a relatively smaller apparent decline in occupancy probability after the fire (from 0.59 in 2014 to 0.40 in 2015), but then remained between 0.42 and 0.55 over the period 2016–2020 (Fig. 3). The probability of occupancy for unburned sites appeared to remain stable or slightly increase following the King Fire (Fig. 3).

Discussion

We have shown that a large, severe “megafire” of a type that is becoming more frequent in some forest ecosystems can lead to dramatic and persistent local population declines. Following the 2014 King Fire in the central Sierra Nevada, CA, spotted owls at severely burned sites went locally extinct and did not re-colonize them over a 6-year period following the fire (Fig. 3). These findings support our hypothesis that spotted owls are poorly adapted to survive in post-fire landscapes characterized by extensive severe fire. These results also indicate that initial short-term impacts (1-year post-fire) reported by Jones *et al.* (2016) have persisted and thus do not represent an ephemeral effect. Hence, this megafire event caused a persistent loss of spotted owl nesting habitat, which is a primary factor limiting populations of this species across its range (Ganey *et al.*, 2017). For this reason, we reject the notion that owls experiencing large, severe fires within their territories may simply show an initial abandonment of sites but return shortly thereafter.

Rapidly changing fire regimes could pose an existential threat to spotted owls and other forest-dependent species as ecosystems cross ‘tipping points’ and experience type conversion (van Nes *et al.*, 2016). Altered fire regimes, in combination with other stressors such as climate change and logging, can lead to ecosystem collapse (Lindenmayer, Messier, & Sato, 2016) and has led to long-term declines in tree-cavity-dependent species in Mountain Ash forests in Australia (Lindenmayer & Sato, 2018). Recent fires in

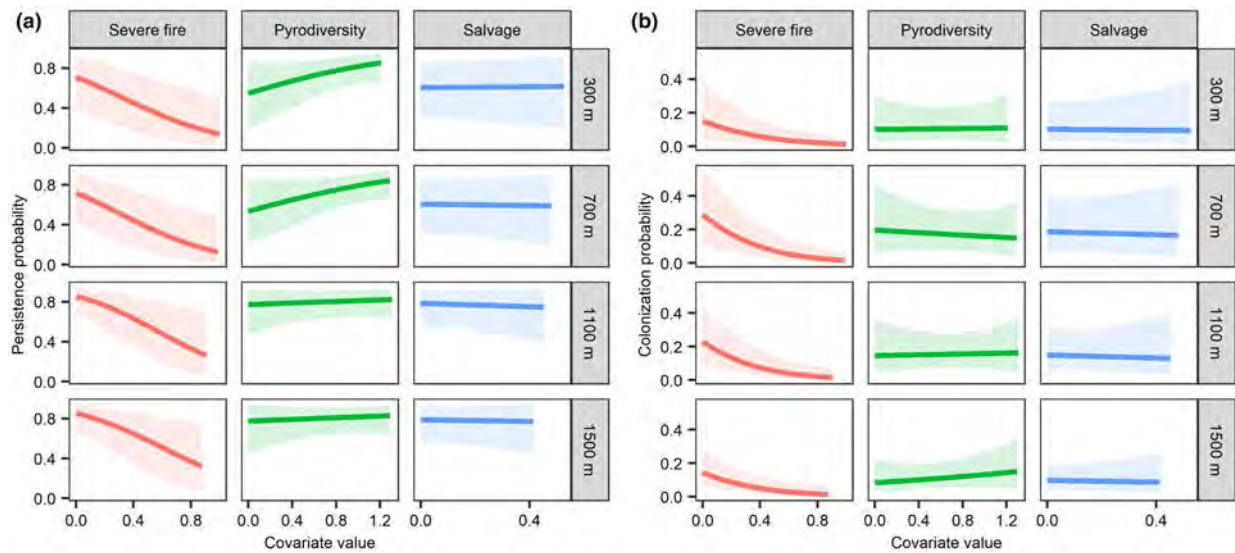


Figure 2 Predicted relationships between covariates (severe fire, pyrodiversity and salvage logging) and dynamic occupancy rates (persistence in panel a; colonization in panel b) across the four scales of analysis (nest area, 300 m; PAC, 700 m; territory, 1100 m and home range, 1500m). The thick colored lines represent the prediction at the posterior mean, while shaded range represents the upper and lower 95% Bayesian credible intervals. Coefficient estimates used to produce figures can be found in the Table S1 in Appendix [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

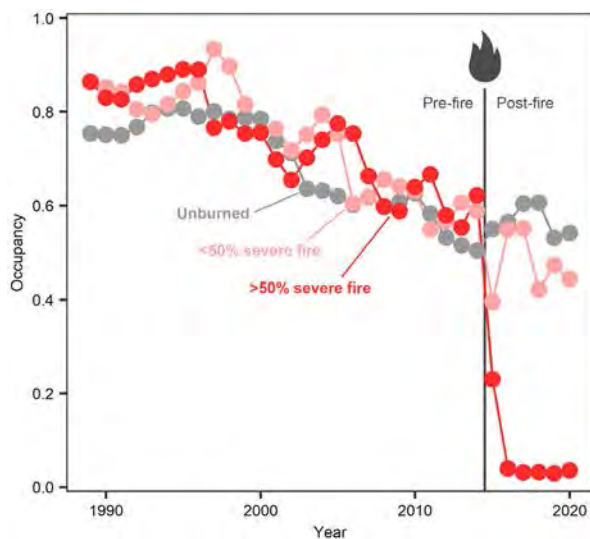


Figure 3 Derived annual occupancy from 1989 to 2020 for spotted owl sites grouped by the percentage of the home-range (1500 m) that experienced severe fire (unburned, <50% severe, >50% severe). The grey vertical line on the x-axis between years 2014 and 2015 indicates the timing of the 2014 King Fire and therefore divides pre- and post-fire occupancy trajectories [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

California, USA have eclipsed the 2014 King Fire in terms of size and severity (e.g., 2020 Creek fire) and these types of fires could contribute to collapse of dry forest ecosystems through regeneration failure and persistent type conversion (Davis *et al.*, 2019; Stevens *et al.*, 2017). If owl populations

are responding similarly to more recent and widespread fire events, landscape-scale population viability over the coming decades could be threatened. Therefore, our results suggest that forest restoration intended to reduce megafires and increase long-term forest resilience are likely to provide co-benefits for this species, forest ecosystems and the people that depend on long-term sustainability of forest ecosystem services (Stephens *et al.*, 2020; Wood & Jones, 2019), so long as keystone structural features of these ecosystems are retained (Jones, 2019; Jones *et al.*, 2018; Tempel *et al.*, 2014).

Many terrestrial vertebrates may respond positively to forest restoration. Mechanical thinning and fire mosaics produced through prescribed and managed fire (i.e., pyrodiversity) can increase structural diversity in homogenized forests, which could result in increased biodiversity (Fontaine & Kennedy, 2012; Steel *et al.*, 2019; Tingley *et al.*, 2016). It has generally been assumed, however, that spotted owls and other sensitive old-forest species will respond negatively to restoration treatments because these species tend to be associated with 'dense' and fire-prone forests. Yet for spotted owls, empirical evidence for negative effects of restoration treatments is sparse. Studies that have inferred or are often cited as evidence for negative treatment effects to owls have demonstrated weak effect sizes (Tempel *et al.*, 2014) or did not distinguish between fire and treatment effects (Seamans & Gutiérrez, 2007). Observed owl declines following restoration treatments in another study occurred alongside declines in control groups, such that effects could not be attributed to treatments themselves (Stephens *et al.*, 2014). Still, other studies have found no measurable effects of treatment, or otherwise weak positive

(beneficial) effects (Tempel *et al.*, 2016). Indeed, restoration that increases landscape-scale heterogeneity in otherwise fire-suppressed, homogenized forests could directly benefit owls by promoting diverse prey habitat and population stability (Hobart *et al.*, 2019). Moreover, restoration that increases the scale of low-severity fire effects through prescribed fire is likely to recruit preferred owl foraging habitat in the short term (Kramer *et al.*, 2021). Therefore, it is likely that although restoration treatments could in some contexts result in weak negative effects, these effects are substantially exceeded by negative effects of megafires over the long term (Jones, 2019; Tempel *et al.*, 2015).

Observations of ecological phenomena are scale dependent (Levin, 1992; Wiens, 1989), which has led to adoption of multi-scale perspectives in ecological analyses (Jackson & Fahrig, 2015; McGarigal *et al.*, 2016). Scale dependence is also apparent in analyses of the effects of ecological disturbances on biodiversity (Hamer & Hill, 2000; Wan, Cushman, & Ganey, 2020). Using four biologically relevant spatial scales (nest area, activity center, territory and home range), we determined that while some disturbance effects were scale invariant, others were scale dependent. The effect of severe fire on both site colonization and persistence was scale invariant; severe fire had clear negative effects on both parameters across all scales examined, with very little variation in effect size or uncertainty (Fig. 2, also see Table S1 in Appendix). This observation may be related to the patterns of severely burned forest within the King Fire where extremely high spatial contagion (Stevens *et al.*, 2017) rendered homogenous severe fire effects across scales. In contrast, higher pyrodiversity has led to increased persistence at finer spatial scales but not at broader spatial scales. Consequently, pyrodiversity at finer scales may result in greater likelihood of nest stand structure preservation or lead to increased diversity of prey habitat near the nest stand (Hobart *et al.*, 2021). The effect of pyrodiversity may diminish at broader scales because these larger scales are more associated with foraging habitat and foray behaviors (Blakey *et al.*, 2019), the former of which is more flexible for spotted owls than is their choice of roosting and nesting habitats (Atuo *et al.*, 2019; Call, Gutiérrez, & Verner, 1992; Williams *et al.*, 2011). This result suggests a potential benefit to increased use of prescribed and managed fire resulting in diverse post-fire conditions in spotted owl core areas and at the scale of protected activity centers (Kramer *et al.*, 2021). Moreover, this result has broader implications for pyrodiversity research, as little existing work has explored the role of scale in mediating pyrodiversity effects on wildlife and the pyrodiversity–biodiversity hypothesis (Jones and Tingley, *in press*).

Following large disturbance events such as megafires, windstorms and droughts, land managers will often engage in post-fire management such as salvage logging and reforestation to recover some economic loss and attempt to rebuild resilient forest ecosystems (North *et al.*, 2019). Salvage logging, in particular, is a controversial practice because of its negative effects on certain taxa and ecosystem processes (Lindenmayer *et al.*, 2008; Thorn *et al.*, 2018). In some cases, scientists have debated whether it is the disturbance itself (e.g.,

fire) or the subsequent management activities (e.g., salvage logging) that has caused estimated effects on sensitive wildlife species such as spotted owls (Hanson, Bond, & Lee, 2018; Jones *et al.*, 2019). It is often the case that fire and salvage effects are confounded and thus cannot easily be separated (Clark, Anthony, & Andrews, 2013; Lee, Bond, & Siegel, 2012). In our study, we were able to separate these two effects and we unequivocally determined that severe fire, and not salvage logging, was correlated with the observed local declines in spotted owl site occupancy. We, thus, reject the hypothesis that salvage logging drove or even contributed to the observed post-fire decline. Given that both severe fire and salvage logging were included as competing covariates, the salvage effects were uninformative across all scales (Fig. 2).

The relative effects of fire and post-fire management on wildlife may, in part, depend on their relative spatial extent. In our study landscape, the spatial extent of severe fire effects not only eclipsed that of salvage logging, but often did so by an order of magnitude (Fig. 4, Table 1). Sites that experienced extensive severe fire (>50%) but very little salvage logging (many close to 0%) remained unoccupied 6 years post-fire, which further indicated that severe fire was more likely of these two forces driving local extirpation and

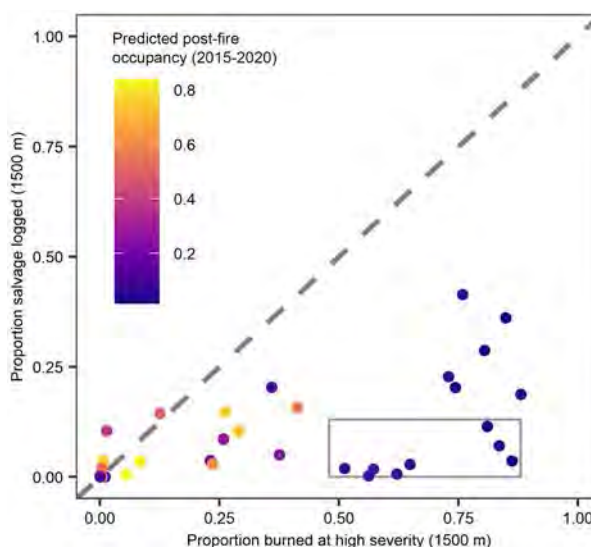


Figure 4 Comparison of the relative extent of salvage logging (y-axis) and severe fire (x-axis) at the home-range (1500 m) scale, where each point represents one spotted owl site. Points are colored by the predicted post-fire (2015–2020) occupancy at each spotted owl site. Points above the grey dashed diagonal 1:1 line indicate sites with a greater extent of salvage logging than high-severity fire; points below the 1:1 line indicate site with more high-severity fire than salvage logging. The grey rectangle in the bottom right surrounds a group of sites that experienced relatively large amounts of severe fire (>50% of home range affected) and relatively little salvage logging (0–12% of home range), highlighting the effect of severe fire on owl occupancy independent of post-fire salvage logging [Colour figure can be viewed at [zslpublications.org/online-library/wiley.com](https://www.zslpublications.org/online-library/wiley.com).]

lack of re-colonization (Fig. 4). In some cases, sites that experienced greater salvage logging had higher post-fire occupancy than sites that had experienced less salvage logging, with differences in occupancy instead being clearly linked to variation in severe fire extent and pyrodiversity, not salvage (Fig. 5). Thus, while it is well known that salvage logging can have negative consequences for spotted owls (Lee *et al.*, 2013; Jones *et al.*, 2020) and biodiversity more broadly (Lindenmayer & Noss, 2006; Thorn *et al.*, 2018), the pattern and extent of salvage logging had no measurable effects on spotted owl occupancy dynamics in this study and was transcended by the extreme nature of the King Fire. It is likely that in other cases where post-fire management (such as salvage logging) is more spatially extensive, determining whether fire or post-fire management caused declines would be challenged because the effects would be confounded.

Long-term monitoring programs offer unmatched value for understanding ecosystem change over prolonged time periods (Hughes *et al.*, 2017; Lindenmayer *et al.*, 2012). Our ability to measure a clear and immediate effect of a random event (the King Fire) on spotted owls was only made possible because of

the intersection of this fire on a long-term population study, even though the original purpose of owl monitoring was to detect population trends, not to detect the effects of disturbance. Our continuing post-fire monitoring of this population has reinforced initial results (Jones *et al.*, 2016), allowed for further accumulation of evidence (Nichols, Kendall, & Boomer, 2019) and expanded understanding of prolonged effects and mechanisms underlying species response. Thus, we emphasize that long-term monitoring can offer surprising and unparalleled opportunities for learning, which allow monitoring programs to provide unexpected value for addressing emerging environmental concerns (Lindenmayer & Likens, 2009). The before–after control–impact natural experimental design – one of the most powerful designs in ecological field studies (Popescu *et al.*, 2012) – is often only possible in the context of long-term monitoring and unexpected environmental changes. In an era of rapid ecological changes and shifting disturbance regimes in ecosystems, the relative value of long-term monitoring programs may increase through time because they will allow researchers to estimate effects of novel changes in ways that more “reactive” research or monitoring may not be able to provide.

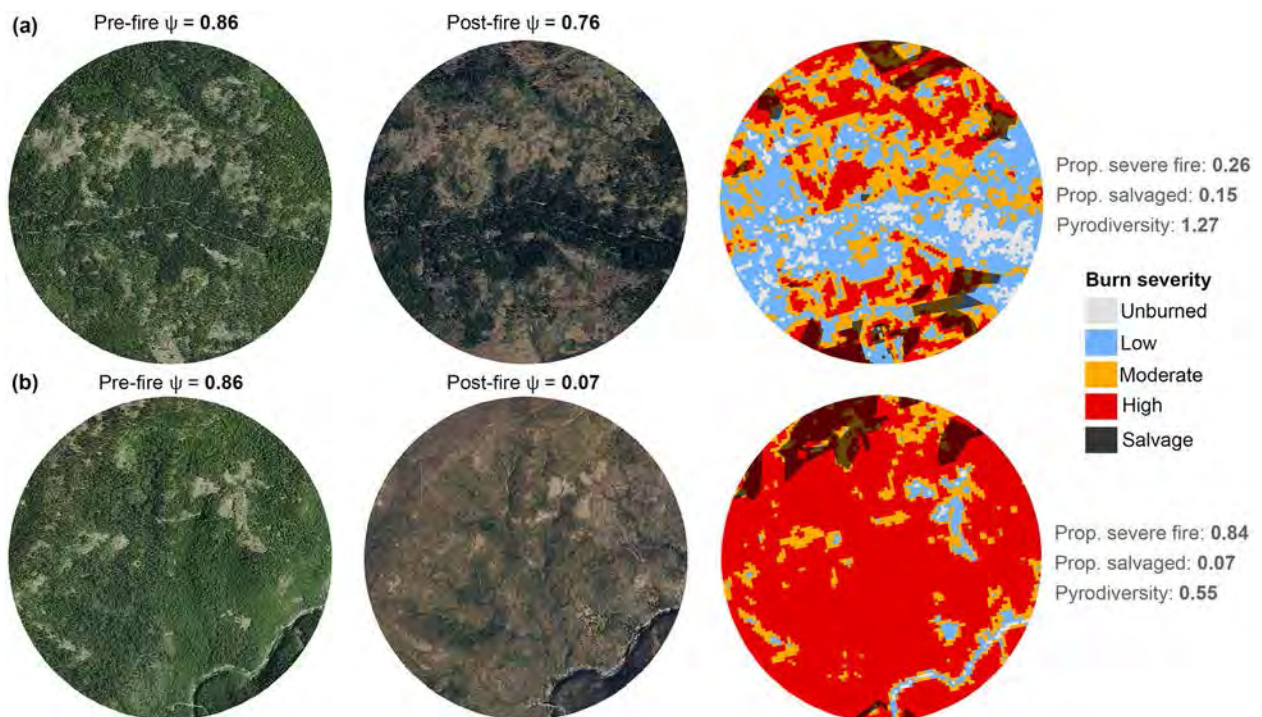


Figure 5 Two selected spotted owl sites (shown at the home-range scale, 1500 m) illustrating the effects of fire severity, pyrodiversity and salvage logging on site occupancy. The owl site in the top row (a; “site A”) and bottom row (b; “site B”) had the same predicted pre-fire occupancy probability ($\psi = 0.86$). After the fire, predicted occupancy declined slightly for site A (0.10 decline) and dramatically for site B (0.79 decline). These different post-fire trajectories can be attributed to differences in high-severity fire exposure and pyrodiversity. Site A experienced relatively little high-severity fire (proportion of home range affected = 0.26) and relatively high pyrodiversity (index = 1.27). Site B experienced extensive high-severity fire (proportion = 0.84) and low pyrodiversity (index = 0.55). Both sites experienced small amounts of salvage logging, with site A experiencing ~2x as much salvage as site B (15% and 7%, respectively). However, salvage logging was an uninformative parameter, so it had no effect on predicted post-fire occupancy. Aerial photos shown in the left and middle columns represent 2014 (pre-fire) and 2018 (post-fire) NAIP imagery. Pre- and post-fire predicted site occupancy was estimated for a 6-year pre-fire period and 6-year post-fire period, respectively [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com).]

Our work offers evidence that the negative effects of novel ‘mega-disturbances’ in some ecosystems may be permanent, not ephemeral, reinforcing the need to re-think the status quo in forest ecosystem conservation (North *et al.*, 2015; Stephens *et al.*, 2019, 2020; Wintle, Legge, & Woinarski, 2020; Wood & Jones, 2019). In this study, there was no evidence of recolonization of sites by owls that burned at >50% high severity even 6 years after the fire. This is not surprising, given that in the Sierra Nevada, the regeneration time for old-forest conditions required by spotted owls exceeds 100 years. However, even a 100+ years hypothesized timeline of habitat regeneration relies on the now questionable assumption that forests will have the capacity to regenerate naturally under climate change and increasing frequency of high-severity fire (Davis *et al.*, 2019; Shive *et al.*, 2018; Stevens *et al.*, 2017). Thus, active management to mitigate disturbance effects, increase forest resilience and/or restore disturbed areas may be required to avoid permanent loss of owl habitat in many areas (North *et al.*, 2019). Forest restoration that increases landscape heterogeneity of forest structure and fuels may increase resilience to disturbances (Koontz *et al.*, 2020). Post-fire reforestation strategies could also increase ecosystem resilience and long-term persistence of seasonally dry forests (North *et al.*, 2019) and the ecosystem services they provide to people (Hurteau *et al.*, 2014; Wood & Jones, 2019). The accumulating evidence, including the evidence provided in this paper, suggests that the conservation of spotted owls, and likely other sensitive wildlife species, and dry forest ecosystem restoration are not in conflict. Therefore, we suggest that sensitive species conservation and forest ecosystem restoration can be mutually reinforcing objectives in bioregional-scale forest management.

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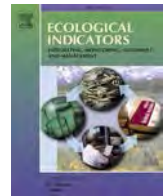
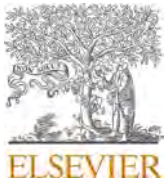
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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Full model results for Bayesian dynamic occupancy models at the four spatial scales examined



Estimating population size for California spotted owls and barred owls across the Sierra Nevada ecosystem with bioacoustics

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ABSTRACT

Monitoring population size at ecosystem scales is difficult for most species of conservation concern. While assessing site occupancy at broad scales has proven feasible, rigorous tracking of changes in population size over time has not – even though it can provide a stronger basis for assessing population status and conservation-decision making. Therefore, we demonstrate how relatively low-intensity, ecosystem-scale passive acoustic monitoring (PAM) can be linked to local-density monitoring to estimate the population size of native California spotted owls (*Strix occidentalis occidentalis*) and invasive barred owls (*S. varia*) across the western Sierra Nevada, California. Based on a PAM sampling grid with 400 ha cells (the approximate home range size of these species), we estimated site occupancy to be between 0.42 (SE = 0.02) and 0.30 (SE = 0.02) for California spotted owls using relatively liberal and strict criteria, respectively, for considering a cell occupied. PAM-based site occupancy estimates within local-scale density monitoring study areas (range = 0.41–0.78 and 0.28–0.76 for liberal and strict criteria, respectively) were strongly and positively correlated with local density (range = 0.08–0.31 owl/km²) for this species. In contrast, ecosystem-wide site occupancy of barred owls was very low based on PAM (0.034, SE < 0.01), as were densities within local monitoring studies (range = 0–0.005 owls/km²). By scaling ecosystem-wide site occupancy estimates to densities estimated with local monitoring studies, we estimated that, depending on occupancy criteria, 2,218 (SE = 278) or 2,328 (SE = 489) California spotted owls occurred in the Sierra Nevada ecosystem in 2021. Thus, while California spotted owls are a rare subspecies, they were well-distributed across the Sierra Nevada. Because there were so few barred owl detections, we could not estimate ecosystem-scale abundance, which reflects the success of prior experimental removals in the region. In conclusion, our study provides a generalizable framework for estimating population size for territorial species with PAM at ecosystem scales when local-scale estimates of density are available. Thus, we demonstrate that this approach can provide novel and valuable insights into monitoring populations to aid species conservation.

1. Introduction

Population monitoring is integral to biodiversity conservation, but monitoring cryptic or rare species over broad spatial scales and long time periods is challenging. Passive acoustic monitoring (PAM) is becoming an increasingly common approach because it can enable

broader and more continuous coverage than conventional, in-person surveys (Darras et al., 2018; Shonfield and Bayne, 2017; Sugai et al., 2019). PAM involves deploying autonomous recording units (ARUs) to record acoustically active species and extracting target signals from the audio data. Animal sounds identified in PAM data can then be readily adapted to detection/non-detection data that can, in turn, inform

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occupancy modeling. The large sample sizes enabled by large-scale PAM projects can yield high statistical power to detect even small changes in occupancy over space and time (Wood et al., 2019b). As a result, there is great potential for PAM to support population trend assessments at greater spatial scales than have previously been possible. Nevertheless, PAM-based estimates of occupancy may not reflect population metrics that are of interest to conservation if ARU sampling is not guided by knowledge of target species' use of any particular area (Wood and Peery, 2022).

For many species, human surveyors either establish or visit what they believe to be biologically meaningful locations, such as historically active breeding areas, to estimate "territory occupancy" as the proportion of potentially occupied territories. For territorial species, territory occupancy can scale directly to population abundance (Conner et al., 2016; Tempel and Gutiérrez, 2013). In contrast, PAM designs often involve deploying ARUs in a randomized subset of grid cells within a larger, grid-based sampling frame without knowing the actual location of resident or territorial individuals. Under this design, "site occupancy" represents the presence of an acoustically active individual of the target species at a survey site (i.e., grid cell). Yet not all observed individuals are necessarily residents of surveyed sites, causing "ecological false positives" which can lead to estimates of site occupancy that exceed territory occupancy rates and are subsequently less closely linked to population size (Berigan et al., 2019; Wood and Peery, 2022). Therefore, ecological false positives can obscure environmental and anthropogenic effects on populations because individuals may visit sites that do not support residents (Berigan et al., 2019).

At least two techniques can be used to mitigate the effects of ecological false positives on inferences about population processes. First, survey sites (e.g., grid cells) can be separated by distances such that it is unlikely territorial individuals will be detected in more than one grid cell. However, this approach reduces sample sizes and thus statistical power to detect changes in occupancy – as well as site-level location information that could be important for management. Second, metrics of acoustic activity (e.g., the count, timing, and types of vocalizations detected as well as identity of vocalizing individuals) can be used to filter out observations less likely to be indicative of residency (Reid et al., 2021) such that only sites at which resident individuals are present are treated as occupied. Criteria can be developed to determine which biological indicators truly constitute site occupancy (i.e., criteria applied to sites by season level) and/or individual detections (i.e., criteria applied to site by sampling period level). However, acoustic-based metrics are not a perfect way to eliminate ecological false positives because resident and non-residents can produce similar levels of vocal activity (Reid et al., 2021; Watson et al., 2023). Thus, there is a need to bridge spatially limited survey approaches that yield estimates of abundance or density and spatially extensive PAM approaches that yield more abstract estimates of site occupancy (Weldy et al., 2023).

We present an approach for combining ecosystem-scale PAM data (tens of thousands of km²) with local-scale monitoring data (tens to hundreds of km²) to strengthen PAM-based approaches for monitoring populations and estimate abundance. Under this approach, estimates of population density are obtained from local-scale monitoring programs; then, in conjunction with ecosystem-scale PAM monitoring data, direct relationships are developed between population density and site occupancy in areas of overlapping coverage to derive ecosystem-scale estimates of population size. Importantly, concerns posed by ecological false positives (Berigan et al., 2019; Wood and Peery, 2022) will be reduced if the relationship between site occupancy and density are consistent across space and time. Accordingly, we demonstrate how combining PAM and local-scale territory occupancy data can be used to estimate population size for territorial species at ecosystem scales in a manner that circumvents some of the aforementioned challenges posed by ecological false positives.

Both local-scale territory occupancy data and ecosystem-scale PAM data exist for the Sierra Nevada population of the California spotted owl

(*Strix occidentalis occidentalis*), an old forest-associated species. Whereas this subspecies of spotted owl has been proposed as threatened species by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 2023), there has never been an estimate of their population size in this large mountain range. Therefore, such an estimation is particularly valuable because the Sierra Nevada constitutes the primary population of this subspecies given that the central coastal and southern California population is highly fragmented and composed primarily of small, declining subpopulations (Barry et al., Under Review; Tempel et al., 2022) that may not be viable. We also estimate PAM-based site occupancy for barred owls (*S. varia*) across the Sierra Nevada – a direct competitor that poses an existential threat to spotted owls (Wiens et al., 2021) – two years after a lethal removal study in the Sierra Nevada (Hofstadter et al., 2022). Although estimates of Sierra Nevada-wide spotted owl occupancy and population size were previously considered unattainable (Peery et al., 2017), we demonstrate that combining local-scale population data with ecosystem-wide PAM data facilitates the estimation of total population size and site occupancy. Thus, our approach constitutes a strategy not only suitable for spotted owl conservation in this ecosystem, but also many other species for which both PAM and local-scale population data are available.

2. Methods

2.1. Study species

The spotted owl is a territorial species associated with mature and old-growth forest that faces several threats in the Sierra Nevada, which is the core range of the California subspecies. First, increasingly large, severe fires are causing localized losses of forest cover and driving potentially decadal population declines in those areas (Jones et al., 2021; Jones et al., 2016). Second, historical harvesting of large trees has caused population declines in some (Conner et al., 2016, 2013; Jones et al., 2018; Tempel et al., 2016) but not all areas (Hobart et al., 2019; Roberts et al., 2017). Third, the barred owl, a competitively dominant invasive species, which is in the process of driving northern spotted owls (*S. o. caurina*) extinct (Franklin et al., 2021; Wiens et al., 2021), has invaded the range of the California spotted owl and recently entered a rapid growth phase in the northern Sierra Nevada (Wood et al., 2019a). The invasion motivated a lethal removal experiment to assess whether barred owl occupancy could be reduced across the Sierra Nevada (Hofstadter et al., 2022). Fourth, although population-level effects are unknown, the California spotted owl is widely exposed to environmental toxicity via anticoagulant rodenticides (Hofstadter et al., 2021). Fifth, rising temperatures driven by climate change will subject California spotted owls to increasing thermal stress (Weathers et al., 2001), which has potential implications for adult survival and reproduction (McGinn et al., in Review).

The California spotted owl faces an array of threats and may soon receive formal protection under the Endangered Species Act. Yet the relative sizes of the native spotted owl and the invasive barred owl populations in the Sierra Nevada are unknown. Despite decades of research, the broad geographic range and secretive nocturnal habits of spotted owls have precluded any spatially comprehensive population assessment. Thus, estimating population size of these species will aid future conservation efforts.

2.2. Study areas and survey design

The Sierra Nevada is the dominant physiographic feature of eastern California, nearly spanning the length of the state. Within this vast ecosystem, we conducted ecosystem-scale PAM surveys and density estimation within four local-scale monitoring studies. Our PAM program spanned the west-slope Sierran mixed-conifer forest, including coverage in all seven National Forests, three of the four National Parks, and some private lands (Fig. 1) because the eastern slope of the Sierra Nevada had

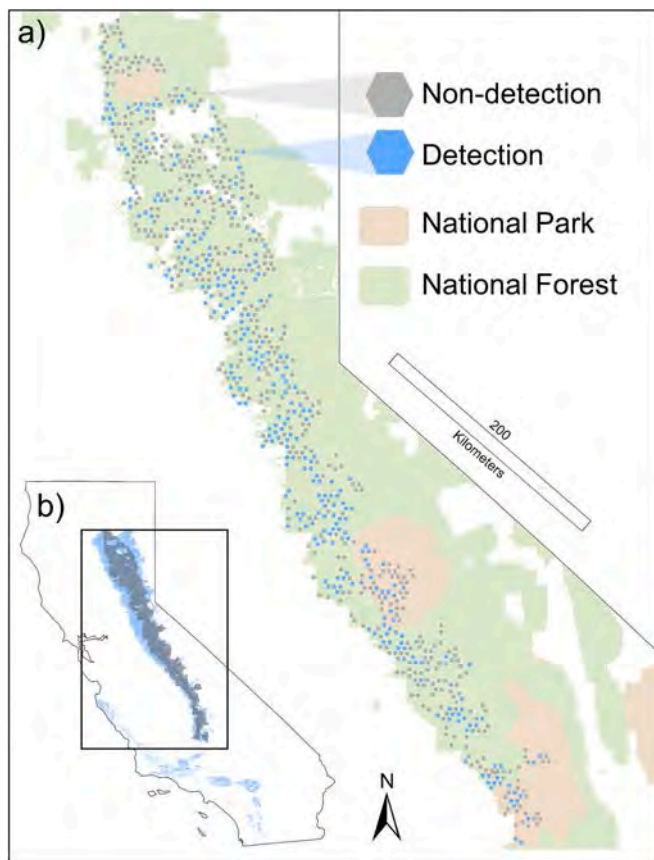


Fig. 1. PAM survey cells and California spotted owl detections. a) PAM surveys were conducted in 851 400-ha hexagonal cells distributed across seven National Forests (green) and three National Parks (brown). California spotted owls were detected (blue) across the Sierra Nevada. b) PAM surveys (grey) occurred across most of the California spotted owls presumed suitable habitat in the Sierra Nevada (light blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

very few owls (Verner et al., 1992). We subdivided this western slope area into 6,236 4 km² hexagonal grid cells, which are approximately the size of a spotted owl territory in this region. Our total sampling area of 24,494 km² (320–2,890 m asl) covered 57% of the California spotted owl's habitat in the Sierra Nevada ecosystem. Candidate cells were excluded if they: intersected highways, were > 50% water, lacked road access in National Forests, or lacked road or trail access (< 4 km from a road or trail) in National Parks. In practice, this also excluded particularly steep and wilderness areas, though they ultimately comprised a very small proportion of the candidate grid cells (< 5%). In 2021, we surveyed 851 non-adjacent grid cells (13.6% of the total area) to reduce the possibility of double-counting owl territories (Wood et al., 2019b).

We deployed one to three, but generally two, ARUs (SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) in each grid cell at acoustically advantageous locations such as ridgetops, with a minimum spacing of 500 m. If a cell overlapped an accessible spotted owl Protected Activity Center (121 ha areas of high-quality habitat around historic spotted owl nest and roost sites) we attempted to deploy at least one ARU inside that Protective Activity Center polygon. Otherwise, deployments were made without specific knowledge of owl occupancy. ARUs had a single omni-directional microphone with –25 dB sensitivity; we programmed them to record 20:00 – 06:00 PDT at a sample range of 32 kHz, 16-bit resolution, and gain of + 33 dB. Deployments began in early-May and lasted through early July, with any given grid cell surveyed for approximately five weeks continuously.

The four local-scale spotted owl monitoring study areas spanned the

length of the Sierra Nevada (Fig. 2). From north to south, the Lassen (1,254 km²; 1,200–2,100 m asl), Eldorado (818 km²; 300–2,500 m asl), and Sierra (693 km²; 300–2,900 m asl), Sequoia–Kings Canyon (343 km²; 425–3,050 m asl) study areas consisted predominantly of land managed by the U.S. Forest Service, with some private lands largely managed for commercial forest products whereas the Sequoia–Kings Canyon study area occurred entirely within two national parks of the same name. All active, historical, and potential spotted owl territories in these study areas have been monitored annually from as early as 1986 to 2021 (Conner et al., 2013; Tempel et al., 2016) using standard call-based spotted owl survey methods (Forsman, 1983). Call-based spotted owl surveys, in which human surveyors imitate or broadcast spotted owl calls, can yield high seasonal detection probabilities for territories (> 0.95) (Wood et al., 2018) such that local spotted owl populations are effectively censused. Thus, we refer to them as “density monitoring study areas” because abundance within a fixed area was estimated annually over time.

Fig. 1.

2.3. Identifying target vocalizations in passively recorded audio

To identify spotted owl and barred owl vocalizations in the passively recorded audio, we used the BirdNET algorithm, a deep convolutional neural network originally designed to identify nearly 1,000 species of North America and European birds (Kahl et al., 2021). We developed a customized version of BirdNET that was overfit to the species and audio characteristics of our PAM program; tests against independent validation data indicated that it could readily identify target vocalizations for two species: the spotted owl's “four-note”, “contact call”, “crow bark”, “monkey hoot”, and juvenile begging, and the barred owl's “eight-note” (or “who cooks for you”) and “hoo-aw” calls. BirdNET's core output is a unitless numeric prediction score, ranging from 0 to 1, for each call type in each 3-second interval of audio data. BirdNET was trained to predict each owl call type individually as well as spotted and barred owl vocalizations generally. Any vocalization above a final species-specific threshold (reported in the results section) was flagged and manually validated. BirdNET's prediction score is not a probability but rather an indication of confidence in the identification with larger numbers indicating greater confidence.

We manually confirmed all putative BirdNET-derived owl observations above species-specific prediction score thresholds for two reasons. First, false positive detections (inferring presence when no individuals occur in the survey area) can inflate occupancy estimates and obscure the effects of environmental factors on occupancy (Berigan et al., 2019). Such false positives can occur because sounds can be misclassified as a spotted owl or barred owl, including calls broadcasted as part of owl surveys. Second, accurate presence data are important to inform forest management activities that could affect spotted owl habitat quality and to locate barred owls for lethal removal.

When selecting specific prediction thresholds above which to manually validate predictions, we considered the trade-off between the effort associated with manual review (to eliminate false positives) and the probability of not detecting territorial owls present within survey cells. Lower (more liberal) prediction thresholds could increase the number of owl calls that are correctly identified; in other words, recall, the proportion of target signals that are recorded and correctly identified as such would likely increase. However, lowering the prediction threshold would also inevitably lead to larger, and potentially intractable, numbers of predictions requiring manual review; in other words, precision, the proportion of predictions that were correct, would decrease. Conversely, higher (more stringent) prediction thresholds would reduce the number of predictions requiring review but could reduce the probability of detecting territorial owls (and thus result in lower detection probabilities estimated as part of the occupancy analyses described below). Thus, in the case of higher prediction thresholds, recall would decrease but precision would increase. Therefore, to

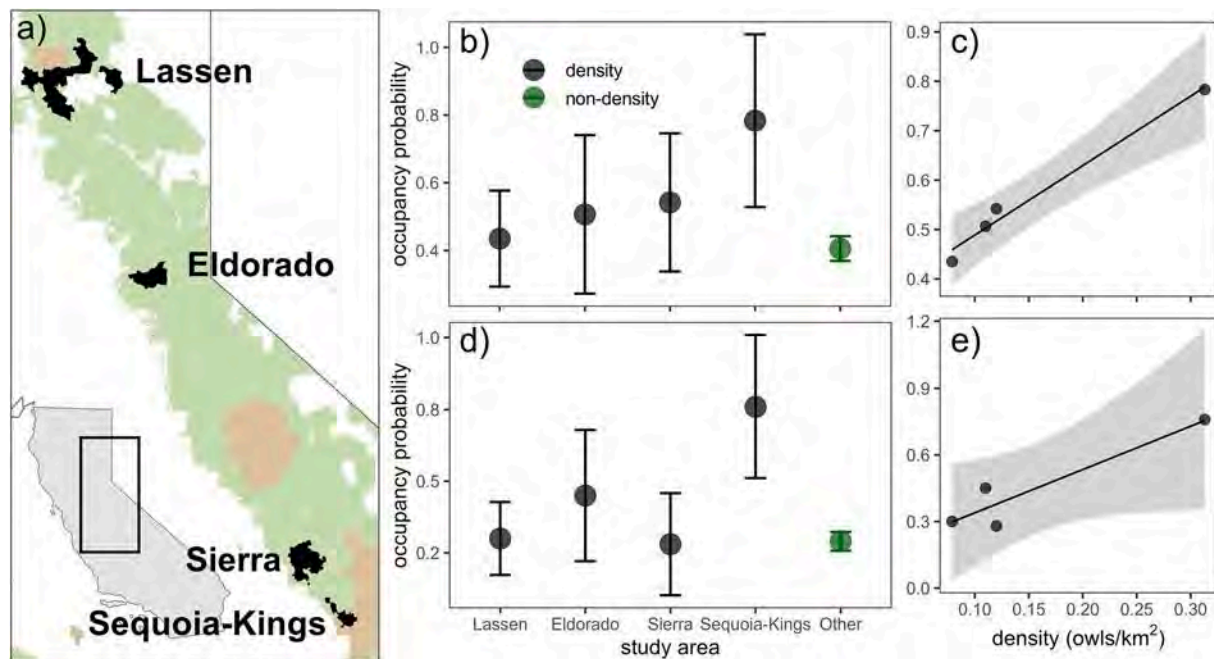


Fig. 2. Acoustic-based site occupancy probabilities for the four local-scale density monitoring study areas (gray points) and all grid cells ($n = 744$) outside those areas (green points). Green indicates National Forests and brown indicates National Parks. The Lassen, Eldorado, Sierra, and Sequoia-Kings density monitoring study areas a) cover a nearly comprehensive latitudinal gradient for the Sierra Nevada. We report b) liberal estimates of occupancy and c) their relationship with density (owls/km²) in black. We also report liberal and strict estimates of occupancy for sites outside density monitoring study areas, or the “non-density” study area, in dark green. Finally, we report d) strict estimates for occupancy and e) their relationship with density. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

evaluate these tradeoffs and select prediction thresholds for spotted owls, we leveraged information from PAM grid cells known to contain residents of either species to calculate two key statistics across a range of BirdNET prediction scores (0.969, 0.979, 0.989, and 0.999 for spotted owls, and 0.960, 0.970, 0.980, and 0.990 for barred owls). We calculated (i) the number of BirdNET predictions requiring manual review, and (ii) the proportion of those cells containing a territorial owl that had a confirmed vocalization at or above that threshold. For each species, we selected prediction score thresholds that yielded high probabilities of observing territorial individuals while only requiring that a tractable number of predictions be manually reviewed. For spotted owls, we drew on data from 17 PAM-surveyed grid cells in the Eldorado density monitoring area that contained nesting or roosting spotted owls in 2021. For barred owls, the number of PAM cells with territorial barred owls for this test was small given recent barred owl removals in the region (Hofstadter et al., 2022); we used information from two grid cells known to contain territorial barred owls.

When conducting our manual review of predictions above the selected thresholds, we removed false positives from our dataset caused by spotted owl and barred owl surveys with two methods. First, we manually reviewed the audio data associated with all potential observations and eliminated any potential observations that were not clearly a spotted owl. This included recognized recorded or mimicked spotted owl vocalizations by surveyors, as well as other acoustic indications that linked a given potential observation to a surveyor (e.g., human voices and repetitive calling sequences indicative of playback surveys). Second, we obtained spatial data from all known organizations conducting spotted owl surveys in the Sierra Nevada in 2021 and eliminated any potential observations that occurred within 1.5 km of a human surveyor on the same night. While this second precaution may have eliminated some true observations of spotted owls, we prioritized eliminating false positives over false negatives given the ability to model detection probability as part of occupancy modeling.

2.4. Estimating owl site occupancy

We estimated site occupancy rates for spotted owls and barred owls using single-season occupancy models (MacKenzie et al., 2002) applied to detection histories derived from manually validated observations generated by BirdNET. Entire grid cells were considered survey sites such that either or both ARUs therein could contribute owl observations to its occupancy status. For both species, we attempted to conduct two separate sets of occupancy analyses for each species representing two acoustic-based detection criteria. The acoustic-based detection criteria were the one-night (a single confirmed owl observation constituted “detected”; i.e., unfiltered) and two-night (“detected” required confirmed owl observations on two or more nights) thresholds for determining the occupancy status of any given site (i.e., grid cell). The one-night threshold represents the liberal, or more relaxed definition of occupancy, while the two-night threshold represents a stricter definition of occupancy. For both analyses, our season entailed eight one-week-long secondary sampling periods starting 10 May and ending 12 July.

With encounter histories generated based on both acoustic-based detection criteria, we constructed several competing full-Sierra Nevada occupancy models in which both detection and occupancy probabilities varied in space and time -with separate model sets evaluated for each of the two criteria. We evaluated model support using Akaike’s Information Criterion (AIC) at each stage of analysis and considered models within 2.0 AIC units of the top-ranked model to be competitive (Burnham and Anderson, 2002). First, while holding occupancy constant, we tested for variation in detection probability. We considered survey effort and time separately, and then combined the most-supported variables from each approach into an additive model, which was then compared to the original individual models. In terms of survey effort, detection could be constant or vary as a function of: (i) the number of ARUs deployed in a cell (1 vs ≥ 2), or (ii) the cumulative number of hours ARUs were deployed. In terms of time, detection could also vary: (i) among individual secondary sampling periods (p_i), (ii)

linearly over time across secondary sampling periods (p_T), or (iii) via a non-linear, natural-log trend ($p_{\ln T}$). Once the most supported detection model structure was determined, we evaluated support for models where occupancy was constant, varied by elevation (linearly, log-linearly, and quadratic), and varied by latitude (linearly, log-linearly, and quadratic). If support existed for multiple effects (i.e., ΔAIC of both models < 2.0), these terms were combined and evaluated as additive models.

2.5. Estimating owl abundance

We estimated the abundance of spotted owls and barred owls in the Sierra Nevada ecosystem by (i) relating PAM-based estimates of site occupancy (ψ_s) within the four local-scale density monitoring study areas to the density of territorial individuals (D_s) in these areas; and then (ii) using these relationships to convert Sierra Nevada-wide PAM-based estimates of site occupancy (ψ_{Sierra}) to a density estimate that applied to the entire ecosystem (D_{Sierra}). We estimated ψ_s based on a single season occupancy model where occupancy was allowed to vary among local-scale study areas (Lassen, Eldorado, Sierra, Sequoia-Kings, and all other grid cells outside of those study areas) – using the best detection model structure from the occupancy described above. We fit a study area effect occupancy model using both one- and two-night detection criteria. We estimated D_s by dividing the number of territorial individuals (N_s) found with our call-based surveys within each of the four density monitoring study areas in 2021 by their respective areas under the assumption that these local populations were effectively censused given the high detection probabilities associated with these surveys (Wood et al. 2018). Note that the number of spotted owls and barred owls in the Lassen study areas was enumerated using 2020 because the > 389 thousand ha Dixie Fire in late summer 2021 required terminating surveys one month earlier than in other years. However, spotted owl populations in the Sierra Nevada typically exhibit little interannual variation (typically $< 2\%$ /year (Conner et al., 2013; Tempel et al., 2016)), suggesting that using 2020 abundance data for one local population had little effect on the ecosystem-scale estimate of abundance in 2021. We then calculated four local-scale study area-specific density:occupancy ratios (R_s): $R_s = \frac{D_s}{\psi_s}$ and an area-weighted mean density:occupancy ratio ($\bar{R}$).

Site occupancy across the Sierra Nevada (ψ_{Sierra}) was calculated from our null occupancy model. We assumed that $\bar{R}$ was representative of the (unmeasured) full Sierra Nevada ratio (R_{Sierra}) given the study areas spanned the nearly the entire latitudinal and elevational gradient in the region and incorporated all major land management regimes (national forests, national parks, and private lands). Under this assumption, we solved for Sierra Nevada-wide density as: $D_{Sierra} = \psi_{Sierra} * R_{Sierra}$. We then converted D_{Sierra} to an estimate of the abundance of spotted owls in the Sierra Nevada as follows: $N_{Sierra} = D_{Sierra} * A$, where A was the area ($24,856 \text{ km}^2$) encompassed by our entire survey grid in the Sierra Nevada. We applied the density estimate to the entire grid, not just the sampled grid cells because local-scale density was estimated across both sampled and unsampled grid cells in the subset analyses. Standard errors for N_{Sierra} were estimated using Monte Carlo simulations where we randomly generated 1000 values of site occupancy for each local study area using normal distributions parameterized with our point estimates of occupancy and their standard errors – and then computing 1000 values of abundance using the aforementioned calculations.

3. Results

3.1. Identifying target vocalizations in passively recorded audio

We deployed 1,651 ARUs in 851 surveyed grid cells, with an average of 1.94 ARUs per cell in 2021. Deployments spanned almost all suitable California spotted owl habitat on the west slope of the Sierra Nevada

ecosystem. The earliest ARU deployment was 3-May, and the final ARU retrieval was 21-July. Thus, we recorded 557,000 h (63.5 years) of audio data, with a mean of 335 h per ARU and 652 h per cell.

The number of BirdNET predictions for either species increased exponentially as the score threshold decreased (Supplemental Table 1). We had substantial but finite capacity to manually review tens of thousands of predictions, and we utilized all expert staff time we allocated for that task based on thresholds of 0.989 for spotted owls and 0.970 for barred owls, which yielded 22,828 and 7,254 predictions, respectively. Our review yielded 18,568 confirmed spotted owl observations and 903 confirmed barred owl observations. After removing 1,807 spotted owl and 136 barred owl predictions that occurred within 1.5 km of call-based owl surveys on the same night, the spotted owl and barred owl precision were 0.813 and 0.124, respectively, at our chosen thresholds.

We then measured recall at the seasonal level (as opposed to the call level) because we had no need to identify all vocalizations at any given location, but we did want to minimize or eliminate the number of locations at which an owl was recorded but never identified by BirdNET at or above our chosen score threshold. To do so, we calculated the proportion of cells which would be considered occupied at different BirdNET score thresholds and occupancy criteria (liberal one-night or conservative two-night criteria) for the 17 and two PAM grid cells known to contain occupied spotted owls and barred owls, respectively. We found that a spotted owl territory would be observed 98% and 92% of the time at the one night and two night criteria at our chosen BirdNET score (0.989); barred owl territories (albeit $n = 2$) were always observed across our score thresholds (Supplemental Table 1). These estimates of recall are confounded with other factors, notably bird vocal behavior, that influence detection probability outside of detector recall, but collectively they indicated that we did not fail to observe the target species over the course of the season due to deficiencies in BirdNET at the score thresholds we used. Users of the BirdNET global model, rather than our custom model, are likely to achieve slightly lower performance at the same thresholds. Thus, while call-by-call recall may have been relatively low, our seasonal-level recall, or our ability to observe an animal acoustically during the entire sampling period, was sufficiently high (Wood et al., 2019b).

3.2. Ecosystem-scale estimates of spotted owl and barred owl occupancy

The detection model $p_{T+ARU\text{hours}}$ received 81% of the AIC weight using the liberal, one-night criterion and p_T received 100% of the AIC weight for the strict, two-night criterion (Supplemental Table 2). Under either criterion, detection varied among secondary sampling periods (p_i); under the one-night criterion, detection also increased with the number of recording hours in each cell (Table 1). Therefore, these detection models were carried forward to the occupancy modeling phase. The most supported occupancy model was $\psi_{\text{lat}+\text{lat}2+\text{elev}+\text{elev}2}$ and received 100% of the AIC weight for both criterion (Supplemental Table 2). Under either criterion, the probability of site occupancy varied nonlinearly with elevation and latitude, such that occupancy probability peaked at mid-elevations and mid-latitudes (Table 1). Based on the null model using the liberal, one-night occupancy criterion, detection probability for spotted owls was 0.50 (SE = 0.01) and site occupancy for the entire Sierra Nevada ecosystem (ψ_{Sierra}) was 0.42 (SE = 0.017). Based on the null model using the strict, two-night occupancy criterion, detection probability was 0.62 (SE = 0.01) and ψ_{Sierra} was 0.30 (SE = 0.02).

Naïve barred owl occupancy with the liberal criterion was just 0.011 (9 of the 851 cells had detections), so we did not apply the strict criterion. Additionally, detection probability could not vary between secondary sampling periods or between the number of ARUs in each cell because there were so few detections and insufficient variation in these factors among cells with detections. The most supported detection model, $p_{T+ARU\text{hours}}$, received 47% of the AIC weight and the second-ranked model, $p_{\ln(T)+ARU\text{hours}}$, received 32% of the AIC weight

Table 1

Site occupancy estimates for spotted owls. For each occupancy criterion (site occupancy defined as a confirmed on at least one night or at least two nights), one model had an AIC model weight of 1.00; β -estimates of model covariates for detection (p) and occupancy (ψ) and their corresponding Upper (UCL) and lower (LCL) confidence intervals are reported (95% CI). All covariates were standardized prior to fitting models, and all models included intercepts, but values are not reported in the table.

Species	Occupancy criterion	Parameter	Covariate	β	LCL	UCL
Spotted Owl	Liberal (one night)	p	t^a	0.76	0.13	1.39
		p	ARU _{hours} ^b	0.00	0.00	0.00
		ψ	lat	15.71	7.11	24.31
		ψ	lat ²	-16.17	-24.77	-7.57
		ψ	elev	3.00	1.96	4.04
		ψ	elev ²	-3.33	-4.43	-2.23
	Strict (two night)	p	t^a	-0.37	-1.06	0.32
		ψ	lat	14.36	9.13	19.59
		ψ	lat ²	-14.80	-23.95	-5.65
		ψ	elev	2.68	1.56	3.80
		ψ	elev ²	-3.03	-4.19	-1.87
		ψ	T^c	-7.25	-11.80	-2.70
Barred Owl	Liberal (one night)	p	ARU _{hours}	0.09	0.031	0.15
		ψ	lat	-50.04	-103.65	3.57
		ψ	lat ²	51.37	-2.94	105.68
		ψ				

^a Categorical time effect. Median β -estimate for secondary sample period shown.

^b Values rounded. 95% CI = 0.001–0.003.

^c Continuous time effect.

(Supplemental Table 3). The top-ranked model was carried to the next modeling stage in which $\psi_{lat+lat^2}$ received 52% of the AIC weight (Supplemental Table 3). Detection probability increased with the number of recording hours in each cell and decreased throughout the season, though we could not determine whether this decrease was linear or logarithmic (Table 1). The probability of site occupancy varied non-linearly with latitude, such that occupancy probability peaked at higher and lower latitudes (Table 1). Of the nine cells in which barred owls were detected, eight were in the northern Sierra Nevada (Lassen, Plumas, and Eldorado National Forests) and one was in the southern Sierra Nevada, which created a peak in occupancy at low latitudes. Based on the null model, Sierra-wide detection probability for barred owls was 0.23 (SE = 0.08) and ψ_{Sierra} was 0.03 (SE = 0.02).

3.3. Spotted and barred owl abundance across the Sierra Nevada

Spotted owl site occupancy varied among density monitoring study areas as models with a study area effect outperformed liberal and strict null ecosystem-scale models (Supplemental Table 2; $\Delta AIC = -0.57$ and -4.34 , respectively). Based on these top models, study area-specific occupancy estimates ranged from $\psi_s = 0.435$ to 0.784 for the one-night criteria and $\psi_s = 0.283$ to 0.760 for the two-night criteria (Table 2, Fig. 2). Occupancy was greatest for the Sequoia-Kings study area and was generally higher within study areas than outside of the study areas compared to nearby surrounding areas (Table 2).

We detected 39 to 99 territorial individuals in the four density study areas (i.e., N_s) with local densities D_s ranging from 0.079 to 0.313 owl/km² (Table 2). Site occupancy was strongly correlated with density based on both the liberal ($r = 0.99$) and strict thresholds ($r = 0.94$) – although this relationship was driven by the Sequoia-Kings Canyon study area (Fig. 2). The area-weighted mean density:occupancy ratio ($\bar{R}$)

was 0.213 and 0.308 for the one- and two-night criteria, respectively. Based on these local-scale site occupancy and density estimates, we estimated that 2,218 (SE = 278) and 2,328 (SE = 489) territorial spotted owls occurred in the Sierra Nevada based on the liberal and strict thresholds, respectively.

We could not estimate abundance for barred owls because very few individuals occurred in our > 24,800 km² PAM study area. In addition to ecosystem-level PAM-based occupancy being extremely low ($\psi_{Sierra} = 0.03$; see above), there was only one acoustic detection within the boundaries of the density monitoring study areas, which precluded comparisons of density and occupancy estimates across those areas. Further, no barred owls were detected by call-based spotted owl surveys in three of the four density monitoring study areas; only six individuals across five locations were detected in the Lassen study area, the northernmost such study and presumed forefront of the barred owl range expansion from the Cascade ecoregion (Wood et al., 2019a). None of those six individuals occurred in cells surveyed using PAM. Thus, barred owl densities ranged from 0 (three sites) to 0.005 owls/km² within (spotted owl) density monitoring study areas.

4. Discussion

The rich and extensive body of literature surrounding the spotted owl contains numerous examples of geographically extensive meta-analyses involving multiple local monitoring studies (e.g., Franklin et al., 2021; Jones et al., 2018; Tempel et al., 2016; Wiens et al., 2021). Moreover, recent work demonstrates how broad-scale PAM and territory occupancy data from local monitoring studies can be integrated to expand the area over which occupancy is inferred and increase the precision of estimates (Weldy et al., 2023). Here we conducted the first systematic, ecosystem-scale population assessment for spotted and barred owls, which has important implications for forest and wildlife management

Table 2

Local-scale spotted owl density monitoring study areas in the Sierra Nevada yielded comprehensive density estimates which we related to site-occupancy estimates (ψ) derived from a subset of the broader PAM project.

Study Area	Number of Owls	Area (km ²)	Density (owls/km ²)	ψ (one-night)	SE	ψ (two-night)	SE
Lassen	99	1254	0.079	0.435	0.072	0.302	0.065
Eldorado	39	355	0.110	0.507	0.119	0.445	0.117
Sierra	64	535	0.120	0.542	0.104	0.283	0.091
Sequoia-Kings	57	182	0.313	0.784	0.130	0.760	0.127
Other ^a				0.406	0.019	0.294	0.017

^a Sites outside the boundaries of local-scale study areas in the Sierra Nevada.

across the state of California. With 1,651 ARUs spanning over six million acres (24,856 km²) across seven national forests and three national parks, ours is the first study to provide near-total survey coverage of a relevant ecosystem (Fig. 1) as opposed to synthesizing data from smaller (300–1,200 km²) non-adjacent study areas (e.g., Jones et al., 2018; Tempel et al., 2016; Fig. 2). However, those intense, smaller-scale monitoring efforts were pivotal in providing data to hone our models. By combining occupancy estimates from those smaller, geographically specific studies with our Sierra-wide PAM data, our estimates of 2,218 or 2,328 territorial California spotted owls in the Sierra Nevada ecosystem highlights the potentially at-risk status of this subspecies given the large declines and population rarity observed in the Southern California population (Tempel et al., 2022).

Our finding that barred owl site occupancy across the Sierra Nevada was very low has important implications for the management of both spotted and barred owls. The functional absence of barred owls in 2021, two years after an extensive experimental removal effort (Hofstadter et al., 2022), suggested that only very limited recolonization and *in situ* reproduction had occurred. After our surveys were complete, eight barred owls were lethally removed from seven survey cells, including four of the nine cells in which they were observed via PAM. A lack of recolonization in the Sierra Nevada following barred owl removal is a key contrast between removal efforts within the range of the California spotted owl and those within the range of the northern spotted owl. Moreover, Hofstadter et al. (2022) found that California spotted owls were recolonizing historically active territories within weeks of barred owl removals in 2019, suggesting that the barred owl invasion had driven a decrease in territory occupancy but not yet a decrease in adult survival. Our findings corroborate that conclusion; in the Lassen density monitoring study area, which is the northern most study area closest to the barred owl invasion front, the PAM-based estimate of 2021 spotted owl site occupancy using the one-night occupancy criterion ($\psi_{Lassen} = 0.44$) was almost identical to a 2018 estimate of site occupancy in that area that also used a one-night occupancy criterion ($\psi_{Lassen\&Plumas} = 0.46$; Wood et al., 2020).

While California spotted owls are rare, our results also indicate that they nevertheless remain well distributed across the Sierra Nevada (Fig. 1) despite the well documented adverse effects of large, severe wildfire on nesting and foraging habitat and occupancy and demographic rates (Jones et al., 2016; Jones et al., 2021; Rockweit et al., 2017). However, PAM sampling occurred from May to July of 2021, immediately before two “megafires.” The Dixie and Caldor Fires burned 4,796 km², >50% of that at high severity ($\geq 75\%$ canopy mortality) from July to October of 2021, which likely caused substantial losses of spotted owl habitat in the northern and central Sierra Nevada. Thus, while our population size estimate is likely reasonable for the 2021 breeding season, the current population size may be lower. Nonetheless, declines caused by recent megafires do not obviate the near-certain barred owl-driven declines that have been averted because of experimental removal. Alleviating pressure on the California spotted owl by means of a highly effective ecosystem-scale experimental removal of an invasive competitor better enables the population to endure other pressures. Such pressures include i) large, severe wildfires that are increasingly defining forest dynamics in the Sierra Nevada and across the western U. S. (Cova et al., 2023); ii) rising temperatures that will lead to increased thermal stress in an ecosystem from which key habitat features, namely ancient trees, have been reduced in density (McGinn et al., 2023b; McGinn et al. in Review); and iii) pervasive environmental toxicants display in-utero transmission (Hofstadter et al., 2021). Even threats that pose low individual risks of extinction can have substantial additive effects over time, and synergistic effects can rapidly increase extinction risk (Kimmel et al., 2022). Mitigating one threat among several is insufficient for long-term conservation success, but it is a necessary first step – particularly when that threat has been demonstrated to cause a rapid decline in a population.

We believe our estimate of population size for California spotted

owls is reasonable for several reasons. Site occupancy was strongly and positively correlated with density under both liberal and strict occupancy criteria within four local-scale density monitoring study areas ($r = 0.99$ and 0.94 , respectively; Fig. 2). Thus, PAM-based site occupancy was predictive of density in our system despite the aforementioned sources of ecological false positives that can decouple site occupancy from density, such as movements of individuals among multiple sampling sites. Limiting passive acoustic sampling to non-adjacent grid cells, coupled with the relatively small area over which spotted owls vocalize (compared to their home range size; (Reid et al., 2022)), may have reduced this form of false detections. Alternatively, ecological false positives may have occurred frequently, but their effects were similar across the range of densities we sampled in local study areas.

Our approach for estimating population size does not require an assumption of equal densities inside versus outside density monitoring study areas so long as density-occupancy relationships estimated within local density monitoring study areas apply to the broader sampled with PAM. Thus, differences in densities among public and private lands (Bias and Gutiérrez, 1992; Hobart et al., 2019; Roberts et al., 2017) were not expected to lead to an appreciable bias in our estimate of population size for California spotted owls despite that fact that ARUs were mostly deployed on public lands. We acknowledge that the assumption of stable density-occupancy relationships cannot be tested outside of density monitoring study areas, but the relative consistency we observed in density-occupancy ratios (Fig. 2c and 2e) across the gradient of spotted owl densities in the four density study areas suggests that the assumption was reasonable. Further, site occupancy outside of the local density study areas was similar to site occupancy inside of the local study areas with the lowest occupancy rates (Table 2). However, additional work that evaluates stability in occupancy-density relationships over time is needed to ascertain whether our approach can provide reasonable estimates of temporal trends in regional population size.

Our ecosystem-scale, bioacoustics approach for monitoring spotted owl population size rather than site occupancy presumably reduces the effect of ecological false positives and should therefore, over time, improve our understanding of how the California spotted owl is responding to environmental change. Prompt annual population assessments will enable a more rapidly adaptive approach to ecosystem management, but continued coordination among survey efforts (i.e., PAM and active surveys) will be essential to maintaining data quality. It may be possible to better elucidate habitat relationships by using spotted owls' sex-specific vocalizations to implement multi-state occupancy models that relate pair occupancy to particular habitat features (Appel et al., 2023; Wood et al., 2020). Identification of demographically important vocalizations, notably juvenile begging (McGinn et al., 2023a), could further enhance the classification of survey cells (i.e., from occupied to single/pair to single/pair/successful reproduction) and recover some of the demographic information that is lost when switching from local- to ecosystem-scale monitoring. Perhaps most importantly, tracking abundance over time, rather than occupancy, should provide managers with a more detailed understanding of how sensitive species respond to environmental change we incur deliberately, like forest restoration, and environmental change we have set in motion, like changing fire regimes.

The approach we have demonstrated using data from spotted owl monitoring studies would readily be applied to other species for which similar data are available. Indeed, the rise of bioacoustics as an effective population monitoring tool suggests that there is a growing need to reconcile monitoring data derived from human observers and from passive acoustic surveys (Yip et al., 2017), which may present opportunities to integrate broad-scale bioacoustic data with historical local-scale demographic data (Weldy et al., 2023). Historically, conventional human-based surveys have yielded demographically rich but spatially limited data such that localized censuses are attainable. Passive acoustic monitoring can increasingly offer data about entire biological communities at ecosystem scales (Brunk et al., 2023; Wood et al., 2021),

but the resulting animal observations can be difficult to interpret (Wood and Peery, 2022). We have shown that the two approaches can be synthesized to maximize their complementary strengths – leading to new insights for at-risk populations.

CRedit authorship contribution statement

Kevin G. Kelly: Conceptualization, Investigation, Resources, Project administration, Writing – original draft, Writing – review & editing. **Connor M. Wood:** Methodology, Writing – original draft, Writing – review & editing. **Kate McGinn:** Formal analysis, Methodology, Visualization, Data curation, Writing – original draft, Writing – review & editing. **H. Anu Kramer:** Methodology, Visualization, Writing – review & editing. **Sarah C. Sawyer:** Funding acquisition, Supervision, Writing – review & editing. **Sheila Whitmore:** Investigation, Resources, Project administration, Writing – review & editing. **Dana Reid:** Investigation, Project administration. **Stefan Kahl:** Software, Data curation. **Aimee Reiss:** Investigation, Project administration. **Jonathan Eisman:** Investigation, Project administration. **William Berigan:** Investigation, Resources, Project administration, Writing – review & editing. **John J. Keane:** Investigation, Project administration. **Paula Shaklee:** Investigation, Project administration. **Lief Gallagher:** Investigation, Project administration. **Thomas E. Munton:** Investigation, Project administration. **Holger Klinck:** Software, Project administration. **R.J. Gutiérrez:** Investigation, Writing – review & editing. **M.Z. Peery:** Conceptualization, Supervision, Project administration, Funding acquisition, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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HABITAT SELECTION IN A CHANGING ENVIRONMENT: THE RELATIONSHIP BETWEEN HABITAT ALTERATION AND SPOTTED OWL TERRITORY OCCUPANCY AND BREEDING DISPERSAL

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Abstract. Understanding the effect of habitat alteration on avian behavior is important for understanding a species' ecology and ensuring its conservation. Therefore, we examined the relationship between Spotted Owl habitat selection and variation in habitat in the Sierra Nevada. We estimated habitat selection by modeling the probability of territory colonization (γ), territory extinction (ϵ), and breeding dispersal in relation to the amount of mature conifer forest within and among territories. Alteration of ≥ 20 ha of mature conifer forest (coniferous forest with $>70\%$ canopy cover dominated by medium [30.4–60.9 cm dbh] and large [>60.9 cm dbh] trees) within individual territories ($n = 66$) was negatively related to territory colonization and positively related to breeding dispersal probability. Although territory extinction was negatively related to the amount of mature conifer forest, it was not clear whether this relationship was due to variation of mature conifer forest within or among territories. Although modeling results for territory colonization and extinction generally supported the hypothesis that individuals are "ideal" when selecting a habitat in the sense that they settle in the highest-quality site available, we did not find a clear benefit in terms of habitat quality for Spotted Owls that exhibited breeding dispersal.

Key words: breeding dispersal, habitat alteration, habitat selection, occupancy, Spotted Owl, *Strix occidentalis*.

Selección de Hábitat en un Ambiente Cambiante: Relación entre la Alteración del Hábitat y la Ocupación de Territorios y la Dispersión Reproductiva en *Strix occidentalis*

Resumen. Entender el efecto de la alteración del hábitat sobre el comportamiento de las aves es importante para comprender la ecología de una especie y asegurar su conservación. Por lo tanto, examinamos la relación entre la selección de hábitat por parte de *Strix occidentalis* y la variación en el hábitat en la Sierra Nevada. Estimamos la selección de hábitat modelando la probabilidad de colonización de un territorio (γ), de extinción de un territorio (ϵ) y de dispersarse para reproducirse en relación con la cantidad de bosque de coníferas maduro dentro de y entre los territorios. La alteración de 20 o más hectáreas de bosque de coníferas maduro (bosque de coníferas con más del 70% de la cobertura del dosel dominada por árboles medianos [30.4–60.9 cm de DAP] y grandes [>60.9 cm de DAP]) dentro de territorios individuales ($n = 66$) se relacionó negativamente con la colonización de los territorios y positivamente con la probabilidad de dispersarse para reproducirse. Aunque la extinción de los territorios se relacionó negativamente con la cantidad de bosque de coníferas maduro, no es claro si esta relación se debió a la variación en el bosque de coníferas maduro dentro de los territorios o entre territorios. Aunque los resultados del modelado de colonización y extinción de los territorios en general apoyaron la hipótesis de que los individuos son "ideales" al seleccionar el hábitat en el sentido en que se establecen en los sitios disponibles de mayor calidad, no encontramos un beneficio claro en términos de la calidad de hábitat para los individuos que se dispersaron para reproducirse.

INTRODUCTION

The effect of habitat alteration on avian habitat choice is a key issue for conservation (Stamps

2001). If birds choose habitats to increase their fitness (Fretwell and Lucas 1969), habitat alteration, both before and after habitat selection has occurred, has the potential to affect population dynamics, particularly if the alteration affects a large area. The consequence of habitat alteration is especially relevant for territorial species that exhibit limited breeding dispersal (individuals switching territories be-

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tween breeding attempts). Breeding dispersal is likely an adaptive trait although it is thought to occur infrequently in many species (Greenwood and Harvey 1982). Inbreeding avoidance, mate choice, site choice, or social constraints have all been hypothesized to influence breeding dispersal (Greenwood 1980, Greenwood and Harvey 1982, Dobson and Jones 1985, Payne and Payne 1993). Breeding dispersal that is motivated by habitat alteration could be viewed as adaptive in terms of site choice.

The Spotted Owl (*Strix occidentalis*) is a territorial species that has high site fidelity (Gutiérrez et al. 1995, Blakesley et al. 2006). Most habitat studies have indicated that Spotted Owls preferentially select areas of mature coniferous forest (Forsman et al. 1984, Verner et al. 1992, Chatfield 2005), and that this habitat type influences their population dynamics (Franklin et al. 2000, Olson et al. 2004, Seamans 2005). Because mature coniferous forests in the western United States are prized for lumber production and are also highly susceptible to stand-replacing wildfire, alteration of this habitat type is believed to pose a threat to the owl's long-term viability (U.S. Department of Interior 1990, 1993, Verner et al. 1992). Although the alteration of mature forest is believed to have long-term negative consequences for Spotted Owls, there have been few empirical studies that have attempted to quantify how variation in the amount of mature forest may affect territory occupancy.

In this paper we examine the relationship between the amount of mature conifer forest, alteration of mature conifer forest, and Spotted Owl territory occupancy and breeding dispersal over a 15-year period. We use the term "habitat alteration" because we are not sure that all habitat changes in forest structure can be considered "habitat loss." Thus, habitat alteration represents a change from mature conifer forest to some other forest cover type by logging or wildfire. Ideally, a true experiment (i.e., random allocation of replicated experimental units to treatments) should be used to estimate cause and effect relationships between habitat alteration and Spotted Owl population processes. However, designing and executing true experiments has proven difficult because of constraints involved with endangered species management and because the scale of potential

treatments poses significant logistical challenges. Therefore, we used a combination of quasi-experimental (Cook and Campbell 1979) and observational approaches. We accepted treatment units (Spotted Owl territories) as they occurred and recorded observations of forest alteration, territory occupancy, and individual movement among territories over time. Valid inference from this approach required controlling for the confounding effect of variation in the amount of mature conifer forest among Spotted Owl territories. Because of the difficulty in controlling for this confounding effect, and because of the overall study design, we did not infer cause and effect relationships from our results. Rather, our goal was to evaluate whether: (1) alteration of mature conifer forest was correlated with immediate, short-term territory colonization probability (probability of an unoccupied territory becoming occupied), extinction probability (probability of an occupied territory becoming unoccupied), or breeding dispersal probability; (2) alteration of mature conifer forest was correlated with long-term territory colonization or extinction probability; and (3) territory colonization or extinction probability, or breeding dispersal, was related to variation in the amount of mature conifer forest among territories. We sought to increase our knowledge of the relationships between habitat alteration and Spotted Owl habitat choice. Further, our results can be used to identify specific habitat types that should be targeted by experimental studies whose goal is to test the effect of habitat alteration on Spotted Owls.

METHODS

STUDY AREA

Our 925 km² study area was located in the central Sierra Nevada, California, between the North and South Forks of the American River (Seamans et al. 2001). Within this area, we surveyed owls in a 355 km² "density study area" from 1990 to 2004. We surveyed the density study area completely for Spotted Owls each year regardless of land ownership or past occupancy by owls. In 1997 we established a "regional study area," which surrounded the density study area. The regional study area consisted of previously known owl territories and territories that were located from 1997 to

1999. Areas between owl territories in the regional study area were not completely surveyed.

The Sierra Nevada was the dominant physical feature of the area. The study area was typical of the midelevation Sierra Nevada, with mountainous terrain bisected by steep river canyons. Elevations ranged from 366 to 2401 m. Climate was Mediterranean, with cool wet winters and hot dry summers (Olson and Helms 1996). Sierran mixed conifer forest was the principal vegetation type (Sierra Nevada Ecosystem Project 1996) and was dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*) in the canopy and black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflora*), and big leaf maple (*Acer macrophyllum*) in the understory. Red fir forest was less abundant but common at higher elevations, and montane manzanita chaparral, black oak woodland, and barren rock were less abundant but locally important vegetation or landscape features (Sierra Nevada Ecosystem Project 1996).

DATA COLLECTION

Spotted Owl surveys. We surveyed Spotted Owls from 1 April to 28 August of each year from 1990 to 2004, following methods described by Franklin et al. (1996). We used two types of surveys: (1) nighttime surveys to initially locate owls in an area; and (2) daytime surveys to locate roosts and nests, and to capture, band, and assess the reproductive status of owls. Nighttime surveys consisted of imitating Spotted Owl vocalizations between dusk and dawn at established survey locations and listening for a response. Survey locations were consistent from year to year and were placed to obtain complete survey coverage of the density study area and each Spotted Owl territory in the regional study area. There were 5–12 survey points for each Spotted Owl territory, depending on the topography of the territory. A complete survey for a territory was achieved when we imitated owl territorial calls at all survey points within a territory over a four-day period without receiving a response. We conducted up to six surveys at each Spotted Owl territory to determine owl presence.

If an owl responded during a nighttime survey we conducted a daytime survey within

four days of receiving the response. We counted a nighttime survey with a response and the subsequent daytime survey as only one survey for the purpose of modeling occupancy (see below). We attempted to capture and band all Spotted Owls detected using the methods of Franklin et al. (1996). Once captured, we fitted owls with a U.S. Fish and Wildlife Service locking aluminum band on the tarsometatarsus of one leg. On the other leg we marked individuals ≥ 1 year old with a unique color-band and tab combination. We determined the sex of owls based on the pitch of their calls and their behavior (Forsman et al. 1984). We identified four age-classes based on plumage characteristics (Forsman 1981, Moen et al. 1991): juvenile; one-year-old (first-year subadult); two-year-old (second-year subadult); and ≥ 3 years old (adult).

Habitat metrics. Using a combination of aerial photographs, digital-orthophoto-quarter quadrangles, and extensive ground sampling we created a forest cover map with eight vegetation cover types for the entire density study area and a vegetation cover type map for each regional study area owl territory (Chatfield 2005, Seamans 2005). We defined vegetation cover types based on the dominant vegetation structure (tree diameter at breast height [dbh; measured 1.4 m above the forest floor on the uphill side of the tree] and canopy cover). Because Seamans (2005) estimated that the area of coniferous forest with $>70\%$ canopy cover dominated by medium (30.4–60.9 cm dbh) or large (>60.9 cm dbh) trees was the best predictor of demographic parameters for owls in our study population, we chose to examine only the effect of alteration of this vegetation type. Hereafter, we refer to this vegetation type as “mature conifer forest.” Minimum polygon size for mapping was 0.1 ha. Map accuracy for mature conifer forest was 91% (Chatfield 2005).

We estimated the total amount of each of the eight cover types within a 400 ha circle in each owl territory using the spatial analyst extension in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). This area was based on a circle with a radius of 1128 m, which was half the mean nearest neighbor distance of occupied territories in the density study area averaged over the years 1990 to 2002. We determined the center of the circle for each territory by estimating the geometric

center of all owl locations from each year the territory was occupied. The area encompassed by this circle was approximately one-quarter to one-half of the estimated home range size for Spotted Owls in the central Sierra Nevada (Laymon 1988, Call et al. 1992). Although we did not know if the entire 400 ha area was used by owls, the circles did encompass all nests and >90% of all roosts in each territory. We used the term "territory" to depict the spatial location and area for which we estimated habitat metrics because: (1) owls responded to conspecific calls from these areas during surveys; (2) the 400 ha we used for analyses contained all known nest locations of owls responding in that area; and (3) all areas surrounding the nest were vocally defended by owls during daytime surveys.

We used aerial photographs (a complete set was created approximately every four years of study) to determine the location and extent of habitat alteration. We estimated the year of timber harvest based on: (1) our own field notes; (2) USDA Forest Service harvest records; (3) University of California Berkeley Blodgett Experimental Forest harvest records; and (4) core samples of trees. We used an increment borer to extract complete cores of ≥ 4 trees immediately adjacent to a clear-cut or within a forest stand that had been thinned. We then estimated the year of harvest by locating a sustained increase in widths of tree rings, indicating reduced competition from other trees.

STATISTICAL ANALYSES

Territory occupancy. For female Spotted Owls, we estimated territory colonization (γ) and extinction (ϵ) probabilities (vital rates of territory occupancy) following MacKenzie et al. (2003). Territory colonization probability is the probability that a territory unoccupied in year $t - 1$ becomes occupied in year t , and territory extinction probability is the probability that a territory occupied in year $t - 1$ is unoccupied in year t . The probability of occupancy (ψ) in year t can be calculated from γ , ϵ , and ψ_{t-1} (MacKenzie et al. 2003) by:

$$\psi_t = \psi_{t-1}(1 - \epsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}.$$

We modeled occupancy vital rates for females only because the most appropriate method for coding data of single male versus

single female responses from surveys was not clear. Modeling females only was a good indication of pair occupancy of a territory because unpaired females were rare during our study (we located only two females in 15 years that may have been unpaired during a year). Each territory was surveyed up to six times each year for 15 years.

We estimated γ and ϵ using program MARK (White and Burnham 1999). In addition to γ and ϵ , the analytical approach we used directly estimated the proportion of territories occupied in the first year of study. We accounted for imperfect detectability of owls while modeling γ and ϵ . We examined the following temporal structures for detection probability within and among years: constant (means model); linear trend; log-linear trend; and quadratic trend. We fitted a model for each combination of these temporal structures within and among years and ranked models using Akaike's information criterion (AIC; Burnham and Anderson 1998). We used the top-ranked detection probability structure for inference regarding the effect of habitat alteration on γ and ϵ .

We created three statistical models to examine the relationship between mature conifer forest and γ and ϵ . For all models we predicted that: (1) increasing amounts of mature conifer forest would be positively related to γ and negatively related to ϵ ; and (2) alteration of mature conifer forest would be negatively related to γ and positively related to ϵ . The first model included a time-varying individual covariate that depicted the amount of mature conifer forest in each territory each year. For the second model we used a categorical treatment effect with two levels, no alteration of mature conifer forest versus >0 ha mature conifer forest altered, to estimate if alteration of mature conifer forest affected territory extinction or colonization probability the subsequent year. The treatment effect for this model occurred regardless of the amount of mature conifer forest altered. Lastly, we created a third model that hypothesized that the amount of mature conifer forest altered in an individual territory had a long-term effect on colonization and extinction probability. This latter model was essentially an interrupted time series model and included a continuous variable that depicted the total area of mature conifer forest in each territory at the beginning of the

study, and a nominal variable with three levels that depicted the size of treatment: no mature forest altered, between 0 and 20 ha altered, or ≥ 20 ha altered. Unlike the second model above, we coded the categorical treatment variable to carry the effect forward in time. For example, if a territory had 30 ha of mature forest altered in 1992, the model was coded to examine a ≥ 20 ha treatment effect on γ and ε for this territory from 1993 to 2004. Our use of a 20 ha cutoff for the treatment level was arbitrary. We also examined variations of this latter model that included the starting amount of mature forest and a nominal variable with two treatment levels (< 20 ha versus ≥ 20 ha), and an interaction between the starting area of mature forest and the categorical treatment effect. We ranked the plausibility of these competing models using AIC_c (AIC corrected for small sample size) and examined the 95% confidence intervals around the model coefficients to determine whether γ or ε was related to the area of mature conifer forest or categorical treatment effect. For analysis of γ and ε we divided the covariate depicting the total area of mature conifer forest in a territory by 260 to aid numerical optimization. Model coefficients presented in results are based on this transformation.

Breeding dispersal. Before examining the effect of habitat alteration on breeding dispersal, we first examined the probability of breeding dispersal as a function of owl sex, age, social status, and breeding status with the same approach used by Blakesley et al. (2006) in a study of Spotted Owls in the northern Sierra Nevada. We defined breeding dispersal probability as the probability that an individual moved to a different territory between year t and year $t + 1$. We created a dataset comprised of uniquely marked individuals and their dispersal histories. Each observation in the dataset consisted of a two-year period for one individual, whether the individual dispersed (switched territories) between years, and the U.S. Fish and Wildlife Service band number for the individual. We coded the binomial response as "0" for no dispersal and "1" for dispersal. We considered owl sex, age (first-year subadult, second-year subadult, or adult) during year 1, reproductive status during year 1 (successfully produced young or not), and social status (unpaired, paired, or paired but apparent death

of mate during the interval) as factors that might explain variability in dispersal probability. We also considered an interaction term between individual sex and breeding status. We analyzed data using a logistic regression (PROC GENMOD in program SAS release 8.02; SAS Institute Inc., Cary, North Carolina) and considered all possible subsets of factors. We ranked models based on their ability to explain variation in dispersal probability using QAIC (AIC corrected for overdispersion; Burnham and Anderson 1998). We calculated overdispersion of the data as χ^2 divided by the degrees of freedom. We calculated the Pearson χ^2 value using the "AGGREGATE" option of the GENMOD procedure and specified age, sex, social status, and breeding status as subpopulations.

Unlike Blakesley et al. (2006), we did not include a factor depicting territory quality in the all possible subsets modeling of dispersal probability. Instead, we included the variables in the top-ranked model from the all possible subsets regression and constructed two statistical models that were similar to the two treatment models we constructed for γ and ε : (1) a model with a categorical treatment effect with two levels, no alteration of mature conifer forest versus alteration of mature conifer forest; and (2) a model that included a continuous variable that depicted the total area of mature conifer forest in each territory during year 1, and a nominal variable with three levels that depicted the size of treatment (no mature conifer forest altered, between 0 and 20 ha altered, or ≥ 20 ha altered). We also considered variations of this latter model that included only two categorical levels of treatment (< 20 ha versus ≥ 20 ha) and an interaction term between the amount of mature conifer forest in year 1 and treatment level. For the two treatment effect models we used a repeated measures approach with generalized estimating equations (Liang and Zeger 1986) to determine if habitat modification was related to dispersal probability. Observations were repeated on individuals (i.e., the blocking factor was the individual owl) and we determined statistical significance using the 95% CI for the regression parameters.

We compared the quality of the original territory with that of the new territory for owls that dispersed. We estimated the quality of

individual territories based on their expected survival. We calculated expected survival ($E(\phi)$) following Seamans (2005) using the equation:

$$E(\hat{\phi}) = \{ \exp[1.5886 + 0.0420(\text{SEX}) + 1.5938(\text{COR57}) - 1.5602(\text{LAMT1}) - 1.2481(\text{LAMT23})] \} \div \{ 1 + \exp[1.5886 + 0.0420(\text{SEX}) + 1.5938(\text{COR57}) - 1.5602(\text{LAMT1}) - 1.2481(\text{LAMT23})] \}^{-1},$$

where SEX was a dummy variable coded 0 for females and 1 for males, COR57 was the amount (ha) of interior mature forest, LAMT1 was the natural log of the amount of hardwood forest, and LAMT23 was the natural log of the amount of pole, sapling, and brush cover types. Habitat covariates were transformed before estimation of the above equation to improve numerical optimization by dividing COR57 and AMT1 by 160, and AMT23 by 350. This model explained 93% of the variability in survival among territories (Seamans 2005). We did not consider reproduction when estimating habitat quality because the relationship between reproductive success and habitat was unclear for this population (Seamans 2005).

RESULTS

TERRITORY OCCUPANCY

We located and monitored Spotted Owls in 66 territories in our study areas from 1990 to 2004. Detection probability was constant among years, followed a log-linear trend within years, and varied between the density and regional study areas (Fig. 1). The area of mature conifer forest in individual territories ranged from 0 to 257 ha among years. Thirty-eight territories (58%) experienced some habitat alteration during our study. Habitat alteration in two territories was the result of stand-replacing wildfire while habitat alteration in all others was the result of timber harvest.

The probability of territory colonization (γ) and extinction (ϵ) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top three colonization models had essentially the same AIC_c weight (w_i), suggesting a high degree of model selection uncertainty. However, the only

model coefficient (β) with a confidence interval that did not include zero was the categorical effect of alteration of ≥ 20 ha mature conifer forest (gt20). The top model included the amount of mature conifer forest in a territory at the beginning of the study (1990) and the alteration of ≥ 20 ha of mature conifer forest. Alteration of ≥ 20 ha of mature conifer forest was negatively related to γ ; $\hat{\beta}_{\text{gt20}} = -1.16$ (95% CI = -2.02 to -0.29). The beginning amount of mature conifer forest (BMF) in a territory was positively related to γ , but had a confidence interval that included zero; $\hat{\beta}_{\text{BMF}} = 1.34$ (95% CI = -0.70 to 3.39). The top model, $\gamma(\text{BMF} + \text{gt20})$, indicated that territories in which ≥ 20 ha of mature conifer forest was altered experienced a 2.5% decline in occupancy probability.

The top territory extinction model ($\epsilon[\text{CMF}]$; Table 1) suggested that ϵ was negatively related to the amount of mature conifer forest in a territory ($\hat{\beta}_{\text{CMF}} = -2.58$, 95% CI = -4.48 to -0.68). "CMF" was a time-varying individual covariate depicting the amount of mature conifer forest in a territory. Model $\epsilon(\text{CMF})$ was four times as plausible as the second-ranked model; therefore, we chose to use model $\epsilon(\text{CMF})$ for inference. The structure of this model precluded us from separating the confounding effect of habitat alteration within territories versus variation in the amount of mature conifer forest among territories. However, if we assume that differences in mature

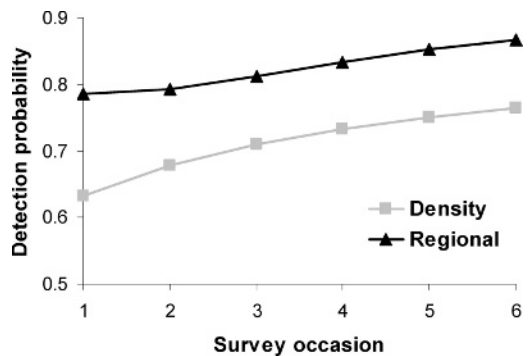


FIGURE 1. Female Spotted Owl within-year detection probability used to model territory colonization and extinction probability in the "density" and "regional" study areas in the central Sierra Nevada, 1990–2004. Each year we surveyed the complete density study area for Spotted Owls, whereas we did not survey areas between owl territories in the regional study area.

TABLE 1. Ranking of models (95% confidence set) depicting the relationship between the amount of mature conifer forest present and altered at individual territories and Spotted Owl territory colonization and extinction probability ($n = 66$ territories), and Spotted Owl breeding dispersal probability ($n = 565$), in the central Sierra Nevada, 1990–2004. Ranking of colonization and extinction models based on Akaike’s information criterion corrected for small sample size (AIC_c), while ranking of breeding dispersal models based on AIC corrected for overdispersion (QAIC). $\text{Log}(\mathcal{L})$ is the log-likelihood, K is the number of parameters, ΔAIC_c is the difference in Akaike’s information criterion from the top model, and w_i is the model weight.

Model ^a	$-2\text{log}(\mathcal{L})$	K	ΔAIC_c^b	w_i
Territory colonization probability (γ)				
$\gamma(\text{BMF} + \text{gt}20)$	3364.84	9	0.00	0.26
$\gamma(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$	3362.79	10	0.01	0.26
$\gamma(\text{BMF} + \text{ltgt}20)$	3362.87	10	0.09	0.25
$\gamma(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	3360.53	12	1.87	0.10
$\gamma(\text{CMF})$	3369.65	8	2.77	0.07
Territory extinction probability (ϵ)				
$\epsilon(\text{CMF})$	3363.84	8	0.00	0.68
$\epsilon(\text{BMF} + \text{ltgt}20)$	3362.55	10	2.81	0.17
$\epsilon(\text{BMF} + \text{gt}20)$	3366.69	9	4.90	0.06
$\epsilon(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	3361.39	12	5.77	0.04
Breeding dispersal probability (d) ^c				
$d(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$	274.83	9	0.00	0.56
$d(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	273.69	11	2.86	0.14
$d(\text{BMF} + \text{gt}20)$	279.95	8	3.12	0.12
$d(\text{gt}0)$	283.13	7	4.30	0.07
$d(.)$	285.31	6	4.48	0.06

^a Abbreviations for model parameters: BMF = individual covariate representing amount of mature conifer forest at beginning of study; CMF = time-varying individual covariate representing amount of mature conifer forest; gt20 = categorical treatment effect for mature conifer forest of <20 ha or ≥ 20 ha; ltgt20 = categorical treatment effect for mature conifer forest of 0 ha, >0 and <20 ha, or ≥ 20 ha; gt0 = categorical treatment effect of mature conifer forest of 0 ha or >0 ha.

^b AIC_c of top colonization model = 3383.07 and of top extinction model = 3385.84; QAIC of top breeding dispersal model = 292.83.

^c All breeding dispersal models included the variables Age (age of owl: 1, 2, or ≥ 3 years old); Reproduction (did owl fledge young the previous year); and Social (a combination of pair status and mate loss).

conifer forest among territories caused the variation in territory extinction probability, model $\epsilon(\text{CMF})$ suggested that occupancy probability increased approximately 1.1% for every 20 ha difference in the amount of mature conifer forest among territories.

BREEDING DISPERSAL

We observed 51 incidences of breeding dispersal among 565 owl-years (i.e., total dispersal opportunities of 159 owls in 15 years of study). Overall, 33 females switched territories (of which 12 were single or had lost their mate), while 18 males switched territories (of which 10 were single or had lost their mate). Overdispersion in the dataset was slight ($\hat{c} = 1.15$). Results from the all possible subsets modeling suggested that owl age, sex, and social status best described variation in the probability of

breeding dispersal. The only two competing models (≤ 4 $QAIC_c$ units from top model) included these same three variables plus: (1) reproductive status (repro) in the previous year; and (2) the interaction of reproductive status in the previous year and owl sex. However, model coefficients for these additional variables had confidence intervals that significantly overlapped zero ($\hat{\beta}_{\text{repro}} = -0.19$, 95% CI = -0.57 to 0.17 ; $\hat{\beta}_{\text{sex} \times \text{repro}} = 0.10$, 95% CI = -0.28 to 0.53). Therefore, we chose to use a model with owl age, sex, and social status for further inference.

The probability of breeding dispersal (d) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top-ranked model, $d(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$, suggested that d was negatively related to the area of mature conifer

TABLE 2. Parameter estimates from the top-ranked logistic regression model examining breeding dispersal probability of California Spotted Owls in the central Sierra Nevada, 1990–2004.

Parameter	Estimate	CI
Intercept	6.42	2.55 to 10.30
Age class (S1)	1.08	0.09 to 2.08
Age class (S2)	1.68	0.79 to 2.57
Sex (F)	1.00	0.24 to 1.75
Social status (Pair)	−1.30	−2.04 to −0.57
Social status (Single)	1.85	0.54 to 3.16
BMF ^a	−0.55	−0.90 to −0.20
gt20 ^b (0)	−8.61	−12.29 to −4.94
BMF*gt20 (0)	0.53	0.19 to 0.88

^a BMF = individual covariate representing amount of mature conifer forest in territory in year prior to potential or actual dispersal; transformed for analysis by dividing raw numbers by 10.

^b Categorical treatment effect for mature conifer forest coded “0” for <20 ha or “1” for ≥20 ha.

forest in a territory just prior to actual or potential dispersal, and positively related to alteration of ≥20 ha of mature conifer forest. Confidence intervals for model coefficients representing mature conifer forest and alteration of ≥20 ha of mature conifer forest did not overlap zero (Table 2). The interaction term suggested a steep increase in d in territories with <150 ha of mature conifer forest that experienced alteration of ≥20 ha of this forest type (Fig. 2). This steep increase in d was disproportional in comparison to territories with lesser amounts of this forest type that did not experience habitat alteration. For example, an individual in a territory with 100 ha of mature conifer forest (median = 99 ha for our study population) in which ≥20 ha were altered was estimated to have a much higher d than an individual in a territory that started with 80 ha yet had no mature conifer forest altered. For owl-specific variables in the top model, d was: (1) 0.09 times higher for first-year subadults than adults and 0.14 times higher for second-year subadults than adults; (2) 0.08 times higher for females; and (3) 0.11 times less for owls that were paired and did not lose their mates than for owls that were paired but lost their mates, and 0.15 times higher for unpaired owls than for paired owls who lost their mates.

Owls that switched territories apparently did not select new territories based on higher quality; only 53% of owls that switched territories moved to a territory with higher

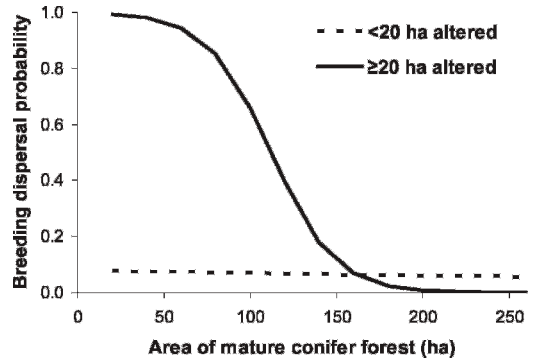


FIGURE 2. The relationship between paired female Spotted Owl breeding dispersal probability and the amount of mature conifer forest in a territory in the central Sierra Nevada, from 1990 to 2004. Dispersal probability increased rapidly at territories with <150 ha of mature conifer forest when ≥20 ha of this habitat type was altered. The x-axis represents the amount of mature conifer forest prior to actual or potential dispersal. The dashed and solid lines represent predicted dispersal probability when <20 ha or ≥20 ha of mature conifer forest were altered, respectively.

expected survival. We estimated that approximately 6% (three of 51) of owls that dispersed were unpaired after they switched territories, compared to 5% (51 of 1092) of all owls during the study. However, in the year prior to dispersal, 45% (23 of 51) of owls that switched territories were either unpaired or had lost their mate. We observed 14 breeding dispersal events in which one or both pair members switched territories and both formed a pair with a new mate.

DISCUSSION

We found that the amount of mature conifer forest was correlated with Spotted Owl habitat choice. Territories with more mature conifer forest had a higher probability of being colonized and a lower probability of becoming unoccupied. Further, alteration of mature conifer forest appeared to decrease the probability of colonization. Although we estimated that breeding dispersal was more likely when habitat alteration occurred, it was not clear if this increase or changes in other demographic processes were responsible for variability in territory extinction probability. For example, because Spotted Owl survival is correlated with the area of mature conifer forest in individual

territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Seamans 2005), it is possible that habitat alteration affected survival, which in turn increased the probability of a territory becoming unoccupied. Conversely, it is possible that habitat alteration did not result in decreased survival but in increased emigration from the study population. In a related study, Olson et al. (2005) estimated that Spotted Owl occupancy declined 5%–15% in three study areas ($n = 125$ to 146 sites) when Barred Owl (*Strix varia*) presence increased, and noted that these declines could have been the result of either death or emigration.

Our use of a categorical variable to depict the amount of habitat altered allowed us to examine the relationship between alteration of mature conifer forest and Spotted Owl habitat selection. However, our use of broad categories may not have adequately represented the effect of very large or very small changes in mature conifer forest. For example, alteration of 20 ha of mature conifer forest was considered the same as alteration of 80 ha. Although this range within the categorical habitat variables likely made detecting statistical relationships more difficult, creating more detailed categories would have resulted in small sample sizes within categories. Thus, the inference that territory extinction was not related to alteration of mature conifer forest because a categorical treatment variable was not in the top model should be made with caution. In addition, the broad range of values in the categorical variable may be partially responsible for the steep increase in dispersal probability in territories with <150 ha of mature conifer forest.

Our estimate of Spotted Owl breeding dispersal probability (9%) is similar to estimates by Forsman et al. (2002; 7%) and Blakesley et al. (2006; 7%) for other Spotted Owl populations. The relationship between breeding dispersal probability and age, sex, and social status appears to be consistent for Spotted Owls. Similar to our study, Forsman et al. (2002) and Blakesley et al. (2006) estimated that younger owls were more likely to disperse than older owls, females were more likely to disperse than males, and unpaired owls were more likely to disperse than paired owls. However, Forsman et al. (2002) and Blakesley et al. (2006) also estimated that owls that nested during the previous year were less likely to disperse than

owls that did not nest, whereas the effect of reproductive status in the previous year was poorly supported in our analysis. Prior to our study, the effect of habitat alteration on dispersal probability had not been examined in depth for the Spotted Owl, although Bond et al. (2002) examined Spotted Owl territory fidelity after wildfire and found that 11% (two of 18) of Spotted Owls switched territories the year after wildfire.

Breeding dispersal is an important life history trait that has likely evolved to increase individual fitness (Greenwood and Harvey 1982). Although the mechanisms behind the evolution of breeding dispersal are unclear, it is generally agreed that breeding dispersal can have significant effects on individual fitness and population dynamics (Greenwood and Harvey 1982, Clobert et al. 2001). Most theoretical models either predict or assume that dispersing individuals should be “ideal” when selecting a habitat, in the sense that they should settle in the highest-quality site available (Fretwell and Lucas 1969, Pulliam and Danielson 1991). Our results regarding the effect of habitat alteration on breeding dispersal, territory colonization, and territory extinction support this hypothesis. However, we did not find that Spotted Owls chose sites with more mature conifer forest, i.e., sites of higher quality, following breeding dispersal. This may indicate that the disturbance associated with habitat alteration, regardless of the extent of area altered, was an important factor motivating breeding dispersal, yet owls were either imperfect in their ability to assess habitat quality of new territories or chose a territory in which to settle based on other factors. It did appear that mate acquisition was a primary factor in selecting a territory; 43% of dispersing individuals were unpaired prior to dispersal compared to 6% after dispersal. Thus, it is surprising that we did not find that previous reproductive success was a good predictor of breeding dispersal probability. Prior reproductive success has been suggested as a primary factor determining breeding dispersal of many bird species (Wiklund 1996, Haas 1998, Catlin et al. 2005), including Spotted Owls (Forsman et al. 2002, Blakesley et al. 2006). Further, Ens et al. (1995) viewed site choice for the Oystercatcher (*Haematopus ostralegus*) as a “career decision” because of the long-term consequences for

individual fitness. We suspect a similar scenario is possible for the Spotted Owls we studied because they exhibited a relatively low probability of breeding dispersal, and because there appeared to be substantial differences among territories in terms of their quality (Seamans 2005).

Individual Spotted Owls may choose territories for something other than their intrinsic quality. We found evidence that selection of new territories by breeding individuals was not correlated with the amount of mature forest, but may have been associated with the presence of a mate. In addition, Seamans and Gutiérrez (2006) estimated that immigrants (it was unknown if they reflected breeding or natal dispersal events) appeared to use conspecifics as cues for settlement, although conspecifics may not always indicate the highest quality territory available. A further confounding factor for estimating the mechanisms responsible for selection of territories is the unknown effect anthropogenic actions have on the selective pressures responsible for breeding dispersal and habitat selection (Stamps 2001). For example, cues (e.g., the amount of mature conifer forest, the presence of a mate, or the occupancy of neighboring territories) that Spotted Owls once used to evaluate habitat quality may no longer reliably indicate quality (Hildén 1965). Our results for breeding dispersal partially support this hypothesis, while our results for territory colonization and extinction probability suggest that Spotted Owls are occupying higher quality territories.

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Sources of variability in spotted owl population growth rate: testing predictions using long-term mark–recapture data

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Abstract For long-lived iteroparous vertebrates that annually produce few young, life history theory predicts that reproductive output (R) and juvenile survival should influence temporal variation in population growth rate (λ) more than adult survival does. We examined this general prediction using 15 years of mark–recapture data from a population of California spotted owls (*Strix occidentalis occidentalis*). We found that survival of individuals ≥ 1 year old (ϕ) exhibited much less temporal variability ($\widehat{CV} = 0.04$), where CV is coefficient of variation, than R ($\widehat{CV} = 0.83$), and that R was strongly influenced by environmental stochasticity. Although λ was most sensitive ($\hat{e}$; log-transformed sensitivity) to ϕ ($\hat{e} = 0.77$), and much less sensitive to either R ($\hat{e} = 0.12$) or juvenile survival (survival rate of owls from fledging to 1 year old; $\hat{e} = 0.12$), we estimated that R contributed as much as ϕ to the observed annual variability in λ . The contribution of juvenile survival to variability in λ was proportional to its $\hat{e}$. These results are consistent with the hypothesis that natural selection may have favored the evolution of longevity in spotted owls as a strategy to increase the probability of experiencing favorable years for reproduction. Our finding that annual weather patterns that most affected R (temperature and precipitation during incubation) and ϕ (conditions during winter related to the Southern Oscillation

Index) were equally good at explaining temporal variability in λ supports the conclusion that R and ϕ were equally responsible for variability in λ . Although currently accepted conservation measures for spotted owl populations attempt to enhance survival, our results indicated that conservation measures that target R may be as successful, as long as actions do not reduce ϕ .

Keywords Elasticity · Fitness components · Life history strategy · Spotted owl · Temporal variability

Introduction

Understanding the link between a species' population dynamics and its life history strategy is important for refining theory regarding life history strategy (Caughley 1994) and for conservation planning (Mills et al. 1999). Because survival and reproductive output (R) determine individual fitness, there is a direct link between demography and the evolution of life history strategy (Stearns 1992). This relationship allows population growth rate (λ) to be considered as a measure of fitness and survival and R to be considered as fitness components (Caswell 2001). For most iteroparous vertebrates that annually produce few young, proportional changes in the survival rate of adults are thought to have a greater effect on λ than proportional changes in all other fitness components, with this relationship apparently strengthening in species with longer generation times that produce fewer young (Gaillard et al. 2000; Sæther and Bakke 2000). It has also been estimated that fitness components that have the greatest influence on λ typically exhibit the least amount of temporal variability (Gaillard et al. 1998). This phenomenon may be caused by canalization

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(a process in which developmental mechanisms reduce phenotypic variation) and should be more pronounced in traits under strong selective pressure (Stearns and Kawecki 1994).

Natural selection in long-lived species is thought to favor mechanisms that buffer adult survival against environmental variation because survival makes such a large contribution to λ (Pfister 1998; Gaillard and Yoccoz 2003). However, the influence that environmental variability has on life history evolution is debatable (e.g., Ricklefs 2000; Orzack and Tuljapurkar 2001). One prediction is that increased temporal variability in R is a consequence of individuals not breeding in a poor-quality year in order to reduce costs that would negatively affect long-term survival. Such a tradeoff to increase fitness has been predicted for organisms in general (Cohen 1966; Schaffer 1974), and may play a role in the evolution of life history (Stearns 1992). A related hypothesis is that uncertainty in juvenile (i.e., pre-reproductive) survival should increase the benefits of iteroparity and increased longevity because an increased number of reproductive attempts increase the chances of reproducing when environmental conditions become more favorable (Murphy 1968).

The spotted owl (*Strix occidentalis*) has been the subject of many population biology investigations because its conservation is linked to the management of mature conifer forests having high economic value (Gutiérrez et al. 1995). Annual variation in spotted owl demographic parameters, such as survival and R , appears to be correlated with weather (i.e., environmental stochasticity; Franklin et al. 2000; Seamans et al. 2002; LaHaye et al. 2004; Olson et al. 2004). For the northern spotted owl (*Strix occidentalis caurina*), it has been estimated that λ is most sensitive to changes in survival of adults (≥ 3 years old) compared to changes in other fitness components (Lande 1988; Noon and Biles 1990). In addition, the spotted owl is apparently similar to many other long-lived species because survival of individuals ≥ 1 year old (ϕ) exhibits the least amount of temporal variability among fitness components (Franklin et al. 2000; Seamans et al. 2002; LaHaye et al. 2004; Olson et al. 2004).

We investigated demographic rates of California spotted owls (*S. occidentalis occidentalis*) under varying weather conditions over a 15-year period in the central Sierra Nevada, California. We examined the following predictions based on life history theory:

1. Environmental variability (temporal variability in weather) has a greater effect on R than on ϕ .
2. λ is most sensitive to annual ϕ and least sensitive to R and juvenile survival.
3. ϕ exhibits the least amount of temporal variability among demographic parameters because of its importance to λ .
4. Juvenile survival and R play a larger role in determining annual variation in λ than expected based on the sensitivity of λ to these parameters.
5. If juvenile survival and R have the greatest influence on annual variation in λ there should be a strong relationship between these parameters, weather, and λ .

Our modeling of empirical data provides a direct approach for testing hypotheses stemming from life history theory and advances our understanding of variability in λ for animal populations.

Materials and methods

Study species

The spotted owl is a medium-sized owl that inhabits mountainous terrain in western North America (Gutiérrez et al. 1995). The spotted owl is territorial and monogamous (Gutiérrez et al. 1995), and generally does not switch sites after establishing a territory (Blakesley et al. 2006). Although floaters (non-territorial individuals of breeding age) exist in populations, only territorial owls are known to breed (Gutiérrez et al. 1995). Noon et al. (1992) hypothesized that because territorial spotted owls have a high annual survival rate (>0.80 ; Franklin et al. 2004), it is likely they have a long lifespan (we have observed both male and female owls as old as 17 years successfully reproducing). One-year-old spotted owls are reproductively mature although they are less likely to breed than older individuals (Gutiérrez et al. 1995). Spotted owls produce a maximum of one brood per year. A pair begins roosting together 1–2 months prior to nesting, and, on our study area, typically initiate nesting by mid-April and fledge young in June (Gutiérrez et al. 1995). Natal dispersal occurs in the fall (Forsman et al. 2002). The critical time for survival is winter (Franklin et al. 2000).

Spotted owl data collection

We surveyed spotted owls from 1 April to 28 August on a 925-km² study area located in the central Sierra Nevada, California (Seamans et al. 2001). Within this area we surveyed owls on a 355-km² Density Study

Area 1990–2004 and a 570-km² Regional Study Area 1997–2004. Each year we completely surveyed the entire Density Study Area for spotted owls while we surveyed only areas in and around known spotted owl territories on the Regional Study Area. We estimated R (the number young fledged per female) and captured and banded owls following Franklin et al. (1996). We identified four age-classes based on plumage characteristics (Forsman 1981; Moen et al. 1991): juvenile; 1 year old (first year subadult); 2 years old (second-year subadult); and ≥ 3 years old (adult).

Weather data

We used data recorded at five local weather stations to depict weather conditions on the study area: Lake Spaulding (39°19'N 120°38'W, elevation 1,572 m); Bowman Dam (39°27'N 120°39'W, elevation 1,641 m); Bald Mountain (38°54'N 120°42'W, elevation 1,341 m); Hell Hole Reservoir (39°04'N 120°25'W, elevation 1,468 m); and Blodgett Experimental Forest (38°55'N 120°40'W, elevation 1,345 m). The latter three stations were on the study area and reported hourly readings for precipitation and temperature. Stations at Lake Spaulding and Bowman Dam were approximately 10–20 km north of the study area and reported daily readings of snow depth. University of California Berkeley Blodgett Experimental Forest (Georgetown, California) supplied data for Blodgett, and other data were obtained from the Western Regional Climate Center (Reno, Nevada). In addition, we used data from the National Weather Service Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/>; accessed January 2005) to estimate the direction (El Niño- or La Niña-like conditions), strength (magnitude of the index) and phase of the Southern Oscillation. Rather than categorize periods as El Niño or La Niña, we used monthly values for the southern oscillation index (SOI) directly. The strength of the Southern Oscillation was correlated with the magnitude of the SOI value.

Weather models

We developed a priori hypotheses to examine how weather influenced survival, R , and λ (Table 1). We developed hypotheses based on our own observations of spotted owls, as well as literature on spotted owls and other avian species (*sensu* Franklin et al. 2000). We formulated hypotheses based on the effects of weather during annual periods that we hypothesized were important for spotted owls or their prey: winter (November–March), fall (September–October), sum-

mer (June–August), incubation (April), and brooding (May). We constructed a statistical model for each a priori hypothesis that represented a predicted relationship between the hypothesized weather effect and a spotted owl demographic parameter (White 2001).

We hypothesized two types of weather effects on owls: direct and indirect. We predicted that weather would directly affect spotted owls by affecting their thermoregulatory requirements and the cost and benefits of foraging activities (Newton 1998; Franklin et al. 2000). Therefore, we hypothesized that survival, R , and λ would be negatively affected by cold and wet (average daily precipitation) conditions during winter (models S1 and R3; Table 1), incubation (S2, R1), and brooding of young (R2). Rather than using mean daily maximum or minimum temperature values, we used the minimum daily energy requirements for spotted owls to depict the effect of temperature. We used the metabolic equations developed by Weathers et al. (2001) for spotted owls and hourly temperature readings to calculate the average daily resting energy expenditure below the thermoneutral zone during annual periods. We also hypothesized that heat stress during the previous summer would have a negative effect on survival because spotted owls are relatively heat intolerant (Weathers et al. 2001) and thus would have to expend more energy for cooling, which might reduce body condition heading into the winter. We quantified the direct effect of hot temperatures by calculating the average daily resting energy expenditure above the thermoneutral zone (Weathers et al. 2001) using hourly temperature readings (S13). Extreme events may also directly affect birds (Newton 1998). Therefore, we hypothesized that extended periods of precipitation during the winter would interfere with hunting and would increase energy demands or reduce foraging time to the point of starvation, thus affecting demographic parameters. The length of time to reach starvation level for spotted owls was unknown; therefore, we used the estimate from Handrich et al. (1993) of 8 days for the barn owl (*Tyto alba*). We considered the number of periods with 8 consecutive days of measurable precipitation (≥ 0.025 cm) during winter (S7, R8), and maximum number of consecutive days of measurable precipitation during winter (S8, R9) as predictive covariates. We hypothesized that average daily snow depth (S5, R6) and the number of days of snow cover during winter (S6, R7) would negatively affect demographic parameters by reducing foraging success. Lastly, we hypothesized that El Niño- or La Niña-like conditions may adversely affect spotted owl demography (S3, S4,

Table 1 A priori models used to examine the relationship between weather and spotted owl survival, reproductive output (R), and population growth rate (λ) in the central Sierra Nevada, 1990–2004. Linear and log-linear forms of each weather covar-

iate were examined unless otherwise noted. All survival models (no lag period) and R models (with a 1-year lag) were used to examine population growth rate. SOI Southern oscillation index

Hypothesis	Model ^a	Predicted effect
Apparent survival (ϕ)		
S1: Negative effects of cold temperatures and high precipitation during winter	$\beta_0 + \beta_1(T_W) + \beta_2(P_W)$	$\beta_1 < 0, \beta_2 < 0$
S2: Negative effects of cold temperatures and high precipitation during incubation, or negative effect of their interaction	$\beta_0 + \beta_1(T_I) + \beta_2(P_I) + \beta_3(T_I \times P_I)$	$\beta_1 < 0, \beta_2 < 0, \beta_3 < 0$
S3: Negative effect of both La Niña- and El Niño-like conditions during winter (quadratic form of SOI)	$\beta_0 + \beta_1(\text{SOI}_W) + \beta_2(\text{SOI}_W^2)$	$\beta_1 > 0, \beta_2 < 0$
S4: Negative effect of El Niño-like conditions during winter or negative effect of La Niña-like conditions during winter (linear SOI)	$\beta_0 + \beta_1(\text{SOI}_W)$	$\beta_1 \neq 0$
S5: Negative effect of mean daily snow depth during winter	$\beta_0 + \beta_1(\text{SNOWD}_W)$	$\beta_1 < 0$
S6: Negative effect of total number of days with snow cover during winter	$\beta_0 + \beta_1(\text{SNOWD}_W)$	$\beta_1 < 0$
S7: Negative effect of multiple periods with precipitation during winter (number of 8-day periods during winter with measurable precipitation)	$\beta_0 + \beta_1(\text{P8DAYS}_W)$	$\beta_1 < 0$
S8: Negative effect of an extended period of precipitation during winter (maximum number of consecutive days with measurable precipitation)	$\beta_0 + \beta_1(\text{PMDAYS}_W)$	$\beta_1 < 0$
S9: Positive effect of mild temperatures during fall	$\beta_0 + \beta_1(T_F)$	$\beta_1 > 0$
S10: Positive effect of warm temperatures during April previous year	$\beta_0 + \beta_1(T_A)$	$\beta_1 > 0$
S11: Positive effect of long growing season previous year (number of consecutive days minimum temperature $> 0^\circ\text{C}$, based on 7-day running average)	$\beta_0 + \beta_1(\text{GROW}_{Y-1})$	$\beta_1 > 0$
S12: Positive effect of high precipitation winter previous year	$\beta_0 + \beta_1(P_{W-1})$	$\beta_1 > 0$
S13: Negative effect of hot summer prior to winter survival period	$\beta_0 + \beta_1(T_S)$	$\beta_1 < 0$
Reproduction (R)		
R1: Negative effects of cold temperatures and high precipitation during incubation, or negative effect of their interaction	$\beta_0 + \beta_1(T_I) + \beta_2(P_I) + \beta_3(T_I \times P_I)$	$\beta_1 < 0, \beta_2 < 0, \beta_3 < 0$
R2: Negative effect of cold temperatures and high precipitation during brooding, or negative effect of their interaction	$\beta_0 + \beta_1(T_B) + \beta_2(P_B) + \beta_3(T_B \times P_B)$	$\beta_1 < 0, \beta_2 < 0, \beta_3 < 0$
R3: Negative effect of cold temperatures and high precipitation during winter preceding reproduction, or negative effect of interaction	$\beta_0 + \beta_1(T_W) + \beta_2(P_W) + \beta_3(T_W \times P_W)$	$\beta_1 < 0, \beta_2 < 0, \beta_3 < 0$
R4: Negative effect of both La Niña- and El Niño-like conditions during winter prior to reproduction (quadratic form of SOI)	$\beta_0 + \beta_1(\text{SOI}_W) + \beta_2(\text{SOI}_W^2)$	$\beta_1 > 0, \beta_2 < 0$
R5: Negative effect of El Niño- or La Niña-like conditions during winter prior to reproduction	$\beta_0 + \beta_1(\text{SOI}_W)$	$\beta_1 \neq 0$
R6: Negative effect of mean daily snow depth winter prior to reproduction	$\beta_0 + \beta_1(\text{SNOWD}_W)$	$\beta_1 < 0$
R7: Negative effect total number of days with snow cover during winter prior to reproduction	$\beta_0 + \beta_1(\text{SNOWD}_W)$	$\beta_1 < 0$
R8: Negative effect of multiple periods with precipitation during winter prior to reproduction	$\beta_0 + \beta_1(\text{P8DAYS}_W)$	$\beta_1 < 0$
R9: Negative effect of an extended period of precipitation during winter prior to reproduction	$\beta_0 + \beta_1(\text{PMDAYS}_W)$	$\beta_1 < 0$
R10: Positive effect of mild temperatures during fall previous year	$\beta_0 + \beta_1(T_F)$	$\beta_1 > 0$
R11: Positive effect of warm temperatures during April previous year	$\beta_0 + \beta_1(T_{A-1})$	$\beta_1 > 0$
R12: Positive effect of long growing season previous year	$\beta_0 + \beta_1(\text{GROW}_{Y-1})$	$\beta_1 > 0$
R13: Positive effect of high precipitation two winters prior to reproduction	$\beta_0 + \beta_1(P_{W-1})$	$\beta_1 > 0$

^a Periods during the year where covariates apply are: current winter (W), incubation (I), brooding (B), fall (F), previous April ($A-I$), summer (S), previous winter ($W-I$), previous year ($Y-I$)

R4, R5). Redmond and Koch (1991) estimated that periods preceded by 4 months of negative SOI values were strongly correlated with El Niño conditions, while periods preceded by 4 months of positive SOI values were generally considered to represent La Niña conditions. Thus, to depict conditions for winter (November–March) we averaged monthly SOI values from the previous August–November. El Niño events (negative index values) in California typically result in higher than average rainfall and warmer temperatures, while La Niña events (positive index values) are typically drier and cooler than average.

Weather may indirectly affect spotted owls by affecting vegetation growth, which would affect either prey numbers or prey availability by enhancing conditions for the owl's prey. For example, warm temperatures and increased precipitation may increase vegetative growth and seed production. *Neotoma* spp., *Peromyscus* spp., and *Glaucmys sabrinus* were the primary prey for owls on our study (Gutiérrez et al. 1995). These mammals obtained their food from seeds, vegetation, and fungi (Williams et al. 1992; Pyare and Longland 2002). Therefore, we hypothesized that average daily precipitation during the previous winter (S12, R13) would have a positive effect on vegetative growth, small mammal populations, and spotted owl demographic parameters (Seamans et al. 2002; LaHaye et al. 2004). The dominant oaks in our study area (*Quercus kelloggii* and *Quercus chrysolepis*) were 2-year oaks (pollination in spring year t , with acorns dropping in the fall year $t + 1$), and temperatures during pollination may influence their mast production (Koenig et al. 1999). A similar relationship, with the same 1-year lag, has been suggested for Ponderosa pine seed production (Maguire 1956). Therefore, we hypothesized that warm temperatures (average daily temperature) during spring (S10, R11) would positively affect the acorn crop, which would affect *Peromyscus* spp. (Gashwiler 1979) and *Neotoma* spp. (Kelly 1990) survival and reproduction, and, consequently, spotted owl demographic parameters the following year. We did not know if weather limits *G. sabrinus* populations (Rosenberg et al. 2003; Ransom and Sullivan 2004). However, research on small mammals has shown that they may take advantage of favorable conditions and expand their breeding seasons (Modi 1984; Kelly 1990). Therefore, we also hypothesized that mild conditions in the fall (S9, R10; average daily temperature) or an extended growing season (S11, R12) would positively affect the owl's winter survival or next year's R . We approximated the length of the growing season by calculat-

ing the number of consecutive days with minimum temperature $>0^{\circ}\text{C}$, based on 7-day running averages.

Estimation of demographic parameters and their variability

We considered each weather-related hypothesis (Table 1) as an a priori model representing the effect of specific environmental conditions on variation in survival and R . We modeled λ using all a priori survival and R models. For each R model used to model λ we used covariate values from the previous year. For example, precipitation and temperature during incubation in 2000 were used to estimate R in 2000 (Table 1; model R1) and λ in the interval 2000–2001. We considered all of the a priori hypotheses for each parameter to be competing models. We did not use highly correlated ($r > 0.5$) weather covariates in the same model. We used an information theoretic approach to compare models based on their relative ability to explain variation in the data (Burnham and Anderson 1998). We ranked competing models that represented the relationship between weather and demographic parameters using Akaike's information criteria (AIC) corrected for small sample size (AIC_C). We addressed uncertainty in selecting the best models by calculating AIC_C weights (w_i ; Burnham and Anderson 1998).

We used an open population Cormack–Jolly–Seber model in program MARK (White and Burnham 1999) to estimate annual “apparent survival” of owls ≥ 1 year old (ϕ) using the capture histories of subadult and adult females and males from 1990 to 2004. We considered our estimates of survival to be “apparent survival” because they represented the probability of a banded owl surviving and remaining within the study population. We could not model juvenile survival because too few of the banded juveniles were recaptured in subsequent years (Franklin et al. 2004). Before analysis of weather models we examined the survival dataset for overdispersion ($\hat{c}$) using a global model in program Release (Burnham et al. 1987). We found no evidence of overdispersion ($\hat{c} < 1$). When estimating ϕ and recapture rates, we considered age (AGE; subadult or adult), sex (SEX), and time [each interval is a categorical variable (t), linear time trend (lt), or quadratic time trend] constraints in addition to weather covariates. We combined 1- and 2-year-olds into one age-class (subadults) after modeling them separately and finding no difference in survival. We first used a global structure (AGE, SEX, and categorical time) on ϕ and modeled recapture rates with the following constraints: intercept only, age, sex, time, and annual

survey effort (Franklin et al. 2004). Annual survey effort was the number of total hours within a year dedicated to capturing and recapturing owls and assessing reproduction. We selected the best recapture rate structure based on AIC_C , and then used this structure for all subsequent ϕ models. We next modeled ϕ using only sex, age, and time constraints, and their interactions. We then used the best sex and age structures when modeling weather covariates. We estimated total temporal process variation ($\hat{\sigma}_{\text{temporal}}^2$; the natural variation in annual survival rates attributable to differences among years) using an intercept-only model in the variance components module of program MARK (Burnham and White 2002). We assessed the performance of our best weather model by examining the change in $\hat{\sigma}_{\text{temporal}}^2$ between the intercept-only model and best weather model.

We estimated annual R (annual number young fledged per female) from 1990 to 2004 using PROC MIXED in program SAS (Littell et al. 1996). We used a mixed model ANOVA (Searle et al. 1992) with the number of young fledged as the dependent variable, age of female [AGE; subadult (1 and 2 year olds) or adult (≥ 3 years old)] and weather covariates as fixed effects, year as a random effect, and individual female as a random blocking factor. We considered year as the experimental unit in a repeated measures design (Franklin et al. 2000, 2004). We first used restricted maximum likelihood estimation to model the following block covariance structures: log-linear variance; compound symmetric; first order autoregressive; and heterogeneous autoregressive (Littell et al. 1996). We selected the best covariance structure based on AIC_C , and then used this structure with full maximum likelihood estimation to model fixed effects. We estimated $\hat{\sigma}_{\text{temporal}}^2$ of R using an intercept-only model within the restricted maximum likelihood approach. Temporal process variation explained by a weather model was calculated as $\hat{\sigma}_{\text{temporal}}^2$ from an intercept-only model minus $\hat{\sigma}_{\text{temporal}}^2$ from the weather model (i.e., the remaining process variation left unexplained by the weather covariates).

To examine the effect of weather on λ , we estimated the annual rate of population change in territorial owls (λ_t) directly from spotted owl capture histories using Pradel's "reverse-time" model (Pradel 1996; Nichols and Hines 2002; Franklin et al. 2004) in program MARK. We use the acronym " $\hat{\lambda}_t$ " to distinguish the Pradel estimate from the estimate of λ using a projection matrix (see below). We only used the capture histories of individuals on the Density Study Area to estimate λ_t . We used the best recapture rate structure from our survival analysis and a categorical time

structure on ϕ for all λ_t modeling. We did not include the first estimable λ in models because of a possible learning effect by observers (Franklin et al. 2004). In addition to weather covariates, we also examined categorical time (each interval is a categorical variable; t), $1t$, and quadratic time trend constraints on λ_t . We estimated temporal process variation ($\hat{\sigma}_{\text{temporal}}^2$) using an intercept-only model in the variance components module of program MARK (Burnham and White 2002). We assessed the performance of our best weather model by examining the change in $\hat{\sigma}_{\text{temporal}}^2$ between the intercept-only model and best weather model.

Contributions of demographic parameters to λ and variability in λ

We used a single-sex projection matrix to estimate asymptotic λ , which allowed for estimation of the proportional contribution of each matrix element to λ using elasticity analysis (Caswell 2001). Elasticities can be used for comparison of life history strategies within and among taxa (de Kroon et al. 2000) and for assessing the relative contribution of fitness components to variation in λ (van Tienderen 1995; Horvitz et al. 1997). We used the acronym " $\hat{\lambda}_{\text{PM}}$ " to identify the estimate of λ using the projection matrix. We used our estimates of R and ϕ as matrix elements. We divided R by 2 to estimate the number of female offspring per female. We did not have an estimate of juvenile survival so we used an estimate from a study of California spotted owls in the San Bernardino Mountains (LaHaye et al. 2004; $\phi_{\text{juvenile}} = 0.368$). The juvenile age-class used by LaHaye et al. (2004) began at the time of fledging and ended the first spring after fledging.

We assessed the sensitivity of λ to individual fitness components by calculating the elasticity ($\hat{e}$) of model parameters (Benton and Grant 1996; Caswell 2001). The relative sensitivity of $\hat{\lambda}_{\text{PM}}$ to variation in fitness components (i.e., R , ϕ , and juvenile survival) depends on both the $\hat{e}$ and the temporal variation of the fitness components (Horvitz et al. 1997; Gaillard et al. 2000). For example, ϕ may have high elasticity but have less importance in determining annual changes in λ than components with lower elasticity yet greater temporal variability. We estimated the variance of λ [$\text{var}(\lambda)$] following Tuljapurkar and Caswell (1997):

$$\text{var}(\lambda) = \sum_{ij} \hat{e}_{ij} \times \widehat{\text{CV}}_{ij}^2$$

where $\hat{e}_{ij}$ was the elasticity of the element (θ) in row i and column j in the matrix, and CV was the element's

Table 2 Models (95% confidence set) relating spotted owl survival, R , and λ to weather in the central Sierra Nevada, 1990–2004. Models are ordered by Akaike's information criteria (AIC) corrected for small sample size (AIC_C), and w_i is the model weight. Acronym in parentheses following model ranking refers to model description in Table 1. SEX Sex effect, AGE age effect (1 and 2 year olds versus individuals ≥ 3 years old); for other abbreviations, see Table 1

Model	AIC _C	ΔAIC_C	w_i	Model likelihood	K^a	Model coefficients					
						β_0	β_1	β_2	β_3	β_4	β_5
Apparent survival (ϕ)											
1. (S5) $\beta_0 + \beta_1[\text{LN}(\text{SNOWD}_w)] + \beta_2(\text{SEX})$	1,192.2	0.0	0.186	1.000	5	0.76	3.46	0.37	–	–	–
2. $\beta_0 + \beta_1(\text{SEX})$	1,193.8	1.5	0.086	0.461	4	1.36	0.37	–	–	–	–
3. (S3) $\beta_0 + \beta_1(\text{SOI}_w) + \beta_2(\text{SOI}_w^2) + \beta_3(\text{SEX})$	1,193.9	1.7	0.080	0.428	6	1.46	-0.16	-0.07	0.36	–	–
4. (S9) $\beta_0 + \beta_1(T_F) + \beta_2(\text{SEX})$	1,194.7	2.5	0.053	0.284	5	-0.61	7.08	0.37	–	–	–
5. (S2 + S4) $\beta_0 + \beta_1(\text{SOI}_w) + \beta_2(T_1) + \beta_3(P_1) + \beta_4(T_1 \times P_1) + \beta_5(\text{SEX})$	1,194.9	2.6	0.050	0.267	7	2.02	-0.14	-0.01	-4.85	0.03	0.37
6. (S6) $\beta_0 + \beta_1(\text{SNOWC}_w) + \beta_2(\text{SEX})$	1,195.0	2.8	0.045	0.244	5	0.81	0.68	0.37	–	–	–
7. (S10) $\beta_0 + \beta_1(T_A) + \beta_2(\text{SEX})$	1,195.2	2.9	0.041	0.271	5	2.37	-0.02	0.37	–	–	–
8. β_0 (intercept only)	1,196.1	3.9	0.027	0.142	3	1.52	–	–	–	–	–
(R)											
1. (R1 + R5) $\beta_0 + \beta_1(\text{SOI}_w) + \beta_2(T_1) + \beta_3(P_1) + \beta_4(T_1 \times P_1) + \beta_5(\text{AGE})$	968.0	0.0	0.996	1.000	23	2.89	-0.25	-0.02	-9.13	0.06	0.18
2. (R1 + R7) $\beta_0 + \beta_1(\text{SNOWC}_w) + \beta_2(T_1) + \beta_3(P_1) + \beta_4(T_1 \times P_1) + \beta_5(\text{AGE})$	982.1	14.1	0.001	0.001	23	2.26	0.01	-0.03	-7.07	0.06	0.18
3. $\beta_0 + \beta_1(\text{AGE})$	986.4	18.4	0.000	0.000	19	0.59	0.18	–	–	–	–
λ											
1. $\beta_0 + \beta_1$ (linear trend)	1,881.8	0.0	0.265	1.000	19	0.12	-0.02	–	–	–	–
2. (S3) $\beta_0 + \beta_1(\text{SOI}_w) + \beta_2(\text{SOI}_w^2)$	1,882.1	0.3	0.230	0.866	20	0.03	-0.07	-0.03	–	–	–
3. (S3 + R1) $\beta_0 + \beta_1(\text{SOI}_w) + \beta_2(\text{SOI}_w^2) + \beta_3(T_1) + \beta_4(P_1)$	1,882.2	0.4	0.218	0.823	22	0.41	-0.07	-0.03	-0.69	0.53	–
4. (S12) $\beta_0 + \beta_1[\text{LN}(P_{w-1})]$	1,884.4	2.7	0.070	0.265	19	0.16	-0.56	–	–	–	–
5. β_0 (intercept only)	1,885.8	4.1	0.028	0.107	18	0.00	–	–	–	–	–
6. (S5) $\beta_0 + \beta_1(\text{SNOWD}_w)$	1,886.4	4.7	0.026	0.097	19	-0.10	0.19	–	–	–	–
7. (R1) $\beta_0 + \beta_1(T_1) + \beta_2(P_1)$	1,886.5	4.7	0.025	0.095	20	0.37	-0.63	0.36	–	–	–

^a Number of estimable parameters in model

Table 3 Estimates of temporal variance components of spotted owl demographic parameters (θ) in the central Sierra Nevada, 1990–2004. For other abbreviations, see Table 1

	Apparent survival (φ)	R	λ
$\hat{\theta}^a$	0.8212	0.6392	1.0009
$SE(\hat{\theta})$	0.0129	0.0763	0.0225
$\hat{\sigma}_{\text{temporal}}^2$	0.0009	0.2796	0.0031
	(0, 0.0062) ^b	(0.1447, 0.7504)	(0, 0.0236)
$(CV(\hat{\theta}))$	0.0368	0.8272	0.0556
$\hat{\sigma}_{\text{model}}^2$ ^c	0.0005	0.2350	0.0031
$\hat{\sigma}_{\text{residual}}^2$	0.0004	0.0446	0.0000
	(0, 0.0064) ^b	(0.0166, 0.3176)	(0, 0.0179)
%Explained ^d	60	84	100

^a Mean point estimate for parameter

^b 95% confidence interval

^c Amount of $\hat{\sigma}_{\text{temporal}}^2$ explained by best weather model

^d Percentage of $\hat{\sigma}_{\text{temporal}}^2$ explained by top weather model

coefficient of variation, $\hat{\sigma}_{\text{temporal}}/\theta$. We presented the contribution of each matrix element as a proportion of the total $\text{var}(\lambda)$, thus, the sum of contributions equals 1.0. For juvenile survival, we estimated $\hat{\sigma}_{\text{temporal}}^2$ as the variance of the minimum known proportion surviving from each cohort from the San Bernardino Mountains ($CV = 0.41$). We used the raw data from the LaHaye et al. (2004) study and calculated the minimum known proportion surviving for year t as the proportion of fledglings banded in year t that were subsequently recaptured in a later year (R. J. Gutiérrez, unpublished data). We considered this an approximation of temporal variability in juvenile survival, and, in an exploratory analysis, examined values 50% above and below this value to assess their influence on $\text{var}(\lambda)$.

Table 4 Percentage of temporal variation in λ accounted for by life history characteristics (matrix elements) used in projection matrix to estimate λ of spotted owls in the central Sierra Nevada, 1990–2004. Percentages estimated using a range of values for temporal variation in juvenile survival

Matrix element	$\hat{\epsilon}^a$	Percentage of variability in λ accounted for when coefficient of variation for juvenile survival is:		
		0.21	0.41	0.61
Reproductive output ($\hat{R}^b$)	0.12	51.8	47.5	41.7
Juvenile survival ($\hat{\phi}_j$)	0.12	4.3	12.4	23.0
Survival >1 year olds ($\hat{\phi}$)	0.77	43.9	40.2	35.3

^a Matrix element elasticity

^b Mean estimate of the parameter over all years

Results

Weather and survival

During the 15-year study we identified 246 individuals ≥ 1 year old on 924 capture occasions (does not include multiple captures of the same individual in the same year). The best recapture rate structure indicated recapture rates varied by annual survey effort. We used this structure for all subsequent φ modeling. The capture–recapture data best supported a model that included a sex effect, suggesting males had higher φ than females. Thus, we considered a sex effect on φ in subsequent modeling with weather covariates.

We examined 23 weather models that included linear and non-linear forms of weather covariates (Table 1), and 12 additional models that included weather covariates from winter plus weather covariates from the incubation period. For competing models that included the same weather covariates, one in linear and one in non-linear form, we presented only the model with the lowest AIC_C (Table 2). We estimated that there was little temporal variation in φ (Table 3). Thus, a model with sex effects only was one of three competing models (<2 AIC_C units), although a sex effect explained no temporal variation in φ . Our research question involved quantifying temporal variation in φ , so we chose to use the most competitive weather model for making further inference. However, a sex effect was supported and therefore all top weather models contained a sex effect. The best approximating weather

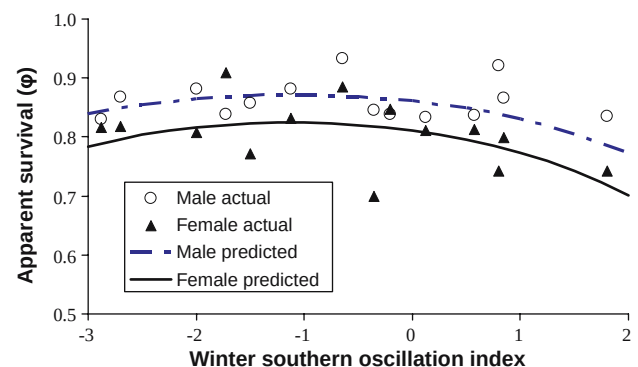


Fig. 1 Actual and predicted annual apparent survival (φ ; probability of surviving and remaining within the study population) of male and female spotted owls (*Strix occidentalis*) ≥ 1 -year-old, based on capture–recapture data for spotted owls from the central Sierra Nevada, 1990–2004. Actual values (open circles male, filled triangles female) are mean estimates for each year from a random effects means model. Predicted values (dotted lines male, solid lines female) are from a weather model containing the quadratic form of the southern oscillation index (SOI) for winter

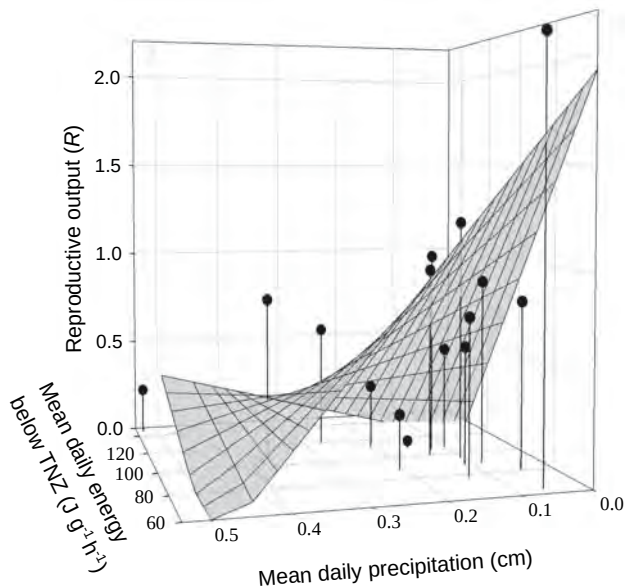


Fig. 2 Actual (filled circles) and predicted (mesh) annual reproductive output (R) for spotted owls (*S. occidentalis*) ≥ 1 year old based on R data for spotted owls from the central Sierra Nevada, 1990–2004. Actual values are mean estimates for each year from a random effects means model. Predicted values are from a weather model with mean daily precipitation and mean daily energy required for thermoregulation for temperatures below the thermoneutral zone (TNZ) during the incubation period

model indicated that ϕ varied by the log of snow depth (Table 2). However, the regression coefficient (β) for snow depth indicated a positive relationship between

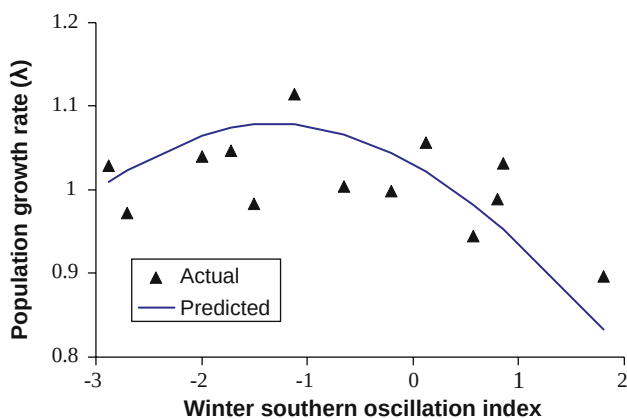


Fig. 3 Actual (filled triangles) and predicted (solid lines) annual population growth rate (λ) for spotted owls (*S. occidentalis*) ≥ 1 year old based on capture–recapture data for spotted owls from the central Sierra Nevada, 1990–2004. Actual values are mean estimates for each year from a random effects means model. Predicted values are from a weather model containing the quadratic form of the SOI for winter

snow depth and survival, which was opposite of what we hypothesized, and had confidence intervals (CIs) that included zero [$\beta(\text{SNOWD}_w) = 3.46$, $\text{CI} = -0.27$ to 7.20]. The next best weather model (Table 2) suggested a quadratic relationship between ϕ and the SOI just prior to winter, with owls experiencing higher survival when conditions were neutral; neither El Niño nor La Niña. For this model, the CI of the regression coefficient for the quadratic terms barely included zero [$\beta(\text{SOI}_w) = -0.16$, $\text{CI} = -0.32$ to 0.00 ; $\beta(\text{SOI}_w^2) = -0.07$, $\text{CI} = -0.16$ to 0.02]. Because the relationship between snow depth and ϕ was opposite of our prediction, we used a model with the quadratic form of the SOI for inference regarding explanation of temporal variance in ϕ by weather. The SOI just prior to winter explained 60% of the estimated temporal process variation in ϕ (Fig. 1, Table 3).

Weather and R

We made 425 independent annual assessments of reproduction of 125 female spotted owls from 1990 through 2004. The best covariance structure for the repeated measures was heterogeneous-autoregressive. Mean annual R ranged from 0.030 to 2.129. We first compared a means model with an age- (subadult vs. adult) structured model. This comparison suggested R varied by age of female [a model with female age (AGE) was 4.7 AIC_C units lower than an intercept-only model; $\beta(\text{AGE}) = 0.18$, $\widehat{\text{SE}} = 0.07$], thus we included female age in all subsequent models. The best weather model (Table 2) suggested that R was related to environmental conditions during incubation, and was negatively correlated to the SOI associated with the winter just prior to nesting [$\beta(\text{SOI}_w) = -0.26$, $\text{CI} = -0.33$ to -0.18]. The main effects of the best model suggested R declined with decreasing temperature (T ; i.e., increasing mean daily minimum energy expenditure) and increasing mean daily precipitation (P) during incubation [$\beta(T_1) = -0.020$, $\text{CI} = -0.030$ to -0.010 ; $\beta(P_1) = -9.132$, $\text{CI} = -14.30$ to -3.96]. The interaction term [$\beta(T_1 \times P_1) = 0.058$, $\text{CI} = 0.021$ to 0.095] suggested R was greatest when conditions during incubation were mild (i.e., low precipitation and minimum energy requirement), and also when conditions were severe (i.e., high precipitation and maximum energy requirement). This was the opposite of our predictions. Examination of predicted values from the best model indicated that increases in R during severe conditions were very slight compared to increases during mild conditions (Fig. 2). Most competing R models included the main effects of, and interaction between, precipitation and the minimum

energy requirement during incubation. In addition, models with these two covariates accounted for nearly all AIC_C weight. The best top ranked weather model explained 84% of the estimated temporal process variation in R (Table 3).

Weather and λ

The top model indicated a negative linear trend in λ_t [Table 2; $\beta(\text{It}) = -0.016$, CI = -0.028 to -0.004]. The best approximating weather model, which was identical to the best survival model, indicated that λ_t varied with the quadratic form of the SOI just prior to winter [Table 2; $\beta(\text{SOI}_W) = -0.070$, CI = -0.119 to -0.022 ; $\beta(\text{SOI}_W^2) = -0.027$, CI = -0.055 to 0.000]. This model suggested λ_t was greatest when conditions were neutral; neither El Niño nor La Niña (Fig. 3). The third ranked model also included the SOI just prior to winter and, similar to the top R model, covariates depicting conditions during the prior year incubation period (Table 2). However, while the relationship between λ and temperature during incubation agreed with our prediction [$\beta(T_I) = -0.692$, CI = -1.376 to -0.008], the covariate depicting mean daily precipitation did not [$\beta(P_I) = 0.526$, CI = -0.268 to 1.321]. The only other competing model suggested λ_t was negatively related to the log of winter precipitation from the prior interval (i.e., a 1-year lag effect) but the CI for the coefficient included zero [$\beta(P_{W-1}) = -0.561$, CI = -1.132 to 0.010]. The SOI just prior to winter explained 100% of the estimated temporal process variation in λ_t (Table 3).

Life history strategy

Use of the San Bernardino juvenile survival estimate ($\phi = 0.368$, SE = 0.038; LaHaye et al. 2004) in the matrix projection resulted in $\hat{\lambda}_{PM}$ equal to 0.950 (SE = 0.025). This growth rate was slightly lower than that estimated using the temporal symmetry capture–recapture methods (Table 3). Although the two methods for estimating population rate of change differ in their interpretation (Franklin et al. 2004; λ_t estimates if territorial individuals are being replaced while λ_{PM} estimates if territorial individuals are replacing themselves) it was not clear why they should differ. However, we felt that our use of the matrix approach was reasonable because we were interested in life history strategy and were not drawing an inference about rate of population change. We used matrix elements that depicted only two age classes (juveniles and owls ≥ 1 year old) because there was an insufficient number of individuals ≥ 1 year old and < 3 years old to

estimate $\hat{\sigma}_{\text{temporal}}^2$ in R and ϕ separately for this age-class.

The dynamics of our study population indicated that ϕ had high elasticity and relatively low temporal variability, R had low elasticity and relatively high temporal variability, and juvenile survival had both low elasticity and low temporal variability (Tables 3, 4). In particular, R had a large influence on the temporal variation in $\hat{\lambda}_{PM}$ (Table 4) relative to its elasticity. Assuming variability in juvenile survival was similar between California spotted owl populations, the contribution of juvenile survival to variability in $\hat{\lambda}_{PM}$ was proportional to its elasticity (Table 4).

Discussion

Demographic analysis is an effective tool for understanding the relative contribution of different life stages to population growth, and for measuring the strength of selective pressure on different fitness components (Stearns 1992; Caswell 2001). It is also useful, in conjunction with an understanding of the range of natural variation in parameters, for conservation planning (Mills et al. 1999; Wisdom et al. 2000). Although comprehensive predictions from life history theory are difficult to formulate because there are always some organisms that serve as exceptions, there are some strong patterns emerging that fit within the theory, such as the relationship between the temporal variation in individual parameters and their relative importance to population growth.

Relationship between weather and variability in parameter estimates

We found that ϕ was relatively high (> 0.80), which was consistent with other spotted owl studies (Seamans et al. 2002; Franklin et al. 2004; Anthony et al. 2006). Our point estimate of R , $\hat{R} = 0.64$ (range 0–2.12 young/female per year), was also within the range reported for spotted owls (Seamans et al. 2002; Franklin et al. 2004; Anthony et al. 2006). Our results supported the prediction that R was affected more by environmental stochasticity than was survival. Further, we found that our weather models explained a large portion of the temporal variability in R whereas they explained less variability in ϕ . In general, we found that the SOI was a good predictor of spotted owl ϕ and R , and that conditions during incubation also had an effect on R . We used the same analytical techniques as Franklin et al. (2000) and Olson et al. (2004) who found that wet

conditions during the nesting period (number of days with measurable precipitation) had a negative effect on R and ϕ for northern spotted owls. Franklin et al. (2000) also found support for a model that indicated increased precipitation and temperature during winter had a negative effect on ϕ . We considered this latter model as depicting conditions that were similar to those depicted by our SOI covariate. Thus, in terms of the demographic rates R and ϕ , it appeared that owls in our study responded similarly to weather conditions as northern spotted owls. We are not aware of another spotted owl paper that presented modeling of λ with weather. Our model selection results indicated that weather covariates that were good predictors of ϕ and R (the SOI just prior to winter and conditions during incubation from the previous year) were also good predictors of λ . This general agreement between weather models for λ and those of ϕ and R was predicted because λ was a function of these parameters. Yet, the covariate depicting precipitation during incubation, which appeared to be a good predictor of current year R , did not agree with our predictions for λ . This may indicate that precipitation during incubation had unpredicted effects on demographic parameters other than R . Alternatively the relationship between R and variability in λ may depend on R from years other than the prior year.

Contributions of demographic parameters to population growth and its variance

Similar to previous studies of spotted owls (Lande 1988; Noon and Biles 1990; Franklin et al. 2000) we found that λ was most sensitive to ϕ , that ϕ exhibited very low temporal variability relative to R , and that R appeared to be more strongly influenced by stochastic variability than ϕ . This was consistent with the prediction for long-lived species where natural selection favors the evolution of high adult survival with low annual variability as a response to environmental stochasticity, whereas reproductive parameters would not provide such a response (Benton and Grant 1996; Gaillard et al. 2000). One shortcoming of our approach was our inability to estimate juvenile survival with data from our study area, which was a consequence of dispersal by juveniles beyond our study area boundary. In addition, we assumed that survival, as used in the projection matrix to estimate $\hat{\lambda}_{PM}$, represented true survival, whereas survival within the Pradel model we used to estimate $\hat{\lambda}_t$ represented the probability of surviving and remaining within the study area. Although our intent was to use the projection matrix to examine spotted owl life history and not to estimate λ , accurate

estimates of vital rates were important for proper interpretation. However, the probability that ϕ was underestimated, and thus elasticity for ϕ was likely greater than we calculated, only strengthens the inference that λ was most sensitive to ϕ .

In general, our estimates of elasticity for ϕ and R placed spotted owls within the range of elasticities for the parameters reported by Sæther and Bakke (2000) for other long-lived avian species. Using methods similar to ours, Doherty et al. (2004) also found a similar pattern of parameter elasticities for red-tailed tropicbirds (*Phaethon rubricauda*), a long-lived seabird. We also found that there appeared to be a tradeoff between variance and elasticity; traits with higher elasticity had lower variation, suggesting that ϕ was canalized in spotted owls. Thus, it appeared that natural selection may have reduced variation in ϕ (Gaillard and Yoccoz 2003), which was consistent with predictions from life history theory (e.g., Gaillard et al. 1998, 2000; Pfister 1998). However, Doherty et al. (2004) found an equivocal relationship between parameter variances and sensitivities for the red-tailed tropicbird after re-scaling sensitivities to account for bounded parameters (i.e., parameters that were the result of probabilities that could only take on values between 0 and 1). We examined this possibility post hoc by scaling survival sensitivities using an arcsine transformation (Link and Doherty 2002), and we found no difference in the rankings or relative differences among sensitivities of parameters.

Although ϕ provided a baseline for the magnitude of λ (Franklin et al. 2000), we found that juvenile survival, and especially R , contributed more than previously estimated to annual variation in λ . Franklin et al. (2000) hypothesized such a relationship for the northern spotted owl but they did not test this prediction. The pattern where a demographic parameter's increasing contribution to variability in λ was associated with decreasing elasticity was consistent with what Gaillard et al. (2000) found for ungulates. In addition, the results from our modeling of λ with weather covariates also supported this pattern; the best weather model for λ suggested that weather patterns that affected both ϕ (the SOI) and R (conditions during the incubation period) were responsible for variability in λ . This result agrees with our conclusion that ϕ and R contributed approximately 40 and 47%, respectively, to variability in λ (Table 4).

It has been hypothesized that animals may use cues to assess quality of the year for breeding before breeding begins (Cohen 1967). Related to this, Gutiérrez et al. (1995) noted that there appears to be considerable variability in the number of spotted owl

pairs that attempt to nest each year. For our study population, we estimated that 0–100% of pairs attempted to nest each year (unpublished data). Thus, a possible explanation for the variability in R that we observed was that spotted owls were tracking resources and only reproducing when conditions were favorable. In addition, because we found similar responses of R and ϕ to weather covariates, this suggested R and ϕ might have shared a common response to environmental stochasticity (i.e., if conditions were poor for survival they were exceptionally poor for reproduction). However, because ϕ exhibited such low temporal variability, we hypothesize that relatively extreme weather patterns such as those caused by a strong Southern Oscillation or those of longer duration provided sufficient selective pressure on these owls that longevity was the consequence. Thus, spotted owls in the central Sierra Nevada, and probably other spotted owl subspecies, may have undergone selection for longevity in order to increase the probability of encountering more favorable years for reproduction.

Conclusions

The spotted owl is an excellent species for testing life history theory because of the many long-term, well-designed demographic studies being conducted on this bird (Franklin et al. 2004; Anthony et al. 2006). Most of these studies employ mark–recapture methodology, thus estimation of many population parameters tends to be precise and unbiased. In addition, field methods are relatively consistent across studies allowing for pooling of data which increases sample sizes. The approach we have taken here could be applied to other spotted owl studies, which would allow a rare comparison of life history strategy within a single species.

Matrix projection and direct estimation methods of λ can benefit species conservation planning by identifying specific life stages that are most likely to increase λ (Wisdom et al. 2000; Nichols and Hines 2002). Our results suggest that either ϕ or R could be targeted for improvement within the context of a conservation strategy, but not one at the expense of the other. However, habitat change may play a larger role in long-term population viability for spotted owls (Akçakaya and Raphael 1998). In particular, natural disturbances or management actions that increase the temporal variability in ϕ will likely have negative consequences for long-term population viability (Lande 1993). For management decisions affecting spotted owls in the Sierra Nevada, we suggest that nothing be done that reduces ϕ , and that habitat manipulation be directed toward increasing R . We

believe more information is needed on juvenile survival and dispersal characteristics to understand their dynamics and to clarify the relationship between habitat and λ .

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California Spotted Owl, Songbird, and Small Mammal Responses to Landscape Fuel Treatments

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A principal challenge of federal forest management has been maintaining and improving habitat for sensitive species in forests adapted to frequent, low- to moderate-intensity fire regimes that have become increasingly vulnerable to uncharacteristically severe wildfires. To enhance forest resilience, a coordinated landscape fuel network was installed in the northern Sierra Nevada, which reduced the potential for hazardous fire, despite constraints for wildlife protection that limited the extent and intensity of treatments. Small mammal and songbird communities were largely unaffected by this landscape strategy, but the number of California spotted owl territories declined. The effects on owls could have been mitigated by increasing the spatial heterogeneity of fuel treatments and by using more prescribed fire or managed wildfire to better mimic historic vegetation patterns and processes. More landscape-scale experimentation with strategies that conserve key wildlife species while also improving forest resiliency is needed, especially in response to continued warming climates.

Keywords: adaptive management, mixed conifer, restoration, Sierra Nevada, wildlife conservation

The role of wildfire in many of the world's forests that are adapted to frequent, low- to moderate-intensity fire regimes has been altered through fire exclusion, timber harvesting, livestock grazing, and urbanization (Agee and Skinner 2005, Collins et al. 2010). In the western United States, these land-use practices have affected forest structure and species composition, increasing surface fuel loads, tree density, the dominance of shade-tolerant tree species, and forest homogeneity (Hessberg et al. 2005, North et al. 2009, Chiono et al. 2012). As a consequence, many forests in the western United States are experiencing higher-severity burns—in some cases, producing large patches of tree mortality that can severely hinder the reestablishment of conifer forests (Roccaforte et al. 2012, Collins and Roller 2013). Consequently, one of the primary focuses of contemporary forest management is the treatment of fuels and vegetation to reduce fire hazards, especially as climate continues to warm (Stephens et al. 2013).

There is increased recognition that forests adapted to low- to moderate-intensity fire regimes experienced some high-severity fire (Perry et al. 2011, Marlon et al. 2012). Patchy, high-severity fire provides opportunities for early-seral habitat development and the production of large pieces of deadwood resources that are important to many wildlife species (Fontaine and Kennedy 2012). As such, forest fuel treatments should not be used to eliminate all

high-severity fire. Rather, treatments should allow for patterns of fire effects that approximate those occurring under more natural forest conditions. What little information we have on fire patterns under these conditions suggests that high-severity fire constitutes fairly low proportions of the overall burned area (5%–15%) in these forest types, which is generally aggregated in relatively small patches (smaller than 4 hectares [ha]), as is the case in the upper mixed-conifer forests in Yosemite National Park (Collins and Stephens 2010, Mallek et al. 2013).

Forest management involving habitat used by wildlife species at risk has been one of the principal challenges to US federal land managers for the last 25 years. In the Sierra Nevada, an ongoing debate is focused on several species that use old-growth forest, including the California spotted owl (CSO; *Strix occidentalis occidentalis*) and the Pacific fisher (*Martes pennanti pacifica*). Forest managers need information on appropriate levels of forest manipulations to create the desired balance between habitat conservation for wildlife populations and modifications of forests to improve their resilience to large high-severity fires that could prove more expensive and detrimental than the short-term effects of restoration treatments.

Fuel-reduction treatments reduce the potential impacts of wildfire by reducing the only aspect of the fire behavior



Figure 1. Fuel treatments implemented in the Meadow Valley project area. (a) Pretreatment mixed-conifer forest. (b) Whole-tree harvester cutting small trees (thinning from below). (c) Small trees, tree tops, and limbs being chipped and shipped by truck to a bioenergy plant to produce electricity. (d) Posttreatment defensible fuel profile zone, taken from the same perspective as in panel (a). Photographs: Keith Perchemlides.

triangle (i.e., topography, weather, fuel) that can be modified by managers: the quantity and continuity of fuel. A number of techniques are employed to reduce fire hazards, and each technique has associated effects on forest structure (Agee and Skinner 2005). Mechanical treatments can reduce stand density, basal area, and ladder and canopy fuel. To reduce accumulated surface fuel and to offset the detritus added from harvest operations, prescribed fire is sometimes used following forest thinning to reduce fire hazards, but whole-tree harvesting (i.e., complete tree removal, with the materials chipped and trucked to a processing facility; figure 1) can also effectively keep much of the harvest detritus from being added to the forest floor. Broadcast burning alone is very effective in elevating canopy base height and in reducing surface fuel (Agee and Skinner 2005).

Recent research confirms the ability of fuel treatments to alter potential fire behavior (Fulé et al. 2012) and actual wildfire effects (Safford et al. 2012). Research has also

determined that fuel-reduction treatments achieve their objectives with generally positive or neutral ecological effects (Stephens et al. 2012); however, almost all research on the effects of fuel treatments has been performed at the stand scale (10–25 ha). Given the large home ranges of many key wildlife species commonly at the crux of forest management issues in the western United States (e.g., the CSO, the northern spotted owl [*Strix occidentalis caurina*], the Pacific fisher), it is important to understand fuel-treatment impacts at larger spatial scales. This is particularly relevant because many fuel-treatment projects are being proposed—and, in a few instances, implemented—at landscape scales (15,000–40,000 ha; Ager et al. 2007, Collins et al. 2010).

Fuel treatments directly alter wildlife habitat by removing both aerial (trees) and ground (coarse wood, shrubs) cover. These altered conditions can affect both habitat suitability, which influences the number of individuals that an area can support, and habitat quality, which directly affects the fitness

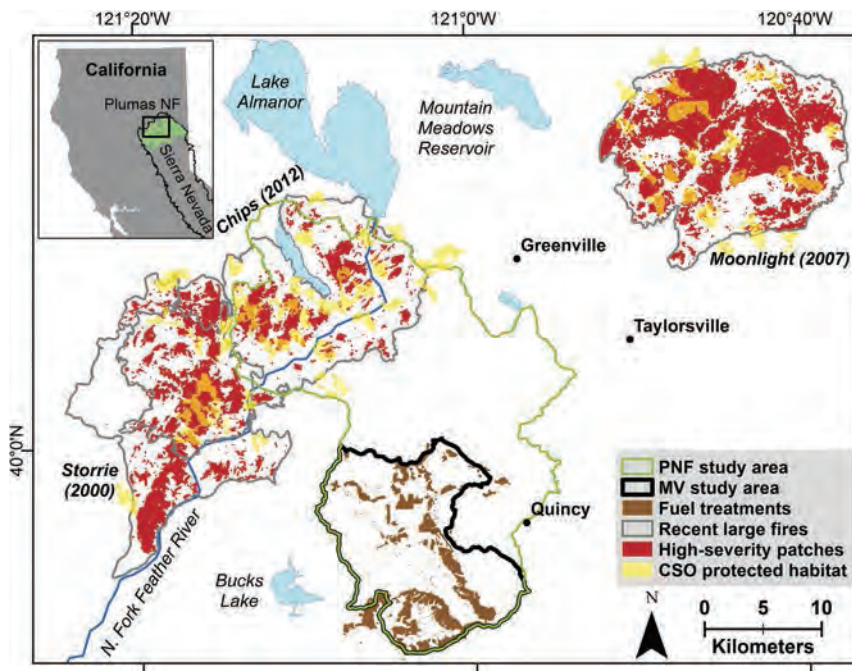


Figure 2. Meadow Valley study area with completed landscape fuel-treatment network. Recent large wildfires and the resulting patches of high-severity fire effects are also indicated. Three wildfires are shown: Storrie (2000), Moonlight (2007), and Chips (2012). These were selected on the basis of the following criteria: proximity to the study area (closer than 25 kilometers), vegetation type (conifer dominated), size (larger than 10,000 hectares), and age (since 2000). Abbreviations: CSO, California spotted owl; MV, Meadow Valley; N, north; NF, national forest; PNF, Plumas National Forest; W, west.

and productivity of individuals. Because more-suitable habitat for certain at-risk wildlife species is associated with greater aerial and ground cover, the effects of fuel treatments are generally perceived as negative. However, large patches of wildfire-caused tree mortality can also negatively affect both habitat suitability and quality (Tempel et al. in press). To the extent that fuel treatments reduce the potential for large patches of tree mortality in wildfire, there may also be an indirect benefit of fuel treatments to certain species' habitat. Finding a balance between these influences is a crucial management need.

Over the past decade, we have studied the ecological effects of one of the few completed landscape-level fuel-treatment networks in western US forests. Here, we distill the results of these efforts. We quantify change in vegetation structure and modeled fire behavior as a result of fuels treatments and assess treatment effects on the CSO, songbirds, and small mammals. Modeling studies have been published in which the trade-offs in these systems have been conceptually examined (Lee DC and Irwin 2005), but this is one of the first studies in which these questions have been empirically examined at landscape scales.

Study area and design

Our study area is located in the Meadow Valley area of the Plumas National Forest, situated in the northern Sierra

Nevada, at 39 degrees (°) 56 minutes (') north, 121°3' west (figure 2). The climate is Mediterranean, with warm, dry summers and cool, wet winters, which is when most precipitation (1050 millimeters per year; Ansley and Battles 1998) occurs. The core study area is 19,236 ha, with elevations ranging from 850–2100 meters (m). The vegetation is primarily mixed-conifer forest, consisting of white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense-cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and other less common hardwood species. White fir is the most abundant tree, although large (e.g., larger than 1 m in diameter) stumps of pines encountered frequently in the forest attest to a change in composition and structure in recent history. Red fir (*Abies magnifica*) is common at higher elevations, where it mixes with white fir. In addition, a number of species are found occasionally in or on the edge of the mixed-conifer forest, including western white pine (*Pinus monticola*) at higher elevations, lodgepole pine (*Pinus contorta* var. *murrayana*) in cold

air pockets, and western juniper (*Juniperus occidentalis*) on xeric sites. California hazelnut (*Corylus cornuta*), dogwood (*Cornus* spp.), and willow (*Salix* spp.) are found in moister riparian areas. Montane chaparral and some meadows are interspersed in the landscape. Tree density varies as a result of recent fire- and timber-management history, elevation, slope, aspect, and edaphic conditions. Historical fire occurrence, which can be inferred from fire scars recorded in tree rings, suggests that the fire regime was predominantly frequent, low- to moderate-severity fires, at intervals ranging from 7–19 years, with the last widespread fires occurring 85–125 years ago (Moody et al. 2006).

Fire activity in the last 15–20 years has been notably higher in the northern Sierra Nevada than in the rest of the range (Collins 2014). Since 2000, there have been three megafires (covering more than 10,000 ha; Stephens et al. 2014) within 25 kilometers (km) of our study area, burning a total of 73,000 ha (figure 2). These fires burned predominantly in mixed-conifer forests, encompassing approximately 60 CSO protected activity centers (figure 2). Cumulatively, 34% of the area burned in these three fires suffered high-severity fire (more than 95% dominant tree mortality; figure 3a; Miller et al. 2009). More important than the total proportion of area severely burned is the distribution of high-severity patches over the burned area, because this can limit tree seed

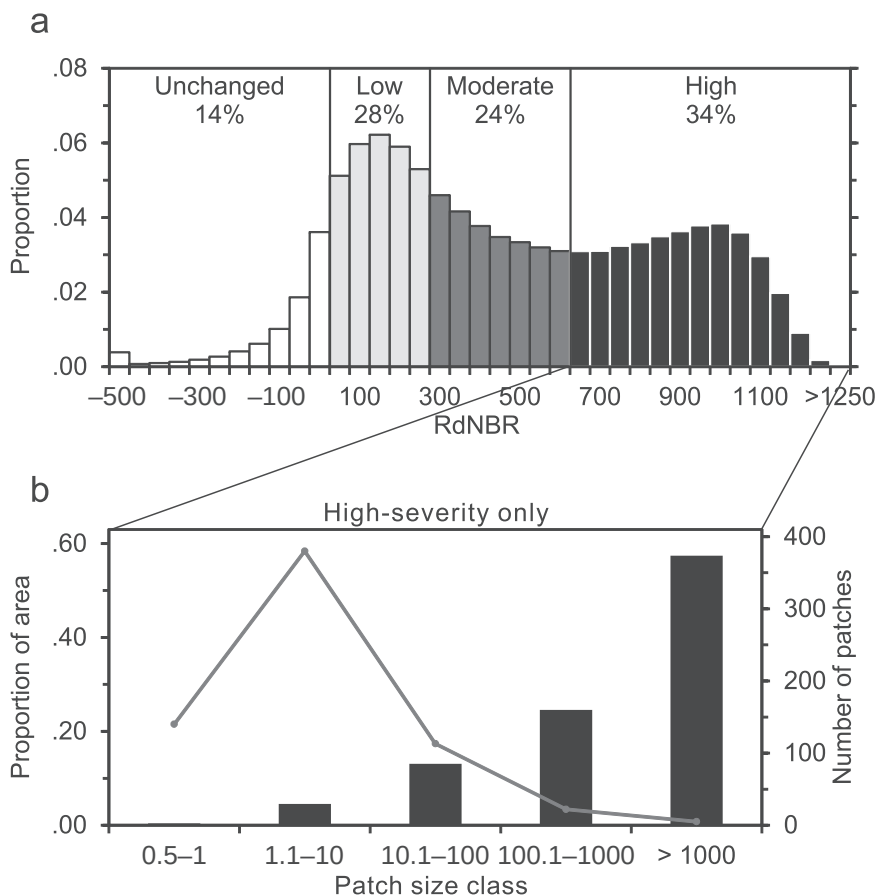


Figure 3. (a) Fire severity distribution for the three recent large fires in the Meadow Valley study area (see figure 2). The fire-severity estimates are based on the relative differenced normalized burn ratio (RdNBR; Miller and Thode 2007). (b) The proportion of total high-severity area (bars) and the number of patches (line) as a function of patch size class.

dispersal from wind and animals (Perry et al. 2011, Collins and Roller 2013). Large patches (defined here as larger than 1000 ha) accounted for a disproportionate amount of the total high-severity-fire area in the recent wildfires near the study area (figure 3b).

The projects that contributed to the fuel-treatment network are part of the larger Herger-Feinstein Quincy Library Group Pilot Project (USHR 1998). This project was directed by the US Congress to involve local communities in forest management. The project objectives included improving forest health, reducing uncharacteristic high-severity fire, conserving wildlife habitats, and stabilizing economic conditions in local communities. The projects in Meadow Valley encompassed a range of treatment types and intensities reflecting changes in regional management directions and differing land-management constraints across a complex landscape (Collins et al. 2010, Moghaddas et al. 2010). The primary fuel treatment used in Meadow Valley was defensible fuel profile zones (DFPZs), which are areas approximately 0.4–0.8 km wide in which surface, ladder, and crown fuel loads are reduced with a combination of moderate

thinning from below (Moghaddas et al. 2010) and prescribed fire treatments (figure 1).

The DFPZs were excluded from portions of the landscape set aside as reserves and from designated CSO protected activity centers, which are 121-ha areas of high-suitability nesting habitat designated by forest biologists. In addition, the project predominantly excluded all riparian habitat conservation areas or stream buffers intended to protect riparian and aquatic resources (figure 4). The activities conducted in the DFPZs were chainsaw thinning and pile burning of trees up to 30 centimeters (cm) in diameter at breast height (dbh); mastication: primarily shrubs and small trees were shredded and chipped in place, with the material left on site; prescription burning: stands were burned under conditions of moderate relative humidity and fuel moisture; and a combination of mechanical thinning and prescription burning of trees up to 51 or 76 cm dbh, depending on whether the stands were in the wildland–urban interface, using a whole-tree harvest system (figure 1) to achieve a residual canopy cover of approximately 40%, and some were underburned (Moghaddas et al. 2010). In addition to the DFPZs, group-selection treatments were implemented as part of the project. The group-selection treatments included the removal of all

conifers up to 76 cm dbh within an area of 0.8 ha, followed by residue piling and burning, then either natural regeneration or replanting to a density of 270 trees per ha with a mix of sugar pine, ponderosa pine, and Douglas-fir. These treatments collectively covered 3688 ha (3448 ha in the DFPZs, 240 ha in the group-selection treatment), or 19% of our study area, and were implemented between 2003 and 2008.

Forest structure and microclimate

Although they are designed to reduce fire hazards, forest treatments alter stand conditions directly by reducing tree density and canopy cover, and indirectly by altering microclimate conditions affecting the understory community. To assess these changes we measured stand structure, light, understory plant cover, micro-meteorological variables, soil moisture, and fuel moisture in replicated control, thinning, and group-selection treatments plots embedded within the landscape-level treatments (see Bigelow et al. 2009, 2011, Bigelow and North 2012 for detailed methods).

The mean forest canopy cover was 69% (standard deviation [SD] = 7%) before treatment; after treatment it was 53%

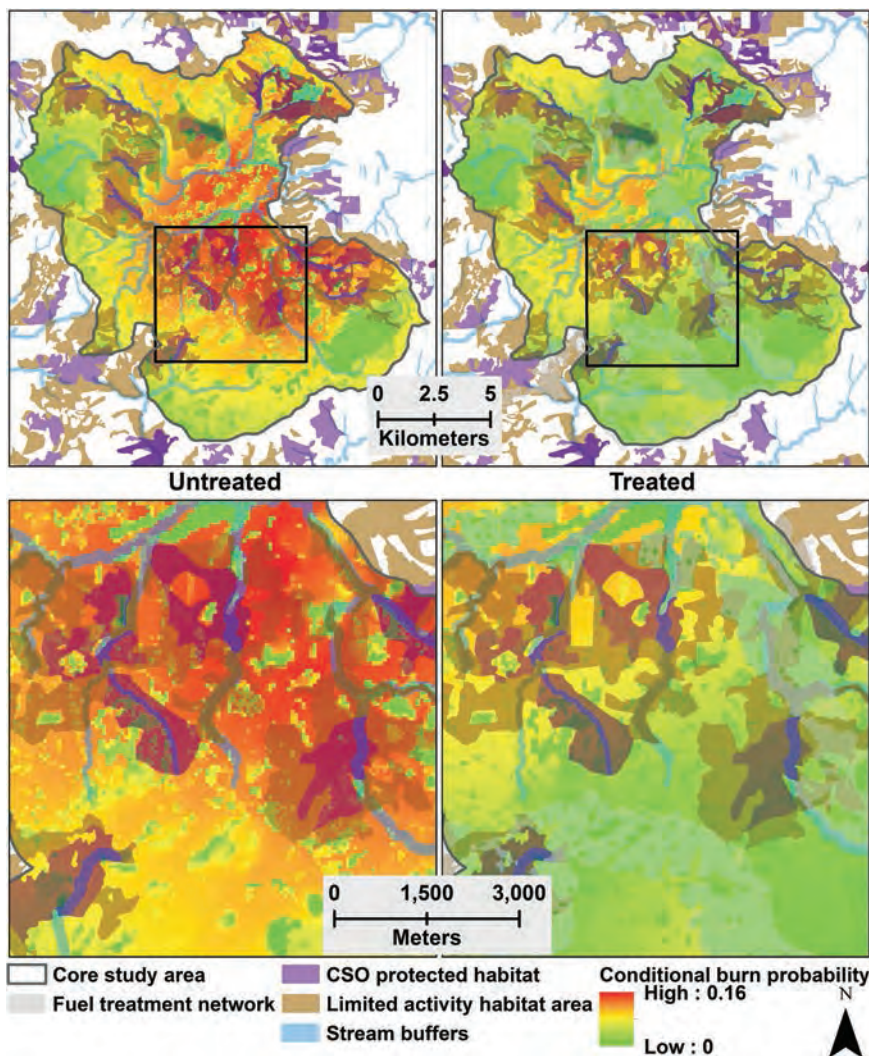


Figure 4. Hazardous fire potential across the Meadow Valley study area for the untreated and treated landscape conditions. This fire potential is based on the conditional burn probability of fire occurring with flame lengths greater than 2 meters, which is consistent with tree torching (see Collins et al. 2013 for specific details). Land designations that often limit or exclude active forest management (e.g., California spotted owl [CSO] protected habitat, stream buffers) are also shown to illustrate off-site effects of the landscape fuel-treatment network. The black square in the upper panels indicates the focal area shown in the bottom panels.

(SD = 7%) in thinned stands and 12% (SD = 6%) in the group-selection openings (Bigelow et al. 2011). These differences were reflected in growing-season understory light, which averaged 17% of full sun before treatment and increased to 26% in thinned stands and 67% in group-selection openings. Models of regenerating tree growth and light availability demonstrated that the height growth rates of shade-intolerant yellow pines (ponderosa and Jeffrey pines) and shade-tolerant white fir were equal at 41% of full sun. Light levels greater than this correlated exponentially with the height growth of the pines. The group-selection treatments provided ample light to recruit shade-intolerant species to the canopy, but only

8% of the sample locations in the thinning treatments had light levels exceeding the 41% crossover point, which suggests that these treatments would not substantially contribute to pine restoration across the landscape. An analysis of hemispherical photographs showed that the treatments decreased canopy closure following thinning. At the plot (1-ha) scale 3 years after treatment, cover of understory plant life-forms only changed under group selection ($p < .05$). Shade-tolerant conifers decreased, and graminoids, forbs, and broad-leaved trees (mainly California black oak and dogwood) increased (figure 5). There was no increase in exotic plant species cover with any of the treatments (Chiono 2012).

Changes in abiotic conditions followed differences in canopy cover for only some of the variables measured (Bigelow and North 2012). Soil moisture increased and duff moisture decreased in the group-selection treatments relative to the thinned and pretreatment conditions. Wind gust speeds (measured 2.5 m above ground) averaged 31% higher in the thinned stands than in the controls, but this was far less than the 128% increase in the group-selection openings. However, there was no difference in air temperature or relative humidity among the treatments, possibly because the increase in understory wind increased air mixing and eliminated any gradients in air temperature and humidity that might have resulted from increased irradiance.

Treatment increased within-stand variability for some vegetation and microclimate conditions but, in general, did not create the landscape-level heterogeneity characteristic of historic forest conditions in the Sierra Nevada (North et al. 2009). Mixed-conifer forests support the highest

vertebrate diversity of California forests (Verner and Boss 1980), and studies suggest that this may result from habitat variability associated with the observed range of tree species diversity, canopy cover, microclimate, and deadwood conditions (Rambo and North 2009, Ma et al. 2010, White et al. 2013). This historic forest heterogeneity appears to reflect differences in fire intensity and site productivity associated with local and large-scale changes in slope, aspect, soil, and slope position (North et al. 2009, Lydersen and North 2012). On average, more mesic sites (e.g., drainage bottoms and north-facing slopes) historically supported greater stem density, canopy cover, and tree basal area, whereas drier and

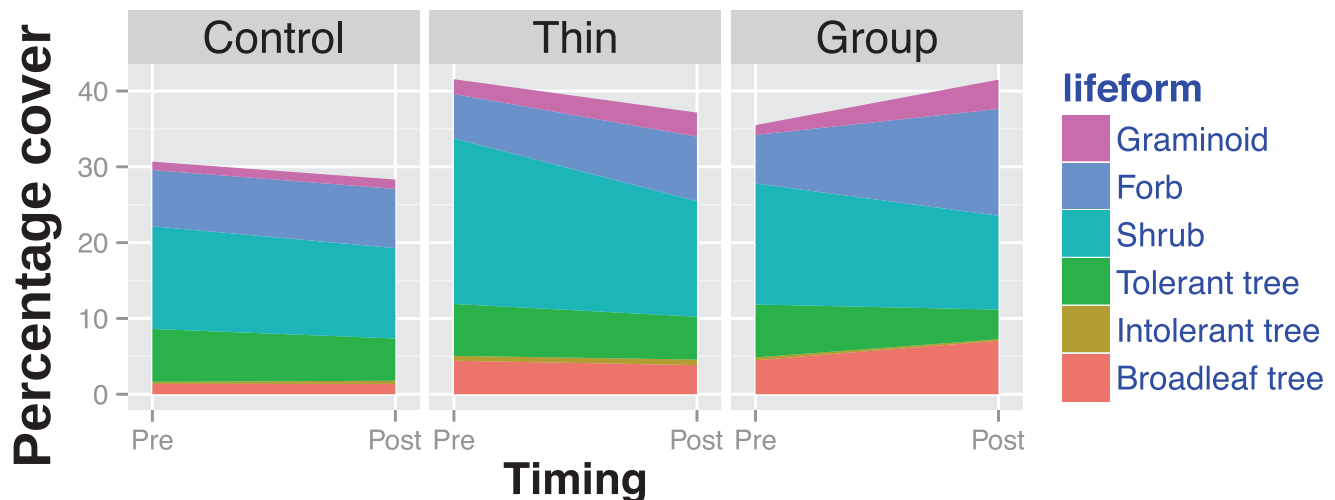


Figure 5. The percentage cover of plant life forms before (pre) and 3 years after (post) fuel-reduction thinning and group-selection treatments ($n = 300$ subplots per treatment) that were implemented in 2007 in Meadow Valley. Changes in understory cover in thinned stands were not significant ($p > .16$). Graminoids, forbs, and broadleaf trees increased and shade-tolerant conifers decreased ($p < .05$) in group selection openings.

steeper areas burned more frequently and intensely, creating more-open, pine-dominated forests (North et al. 2009). Although the Meadow Valley treatments did increase within-stand heterogeneity, they were not explicitly designed to vary with site topography or local productivity to produce this historic landscape variability.

Potential fire behavior

We employed a spatially explicit fire behavior model (Finney et al. 2007) to simulate fire spread across the Meadow Valley area. We simulated 10,000 individual fire events, with random ignition locations, and compared patterns of burn probability based on the number of times a particular area burned with the given ignition locations and simulated flame lengths for the study area prior to and following the implementation of landscape fuel treatments. Each fire event simulated burning for 240 minutes (one 4-hour burn period) under 97th percentile fuel moisture and wind conditions. These are the conditions associated with large-fire growth in this region (Collins et al. 2013). The burn period duration was selected such that the simulated fire sizes (for one burn period) approximated large-spread events observed (daily) in nearby recent wildfires (Collins et al. 2013). One of the primary assumptions with this approach is that, during these large-spread events (burn periods), fire suppression operations have limited impact, which is consistent with observed large-fire occurrence throughout the western United States (Finney et al. 2007). We summarized the burn probabilities across the Meadow Valley area into land allocations determined by the US Forest Service (USFS; Moghaddas et al. 2010).

The simulated fire behavior indicated that the landscape-scale network of DFPZs and prior fuel treatments were effective at reducing conditional burn probabilities across all

land-allocation types, except the small area of off-base lands (figure 4; Moghaddas et al. 2010). Because burn probabilities are correlated directly and positively to fire size (Finney et al. 2007), it is clear that the pretreatment landscape was more conducive to large-fire growth than the posttreatment landscape was (Moghaddas et al. 2010, Collins et al. 2013). Although the influence of the treatments on the modeled burn probabilities of each land allocation varied, the untreated stands (e.g., those designated for protected CSO habitat, riparian and aquatic resources, and reserve lands) and the remaining private and unclassified lands all experienced reduced burn probabilities from the application of fuel treatments at the landscape scale (figure 4; Moghaddas et al. 2010). A similar reduced burn severity immediately adjacent to treated areas has been reported for actual fires across the western United States (Finney et al. 2005).

The substantial reduction in both the total area and the area burned at higher flame lengths under a posttreatment wildfire scenario was notable, given that only 19% of the study area had been treated (Moghaddas et al. 2010, Collins et al. 2013). Both the orientation of the treatments (approximately orthogonal to the predominant wind direction throughout the duration of the simulated fire), and the long, continuous shape of the DFPZs resulted in potential wildfires' intersecting fuel treatments in multiple places. In addition, the treatments were somewhat concentrated in the southwestern portion of the study area (figure 2), which is the dominant direction of strong winds during the fire season (Collins et al. 2013). In combination, these factors limited the ability of the simulated fire to both circumvent the treated areas and to regain spread and intensity after encountering the treatments. These results are important to managers, because similar installations of fuel and restoration treatments are needed in many Sierra Nevada

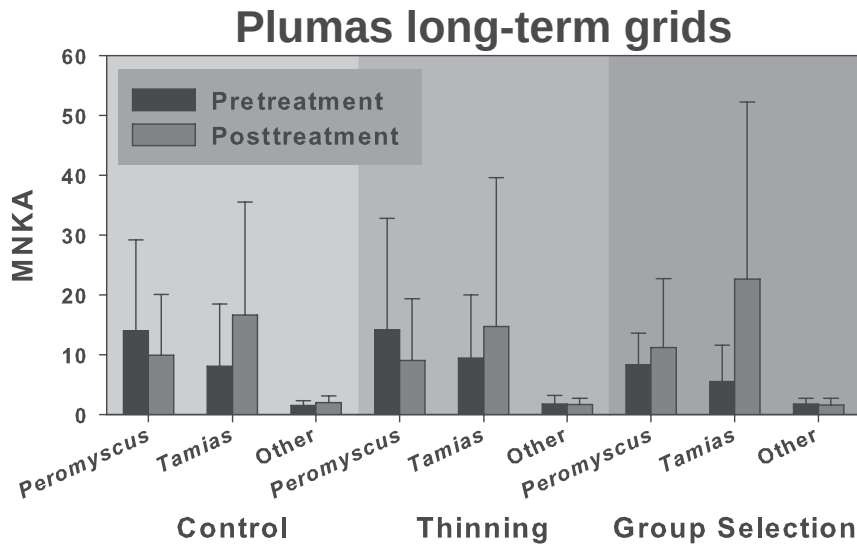


Figure 6. The mean minimum number of small animals known alive (MNKA), recorded before and after fuel treatments in the Plumas National Forest study area. For ease of presentation, we present three species groups (*Peromyscus boylii* and *Peromyscus maniculatus*; *Tamias quadrimaculatus* and *Tamias senex*; all other species; see Kelt et al. 2013 for details). The bars represent the means of the replicate sampling grids. The error bars represent the positive standard deviation.

mixed-conifer forests, where the present treatment rates are very low (North et al. 2012).

Small mammals

The northern Sierra Nevada supports a diverse fauna of small mammals that play key ecological roles as consumers, seed and fungal dispersers, and prey for both terrestrial and aerial predators (Hallett et al. 2003, Kelt et al. 2013). We studied small mammals in the Meadow Valley study area and the greater Plumas National Forest study area (PNFSA; figure 2), with a particular focus on two species that are key prey of the CSO (Gutiérrez et al. 1995): the dusky-footed woodrat (*Neotoma fuscipes*) and the northern flying squirrel (*Glaucomys sabrinus*). Results on focal species efforts have been reported elsewhere (Innes et al. 2007, Smith et al. 2011), but one finding merits emphasis here. California black oak, the primary hardwood in mixed-conifer forests, is an important habitat element for both the woodrat and the flying squirrel. Woodrat density was positively correlated with black oak density (Innes et al. 2007), and both species strongly preferred black oaks for nest sites (Innes et al. 2008, Smith et al. 2011). California black oak may be important for other wildlife species as well (Zielinski et al. 2004), but its persistence in our study landscape is in doubt. California black oak is shade intolerant, and across our study area, there were few thriving seedlings and many mature trees in decline as adjacent conifers overtopped them. California black oak trees were present in only 133 of 602 plots placed randomly in the PNFSA and were in a codominant canopy position in less than 10% of the plots in which it was present (see supplement S1).

Our broader studies on the management needs of entire small mammal assemblages included two complementary efforts. We sampled small mammals annually for 8 years on replicate trapping grids in treated and untreated mixed-conifer forests dominated by white fir in order to evaluate the responses of the small mammal community to canopy thinning (Kelt et al. 2013). To determine whether the habitat associations of the mammals in these forests were similar to those of mammals in other forest types, we expanded our efforts to include stratified random sampling of the PNFSA that encompassed the Meadow Valley study area (figure 2).

Whereas canopy thinning in white-fir-dominated mixed-conifer forests caused some significant changes in forest structure, small mammal assemblages were similar before and after canopy thinning and group selection (Kelt et al. 2013), which suggests a minimal response in the short-term to these treatments

(*contra* Suzuki and Hayes 2003, Gitzen et al. 2007, but see Carey and Wilson 2001). Although each treatment may have elicited somewhat different responses (figure 6), the variance across replicate plots eroded any such differences even in the face of the substantial variation in canopy cover. The lack of a short-term response may not be surprising in a system characterized by high interannual variation in weather and in a system dominated by generalist species; we look forward to resampling these sites after 10–15 years to assess potential longer-term responses. Because our manipulative experiment was focused on white-fir-dominated mixed-conifer forests, we pursued a more general assessment of mammalian responses to habitat and environmental variation across the entire PNFSA, capitalizing on a series of point-count transects established throughout the forest in a stratified (by forest type) random manner (see the “Songbirds” section below). We sampled eight randomly selected points on each of 74 transects to characterize how small mammals respond to broader variation in forest structure.

We assessed assemblage-wide responses to this variation with ordination (canonical correspondence and canonical correlation) and species-specific responses with multiple stepwise regression. All data were standardized (both rows and columns) by centering and normalizing, and the mammal data were log-transformed to prevent domination of the axes by common species. The results from all of the analyses were qualitatively identical to those of the Meadow Valley experimental grids, which indicates minimal responses of small mammal assemblages to variation in forest structure or composition. Although the spatial arrangement of the

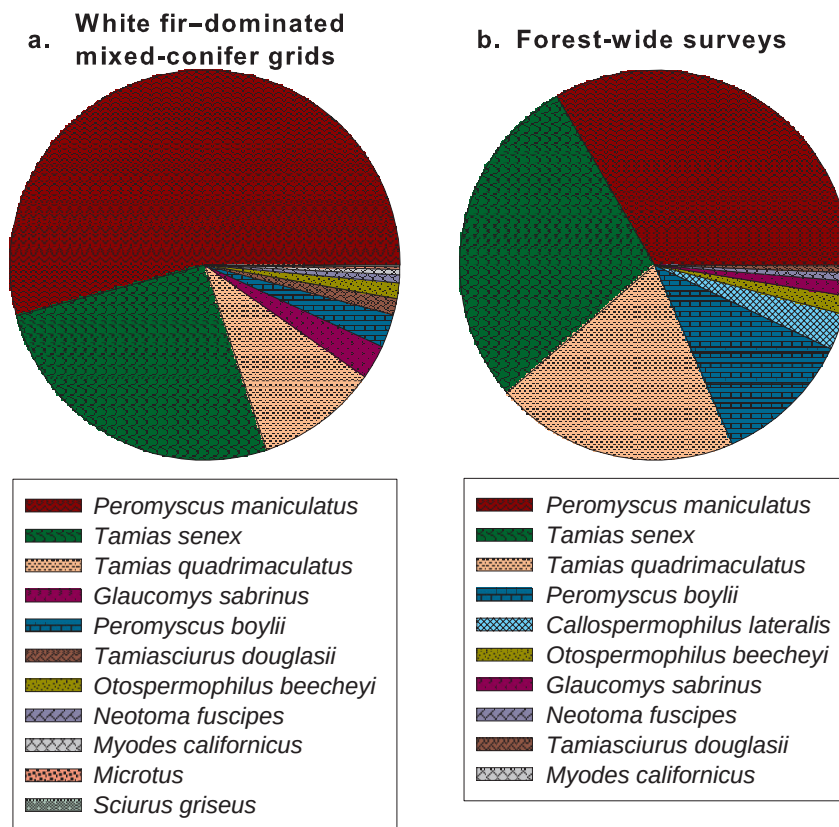


Figure 7. Small mammal composition at two spatial scales in the Plumas National Forest study area. At both scales, captures were dominated by three species. At the forest scale, only one other species was highly represented. All other species at both scales were only minor elements.

small mammal species in the ordination space was ecologically reasonable (e.g., woodrats and brush mice [*Peromyscus boylii*] associated with oaks, and chipmunks [*Tamias*] and Douglas squirrels [*Tamiasciurus douglasii*] associated with conifers and with a high basal area of trees and snags), ordination explained only a small proportion of variance in the distribution of small mammals. Similarly, regression failed to produce compelling associations for any species (or for community metrics such as species richness or diversity). The coefficients for both sets of analyses were universally low (Kelt et al. 2013).

In trapping efforts on the Meadow Valley experimental grids and in the larger PNFSA (figure 2), our captures were overwhelmingly dominated by 3–5 species (figure 7). Deer mice (*Peromyscus maniculatus*) dominated the captures at both spatial scales, comprising a full 55% of the captures on the Meadow Valley experimental grids and just over one-third of the captures in the PNFSA. Two species of chipmunk (*Tamias quadrimaculatus*, *Tamias senex*) represented an additional 40%–44%, and brush mice were an additional 8% in the PNFSA. Therefore, our samples were dominated by ecological generalists known to be tolerant of diverse habitats. What appears to be missing is a reasonable representation of species with more restricted

niche requirements. Our sampling was not designed to sample shrews (*Sorex*), but California red-backed voles (*Myodes* [formerly *Clethrionomys*] *californicus*) may have been more common in this region in the 1940s and 1950s (Kelt et al. 2013) and should have been present in our study. This species forages on fungi, however, and requires large downed woody debris and a closed-canopy forest to allow sufficient moisture retention to promote fungal growth (Alexander and Verts 1992). In 177,216 trap nights of effort, we captured only 11 *Myodes* (all but one on Meadow Valley experimental grids). Other species that are mesic habitat specialists were not sampled (e.g., *Zapus trinotatus*, *Sorex palustris*).

It is not clear whether the taxonomically depauperate assemblage structure documented in our study represents a relatively recent reduction or is more historic for this region. No data on mammal assemblages exist prior to European settlement and the beginning of widespread changes to the Sierra Nevada forest ecosystems (Merchant 2012). However, one implication of this research is that, in spite of nearly a kilometer of vertical elevation relief and diverse forest types from ponderosa pine to red fir, the current forest conditions support a relatively

homogeneous small mammal community dominated by ruderal species. It is unclear whether this reflects a legacy of fire exclusion and the resulting accumulation of fine woody debris or, perhaps, a response to a history of logging and fire suppression in this region. In contrast, other recent work in Yosemite (Roberts et al. 2008) confirms that small mammals respond strongly to variation in burn history. Taken together, these results support the fundamental ecological role of fire and broadscale forest heterogeneity in managing mixed-conifer forests in the Sierra Nevada (North et al. 2009).

Songbirds

To evaluate the effects of the Meadow Valley fuel-treatment network on songbirds, we compared avian community diversity before and after treatment. From 2004 to 2011, we surveyed the breeding community in and adjacent to Meadow Valley, using standardized point-count surveys with a 50-m radius (Ralph et al. 1995). Surveys were conducted at 51 stations where DFPZs were implemented (treated) and 201 stations where no treatments were implemented (untreated), proportional to the 19% of the study area treated. An additional 180 stations were surveyed in adjacent untreated PNFSA (figure 2) watersheds (the reference group). We used geographic information systems to establish locations

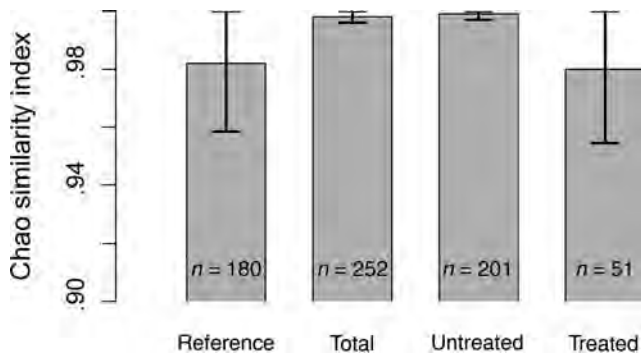


Figure 8. Chao similarity index for the avian community (60 species) before and after treatment at treated and untreated locations in the Meadow Valley study area and reference locations in the adjacent Plumas National Forest study area that also received no treatment. This metric ranges from 0–1, with 1 representing perfect similarity (all species and relative abundances shared among both samples). The error bars are 95% confidence intervals.

for the untreated and reference stations from a randomly selected origin (constrained by slopes lower than 35% and on USFS land) along a random compass bearing in a linear array of 4–12 points. The treated stations were placed within proposed DFPZ treatments across the breadth of treatment types and geography described above. All of the stations were a minimum of 250 m apart.

We surveyed all of the stations in both 2004 and 2005, prior to treatment, and for 2 years after all treatments were implemented (2010–2011). In each year, we surveyed every station twice during the peak of the breeding season (15 May–10 July), with a minimum of 10 days between visits. We limited our analyses to the 60 species breeding in upland habitats that were reliably recorded with point counts (Hutto et al. 1986). The results were summarized at the level of the three treatment groups described above (treated, untreated, reference) and for treated and untreated locations in Meadow Valley combined. For all of the analyses, we summed detections across four surveys (two visits per year over 2 years) for the pre- and posttreatment periods. We compared avian assemblages before and after the treatment with Chao–Jaccard’s similarity index (Chao et al. 2005), calculated using EstimateS (version 9.1, University of Connecticut, Storrs). Chao–Jaccard similarity is sensitive to changes in species composition and abundance. Differences in avian diversity were evaluated using the exponent of the Shannon index (Nur et al. 1999). For both analyses, 95% confidence intervals were derived from estimated standard errors from 1000 bootstrap samples.

Our results indicate little change in the Meadow Valley avian communities in response to treatment. The communities were similar across the treated, untreated, and

reference samples (figure 8). There was some evidence that the treated areas were less similar to each other than were the untreated areas, but this was not statistically significant ($p > .05$). Avian diversity (the Shannon index) was lowest for the treated sample prior to treatment but increased more in the posttreatment period, such that the Shannon index after treatment was equivalent in the treated and untreated samples (figure 9).

Evaluating the effects of fuel treatments with coarse metrics such as similarity and diversity can cause one to overlook large effects on select species (Hurteau et al. 2008). Numerous studies in seasonally dry fire-prone US forests have shown that fuel treatments can result in at least modest changes in the abundance of a broad range of avian species (Fontaine and Kennedy 2012). We recently reported that mechanical fuel-reduction treatments in the northern Sierra Nevada (including Meadow Valley) resulted in modest decreases in the abundance of a few closed-canopy associates and increases in some edge and open forest associates (Burnett et al. 2013). None of the 15 species evaluated in that study showed a significant decline following the construction of shaded fuel break DFPZ treatments—the primary treatment used in the Meadow Valley study area. With the moderate portion of the landscape treated, small differences in avian community similarity and diversity resulting from treatment, and the results from our previous evaluation of individual species response, we conclude that the effects of the Meadow Valley fuel-treatment network on the songbird community were minimal.

The fuel treatments implemented in Meadow Valley were typically less intense than those shown to result in large changes in avian communities (for a review, see Vanderwel et al. 2007). The treatments were applied to 19% of the landscape, and the prescriptions left relatively high canopy cover. Fire suppression and silvicultural practices over the last century have reduced forest heterogeneity and increased stand density (Scholl and Taylor 2010, Collins et al. 2011). In the Sierra Nevada, most fuel treatments changed the forest structure moderately from historic forest conditions (North et al. 2007). The Meadow Valley mechanical treatments primarily removed ladder fuels, which reduced crown fire potential but did not substantially alter the existing habitat features associated with songbirds, such as shrub cover or large overstory trees.

Our results should be considered in the context of the conditions that existed in the study area prior to the implementation of the landscape treatments. If an objective of these treatments was to maintain the existing avian assemblage and diversity, they appear to have been successful. However, a frequently stated objective for fuel reduction is to act as a surrogate for the natural fire regime (Stephens et al. 2012). Therefore, the maintenance of the pretreatment wildlife community may not always be the most desirable outcome in landscapes such as Meadow Valley and the larger PNFSA, where fire has been excluded for 85–125 years (Moody et al. 2006). Creating or enhancing

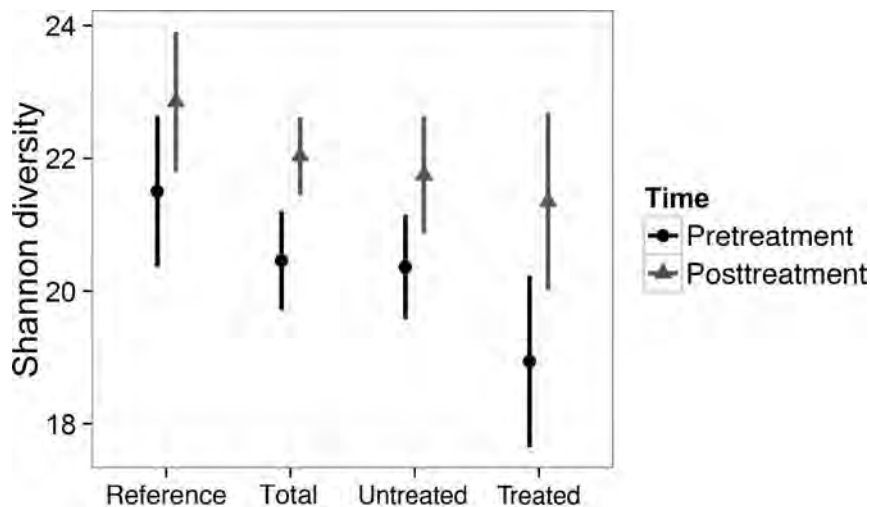


Figure 9. Shannon diversity index of avian diversity before (pretreatment) and after (posttreatment) fuel treatments were implemented at treated ($n = 51$) and untreated ($n = 201$) locations and the first two combined (Total; $n = 252$) in the Meadow Valley study area and in reference locations in the adjacent Plumas National Forest study area, which received no treatment ($n = 181$). The error bars are 95% confidence intervals.

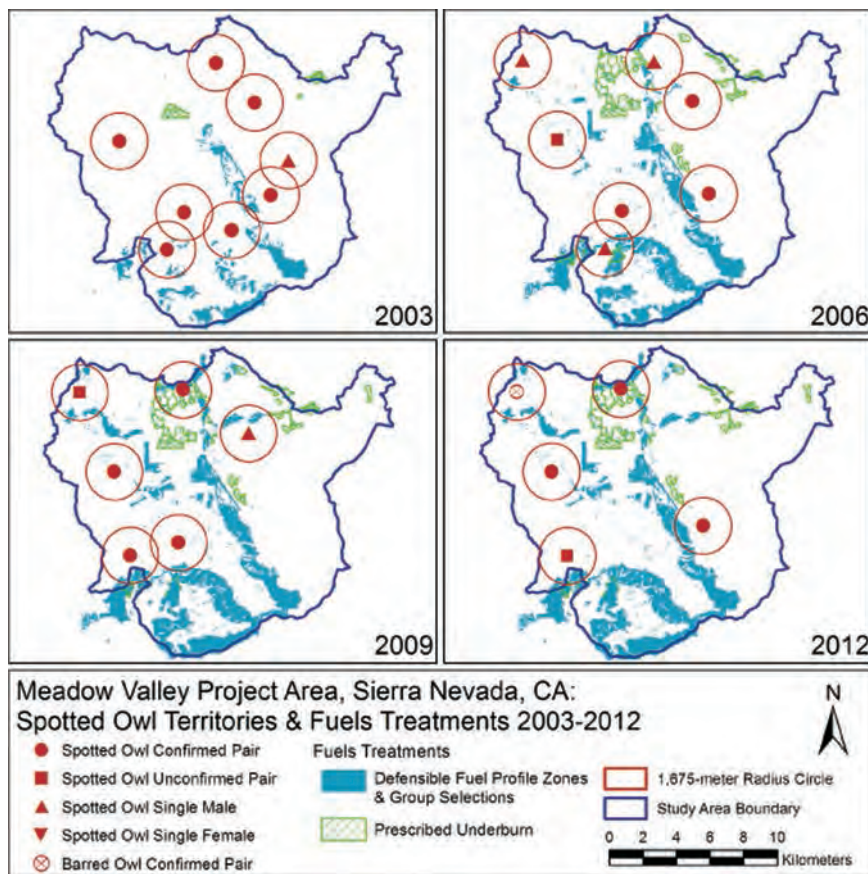


Figure 10. Distribution of territorial California spotted owl sites and landscape forest fuel treatments within the Meadow Valley study area from 2003 to 2012.

conditions for species associated with postdisturbance habitat, some of which have experienced recent declines, may be a prudent approach for achieving some biological diversity objectives (Fontaine and Kennedy 2012). If fuel-reduction treatments are to be a complementary tool to fire in achieving biological objectives, we suggest that they be designed to further increase landscape heterogeneity in fire-excluded forests.

California spotted owls

Modeling studies have projected that fuel treatments on a portion of the landscape (20%–35%) may have minimal effects on owl habitat and that the longer-term benefits of reduced wildfire risk may outweigh the short-term treatment effects on owl habitat (Ager et al. 2007, Roloff et al. 2012). However, no empirical data are available to assess the effects of landscape fuel treatments on the CSO and its habitat.

We used standardized surveys and color banding of individual owls to monitor the distribution, occupancy, survival, and reproduction of CSO sites annually across 1889 square kilometers between 2003 and 2012 in the Plumas and Lassen National Forests. Within this area, four areas were identified for implementation of landscape-scale fuel and restoration treatments. Our initial objectives were to establish baseline values for CSO distribution and abundance and to monitor the owl's response in the treated and untreated landscapes in posttreatment years. However, complete implementation of the fuel-treatment network only occurred on one (Meadow Valley; figure 10) of the four landscapes because of legal challenges to the proposed US Forest Service management strategy.

In the Meadow Valley study area, the number of territorial owl sites declined after treatment. Prior to and throughout the implementation of the treatment, the number of owl sites ranged from seven to nine. Between the final year of the DFPZ and group-selection installations (2008) and 2 years after treatment (2009–2010), the number of owl sites declined by one (six territorial sites), and by 3–4 years after treatment (2011–2012), the number of sites had declined to four—a decline of 43% from the pretreatment numbers

(figure 11). These results mirror similar declines of the CSO in the larger Plumas-Lassen CSO study area over the past 20 years (Conner et al. 2013) but suggest a greater magnitude of decline within Meadow Valley (figure 11).

The CSO nests and roosts in dense, multilayered, mature forest patches, and the adult survival and territory occupancy of these owls is positively correlated to the amounts of mature forest in core areas around CSO sites (Dugger et al. 2011). For foraging, however, the CSO uses a broader range of vegetative conditions. Radio-telemetry conducted in Meadow Valley indicates that the CSO avoids foraging in DFPZs in the first 1–2 years after fuel treatments and that the owl's home range size was positively correlated with the amount of treatment within the home range (Gallagher 2010). Barred owls (*Strix varia*) began to colonize the Meadow Valley study area in 2012 and are likely to become a threat to the CSO and a confounding factor to be accounted for in assessments of forest management effects (Keane 2014).

Although inference must be tempered from a single study, the Meadow Valley area is the first large area to receive full the implementation of landscape-scale DFPZ and group-selection treatments in which CSOs were monitored annually both before and after treatment. CSOs are long-lived (up to 20 years) and exhibit high site fidelity as adults, although there is high annual variation in reproduction associated with weather and food (Gutierrez et al. 1995). Given these traits, individual CSOs may exhibit both short- and long-term responses to fuel treatments or wildfire, and understanding both is important to land-use managers. Our results documented a decline in CSO territories as a result of landscape fuel treatments, but the factors driving the decline remain unknown.

Conclusions

This study has shown that coordinated landscape-scale fuel treatments can substantially reduce the potential for hazardous fire across a large montane region, even when a moderate proportion of the area that could not be treated because of management constraints. In many cases, lands with designated management emphasis, such as wildlife habitat reserves and stream buffers, are distributed throughout the landscape. Creating fuel treatments that exclude these lands can result in a patchwork of treated areas heavily dissected by, for example, untreated stream buffers. Hazardous fire potential decreased in untreated areas, but that effect is not stable over time. Even if the existing network was maintained in a “treated” condition (i.e., periodic prescribed fire to keep surface and ladder fuels low) hazards will continue to increase in untreated areas because of stand development (Collins et al. 2013).

Our results indicate negative CSO responses to treatments, supported by the avoidance of DFPZs by foraging owls, larger owl home ranges associated with increasing amounts of treatment within the home ranges, and a 43% decline in the number of territorial CSO sites across the Meadow Valley study

area within 3–4 years of the implementation of landscape treatments. In addition to changes in the number of owls, we also observed spatial redistribution of owl sites over time across the landscape (figure 10). The specific mechanisms driving these observations are unclear, but given the region-wide decline in the CSO population (Conner et al. 2013) and the increasing barred owl populations, it is difficult to disentangle fuel treatment effects from background or external pressures. Despite the challenges of working at landscape scales, studies such as this provide opportunities for addressing scale-dependent ecological phenomena, such as population-level species responses and responses to management strategies that cannot be addressed at smaller spatial scales.

To date, little discussion has been focused on what may constitute sustainable, viable CSO populations under various landscape conditions designed to address projected fire and climate scenarios. Furthermore, there is not a clear understanding of the balance between the potential short-term impacts from treatments and the longer-term benefits provided by introducing landscape heterogeneity (North et al. 2009), reducing potential for severe fire (Ager et al. 2007, Collins et al. 2013), increasing the potential for more desirable fire effects (North et al. 2012), and increasing resilience to climate change (Stephens et al. 2010). The Meadow Valley study is an important step in learning about the responses of wildlife species to fuel-reduction treatments.

Recent research in Yosemite National Park suggests that CSOs are not adversely affected by low- to moderate-severity fire (Roberts et al. 2011, Lee et al. 2013). Studies of the CSO both in Yosemite and in Sequoia and Kings Canyon National Parks have not shown population declines that have been found in several national forests in California. There are many differences between the two ownerships: National forest lands generally contain younger forests and lack the large tree structures associated with preferred owl habitat. With continued fire suppression, national forest lands continue to develop dense, small-tree stand conditions, reducing the habitat heterogeneity associated with a variety of small mammals that constitute the CSO's prey base. Because of these differences, it is difficult to determine whether more recent mechanical treatments or existing fire-suppressed conditions might be associated with declining CSO populations. Uncertainty also persists regarding the potential thresholds at which the amounts and patch sizes of high-severity fire reduce the postfire probabilities of CSO occupancy, survival, and reproduction. This is a significant information gap, given the trend for increasing amounts and patch sizes of high-severity fire in many Sierra Nevada forests (Miller et al. 2009). Unfortunately, only one CSO pair in Meadow Valley used an area that received prescribed burn treatments, but unlike those in some of the mechanically treated areas, these owls continued to occupy the burned area through the duration of the study and foraged within the burn-treatment areas (Gallagher 2010). The introduction of barred owls to Meadow Valley adds another important factor that may

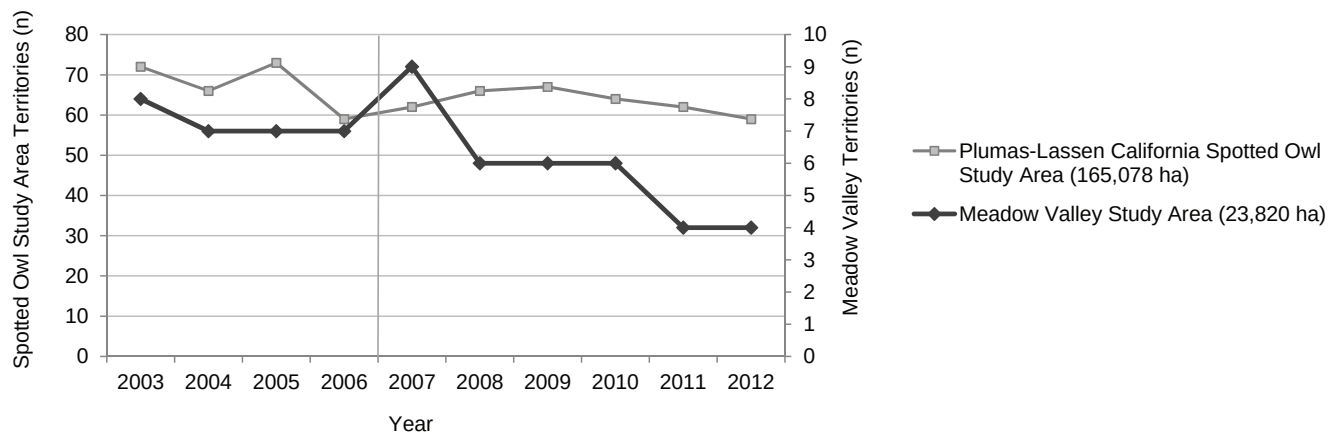


Figure 11. The annual number of territorial California spotted owl sites from 2003 to 2012 within the Meadow Valley study compared with the rest of the Plumas-Lassen study area (in the Plumas and Lassen National Forests). Vertical line represents completion of >80% of treatments.

reduce the population and viability of the CSO, possibly independent of forest structure.

Mechanical treatments can reduce fuels, but, in this study, they also left the largest trees and retained more than 40% canopy cover, two structural characteristics associated with CSO habitat use (Verner et al. 1992). However, although mechanical treatments retain these live features, they often remove snags for operator safety and fuel objectives; reduce tree density and canopy layering; reduce canopy cover to the minimum level (around 40%) considered to function as owl foraging habitat; and simplify the ground structure through a reduction of logs and small trees. Furthermore, DFPZ treatments are often uniformly implemented over large areas along roads, which results in extensive patches of simplified stand structure with regularly spaced trees. Another concern is that treatment size and placement are determined by land-use constraints (gentle slopes, access to roads) and opportunities to affect fire behavior. We have little information about how the location of treatments may affect CSOs' use of areas outside their core nesting locations. Several small mammals appeared to favor sites with steeper slopes (Kelt et al. 2013), possibly reflecting the spatial allocation of treatments in this landscape.

The importance of increasing heterogeneity within stands and across the landscape in mixed-conifer forests is well documented to meet restoration objectives (North et al. 2009, Stephens et al. 2010). Our ability to optimize heterogeneity at large scales may be more effectively achieved with prescribed and managed fires that are allowed to burn under moderate weather conditions. This type of burn often produces variable forest conditions that mimic historic patterns (Collins et al. 2011) to which this fauna, including the CSO, has adapted. Alternatively, mechanical treatments that produce the complex forest structure and composition that more closely mimic the patterns generated under a more active fire regime (North et al. 2009) may provide habitat conditions to support CSOs and a diverse fauna superior to those of the DFPZ and group-selection treatments implemented in Meadow Valley.

Although mean stand conditions (e.g., canopy cover) have often been used to infer management impacts on preferred habitat (Tempel et al. in press), the historic heterogeneity of frequent-fire forests suggests we have yet to identify the optimal scales at which to create variable forest conditions.

We encourage further work to examine landscape-level treatments that are intended to emulate the influence of fire in creating spatial heterogeneity in vegetation and fuel conditions. A working hypothesis is that increased habitat heterogeneity, including the retention and development of currently limited but ecologically important forest conditions (areas of large, old trees) and more-open, patchy, early-seral stage conditions, would promote a diverse wildlife community while providing a more fire-resilient landscape. The results from the Meadow Valley study area illustrate the benefits and challenges of working at the landscape scale. Rigorous and controlled experiments are difficult because of the inherent variability across landscapes, sociopolitical constraints, and competing management objectives that can influence planned treatments. However, inferences from these studies can be strengthened by careful replication of management strategies across multiple landscapes.

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Supplemental material

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Relation between Occupancy and Abundance for a Territorial Species, the California Spotted Owl

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Abstract: Land and resource managers often use detection-nondetection surveys to monitor the populations of species that may be affected by factors such as habitat alteration, climate change, and biological invasions. Relative to mark-recapture studies, using detection-nondetection surveys is more cost-effective, and recent advances in statistical analyses allow the incorporation of detection probability, covariates, and multiple seasons. We examined the efficacy of using detection-nondetection data (relative to mark-recapture data) for monitoring population trends of a territorial species, the California Spotted Owl (*Strix occidentalis occidentalis*). We estimated and compared the finite annual rates of population change (λ_t) and the resulting realized population change (Δ_t) from both occupancy and mark-recapture data collected over 18 years (1993–2010). We used multiseason, robust-design occupancy models to estimate that territory occupancy declined during our study ($\Delta_t = 0.702$, 95% CI 0.552–0.852) due to increasing territory extinction rates ($\hat{\epsilon}_{1993} = 0.019$ [SE 0.012]; $\hat{\epsilon}_{2009} = 0.134$ [SE 0.043]) and decreasing colonization rates ($\hat{\gamma}_{1993} = 0.323$ [SE 0.124]; $\hat{\gamma}_{2009} = 0.242$ [SE 0.058]). We used Pradel's temporal-symmetry model for mark-recapture data to estimate that the population trajectory closely matched the trends in territory occupancy ($\Delta_t = 0.725$, 95% CI 0.445–1.004). Individual survival was constant during our study ($\hat{\phi}_{1993} = 0.816$ [SE 0.020]; $\hat{\phi}_{2009} = 0.815$ [SE 0.019]), whereas recruitment declined slightly ($\hat{f}_{1993} = 0.195$ [SE 0.032]; $\hat{f}_{2009} = 0.160$ [SE 0.023]). Thus, we concluded that detection-nondetection data can provide reliable inferences on population trends, especially when funds preclude more intensive mark-recapture studies.

Keywords: dynamic occupancy model, population dynamics, Sierra Nevada, *Strix occidentalis occidentalis*, temporal-symmetry model

Relación entre Ocupación y Abundancia en una Especie Territorial, el Búho Moteado de California

Resumen: Los manejadores de tierras y recursos a menudo utilizan muestreos de detección-no detección para monitorear las poblaciones de especies que pueden ser afectadas por factores como la alteración del hábitat, cambio climático e invasiones biológicas. En relación con estudios de captura-recaptura, el uso de muestreos de detección-no detección es más rentable, y los avances recientes de los análisis estadísticos permiten la incorporación de la probabilidad de detección, covariables y múltiples temporadas. Examinamos la eficacia del uso de datos de detección-no detección (relativos a datos de captura-recaptura) para monitorear las tendencias poblacionales de una especie territorial, el búho moteado de California (*Strix occidentalis occidentalis*). Estimamos y comparamos las tasas finitas anuales de cambio poblacional (λ_t) y cambio poblacional realizado resultante (Δ_t) tanto para datos de ocupación y de captura-recaptura recolectados a lo largo de 18 años (1993–2010). Utilizamos modelos de ocupación multianuales de diseño robusto para estimar que la ocupación de territorio declinó durante nuestro estudio ($\Delta_t = 0.702$, 95% IC 0.552–0.852) debido al incremento en las tasas de extinción de ocupación de territorio ($\hat{\epsilon}_{1993} = 0.019$ [ES 0.012]; $\hat{\epsilon}_{2009} = 0.134$ [ES 0.043]) y el decremento de las tasas de colonización ($\hat{\gamma}_{1993} = 0.323$ [ES 0.124]; $\hat{\gamma}_{2009} = 0.242$ [ES 0.058]). Utilizamos el modelo de simetría temporal de Pradel para datos de captura-recaptura para estimar que la trayectoria de la población era similar a las tendencias de la ocupación de territorio ($\Delta_t = 0.725$, 95% IC 0.445–1.004). La supervivencia individual fue constante a lo largo de nuestro estudio ($\hat{\phi}_{1993} = 0.816$ [ES 0.020]; $\hat{\phi}_{2009} = 0.815$ [ES 0.019]), mientras que el reclutamiento declinó levemente ($\hat{f}_{1993} = 0.195$ [ES 0.032]; $\hat{f}_{2009} = 0.160$ [ES 0.023]). Por lo tanto, concluimos que los datos de detección-no detección pueden proporcionar

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inferencias confiables sobre las tendencias poblacionales, especialmente cuando los fondos excluyen estudios más intensivos de captura-recaptura.

Palabras Clave: dinámica de poblaciones, modelo de ocupación dinámica, modelo de simetría temporal, Sierra Nevada, *Strix occidentalis occidentalis*

Introduction

A primary responsibility of land and resource managers is to monitor (often over large spatial scales) the population trends of focal species that may be affected by changing future conditions, such as habitat change, climate change, and biological invasions. The use of detection-nondetection data (i.e., occupancy monitoring) may be a cost-effective, robust means of achieving this goal (Noon et al. 2012). Furthermore, recent advances in the statistical analyses of site-occupancy data allow the incorporation of imperfect detection, site- and survey-specific covariates, multiseason dynamics, and multiple states to assess a wide range of ecological and management questions, which enhances the utility of occupancy analyses (MacKenzie et al. 2006; Nichols et al. 2007).

Mark-recapture studies offer an alternative means of monitoring populations and provide more detailed data on demographic vital rates, such as survival and recruitment (Armstrup et al. 2005). However, mark-recapture studies are labor intensive, relatively costly, and generally encompass a small geographic area due to these constraints. In contrast, occupancy studies require surveying for only the presence or absence of a species and generally allow a larger area to be surveyed at a lower cost (Noon et al. 2012). Furthermore, metapopulation models and species-abundance distributions describe a fundamental, theoretical relation between occupancy and abundance so that site occupancy should provide a useful index for population status (Royle et al. 2005; Borregaard & Rahbek 2010). The results of some empirical research support the theoretical relation between occupancy and abundance. For example, Zuckerberg et al. (2009) found strong correlations between regional occupancy and relative abundance for a wide range of bird species in the state of New York (U.S.A.) over 2 periods. For these reasons, researchers have recently used detection-nondetection data, rather than mark-recapture data, to monitor the population status of species over large spatial extents (e.g., Burton et al. 2011; Karanth et al. 2011; Thorn et al. 2011). However, we were unaware of existing studies in which annual trends in site occupancy were compared with annual population trends (estimated with mark-recapture data from the same study population), a comparison that would more convincingly demonstrate a close relation between occupancy and abundance.

The California Spotted Owl (*Strix occidentalis occidentalis*) is a focal management species in the Sierra Nevada because it uses late-seral forests for nesting and

roosting (Gutiérrez et al. 1992). The U.S. Forest Service (USFS) considers the owl a “sensitive” species, which motivated the USFS to develop a Sierra-wide forest management plan (U.S. Forest Service 2004). The owl is highly territorial, displays strong site fidelity, and breeds irregularly, typically producing 1–2 young in years when it reproduces (Gutiérrez et al. 1995). Currently, the USFS monitors owl populations in the Sierra Nevada with long-term, mark-recapture studies designed to detect territorial adults (i.e., those responding to vocal surveys) (Franklin et al. 2004; Blakesley et al. 2010). The vital rates of those individuals are then quantified annually. These studies require intensive survey effort over large areas because California Spotted Owls have large home ranges (mean = 555 ha [SE 100] on the basis of data collected within and near our study area) (Williams et al. 2011). Thus, occupancy studies on a regional scale could be an ideal complement to the mark-recapture studies.

To test the efficacy of using occupancy studies to infer population status, we compared long-term trends (1993–2010), estimated from both occupancy and mark-recapture data, in a California Spotted Owl population in the central Sierra Nevada. We considered each owl territory a site, so the sampling population was similar for both types of data (i.e., all territorial adults on our study area vs. all owl territories). Thus, we expected annual trends in owl site occupancy should be similar to population trends estimated from the mark-recapture data.

Study Area

We conducted our study on a contiguous 35,500-ha area on the Eldorado National Forest in the central Sierra Nevada, California. The Eldorado Density Study Area (EDSA) has been the site of a long-term mark-recapture study of California Spotted Owls (Seamans et al. 2001; Franklin et al. 2004; Blakesley et al. 2010). We surveyed the entire area each year without regard to land cover, topography, access, or land ownership. Approximately 60% of the EDSA was public land managed by the USFS, and 40% was private land managed by timber companies.

The primary vegetation type on the EDSA was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). Common understory species included California black oak (*Quercus kelloggii*), bigleaf maple (*Acer macrophyllum*), and tanoak

(*Lithocarpus densiflorus*). Red-fir (*Abies magnifica*) forest, dominated by red fir and lodgepole pine (*Pinus contorta*), was present at higher elevations. Other local vegetation types and landscape features included chaparral, black oak woodland, and barren rock. Elevations on the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

Methods

Spotted Owl Surveys

We conducted surveys annually for spotted owls from 1986–2010 during the owl breeding season (1 April to 31 August). We did not conduct complete surveys over the entire EDSA in the early years of the study because funding constraints limited our survey effort. Hence, we examined survey coverage of the EDSA (see Survey Coverage of Study Area below) to determine when our survey effort was adequate to include data for analyses. In our surveys we imitated spotted owl vocalizations (vocal lure) for 10 minutes at a survey station or used vocal lures while walking along a survey route. We determined sex of a responding owl by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If owls were detected on nocturnal surveys, we conducted diurnal surveys to band unmarked owls, resight marked owls, assess reproduction, and band fledglings (Franklin et al. 1996). We banded owls with a numbered locking metal band on one leg and a unique combination of color band and color tab on the other leg (Franklin et al. 1996). We included both nocturnal and diurnal surveys in our occupancy analyses. We considered sites a territory where owls responded to vocal lures and were subsequently observed either roosting or nesting.

Survey Coverage of Study Area

To determine the initial year of complete survey coverage of the EDSA, we used ArcGIS 9.3 (ESRI, Redlands, California) to examine annual survey coverage of the EDSA. We drew a 0.80-km (0.5 mile) circle around each survey point where owls were not detected and a 1.61-km (1 mile) circle around each nest or roost location. We chose the 0.80-km distance because we expected surveyors to be able to hear any owls within this distance that responded during the surveys. We chose the 1.61-km distance because it was unlikely that other territorial owls would occur so close to a given territory (mean nearest-neighbor distance between owl territory centers from 1993–2010 was equal to 2.26 km). We then overlaid these circled areas on a map of the EDSA and calculated the proportion of the EDSA contained within the estimated areas of survey coverage each year. We chose 1993 as the starting year for our analyses because it was the first year

that >90% of the EDSA land area was surveyed and >1 survey was conducted at >90% of the owl territories. The surveys conducted prior to 1993 served to develop survey protocols and identify owl territories. Our approach was consistent with previous mark-recapture analyses for the EDSA that did not use data collected prior to 1990 because it was subjectively determined that survey effort was inadequate from 1986–1989 (Franklin et al. 2004; Blakesley et al. 2010).

Occupancy Modeling

We used a multiseason, robust-design occupancy model (MacKenzie et al. 2003) to assess occupancy trends of owls. We divided each breeding season into 10 bimonthly periods (1–15 April, 16–30 April, 1–15 May, 16–31 May, etc.). This approach provided greater biological meaning to the survey occasions at individual territories, relative to sequentially using all surveys conducted at a territory each year. For example, if one territory was first surveyed in early April and another in late May, we believed that it was inappropriate to model the detection probability for the first survey occasion at each site with the same parameter. We chose bimonthly periods to retain as much data as possible without having too many missing observations within a given sampling period. If a territory was not surveyed during a bimonthly period, we treated it as a missing observation. If multiple surveys were conducted within the same period, we assigned a zero to the survey history if no owls were detected during any survey and a one if at least one owl was detected during any survey. Our primary sampling periods were breeding seasons (i.e., years), and our secondary sampling periods were the bimonthly periods within each breeding season.

Our statistical model contained parameters for initial occupancy (ψ_1), local extinction (ϵ_t), local colonization (γ_t), and detection probability ($p_{t,j}$) (MacKenzie et al. 2003). We used PRESENCE (version 3.1) (Hines 2006) to compare models with Akaike's information criterion (AIC) (Burnham & Anderson 2002). We used MARK (version 6.1) (White & Burnham 1999) to obtain model-averaged parameter estimates that were based on Akaike weights (ω_i) (Burnham & Anderson 2002). Both programs also provided annual estimates of occupancy ($\hat{\psi}_t$) and rates of change in occupancy ($\hat{\lambda}_t$), which were derived recursively from $\hat{\psi}_1$, $\hat{\epsilon}_t$, and $\hat{\gamma}_t$ (MacKenzie et al. 2003). We then calculated the geometric mean for the rate of change in occupancy ($\hat{\lambda}$) and estimated the realized change in occupancy (Δ_t) as

$$\Delta_t = \prod_{i=1}^{t-1} \hat{\lambda}_i. \quad (1)$$

Thus, Δ_t was the product of $\hat{\lambda}_{1993} \times \hat{\lambda}_{1994} \times \dots \times \hat{\lambda}_{2009}$ and represented the proportion of the initial population (i.e., the number of occupied territories) remaining in

2010. We obtained variance estimates for $\hat{\lambda}$ and Δ_t with the delta method (Powell 2007).

We conducted the modeling in 2 stages. First, we used the fully parameterized model ($\psi_1, \varepsilon_t, \gamma_t, p_{t,j}$) to model within-season p . We developed 16 models containing covariates that we hypothesized affect p on survey occasion j during year t (Supporting Information). We used month as a covariate because each month corresponded to a different stage of the owl's breeding cycle and breeding-cycle stage affects owl behavior (April, incubation period; May, brooding; June, young fledged from nest; July, fledglings and adults typically near nest tree; August, fledglings and adults typically farther from nest tree) (Gutiérrez et al. 1995). We separated the survey season into pre fledging (1 April to 31 May) and post fledging (1 June to 31 August) periods because the fledging period affects owl behavior. We included time trends (linear, quadratic, and log linear) because Seamans and Gutiérrez (2007) found that p varied in a log-linear trend over the survey season on the EDSA. We specified that p was different on survey occasions after the survey when owls were initially detected at a territory because observers intensified their efforts to relocate detected birds in order to resight or capture birds and assess reproduction (Riddle et al. 2010). Because we expected nesting owls to be more easily detected than non-nesting owls (Nichols et al. 2007; MacKenzie et al. 2009), we used reproductive status as a covariate. Nesting owls may defend their territories more aggressively (i.e., respond more readily to vocal surveys) or spend more time in the territory core area, where most of our survey effort occurred. We did not include any covariates for survey effort because multiple surveys were often conducted within a sampling period at sites where owls were known to be present (i.e., for the demographic study), which created a spurious, positive relation between survey effort and p . We also did not include a covariate for survey type because surveys of different types were often conducted within the same period.

In the second modeling stage, we used the best structure for within-season variation in p and compared models in which ε_t , γ_t , and p_t varied in 5 ways: constant (.), different in each year (t), linear trend (T), quadratic trend (TT), and log-linear trend (lnT). We considered all possible combinations of temporal trends for ε_t , γ_t , and p_t . We did not include additional covariates (e.g., habitat quality within a territory) because our main interest was to obtain the best estimate of temporal trends in occupancy, not to test biological hypotheses related to territory occupancy.

Mark-Recapture Modeling

In prior mark-recapture analyses of some of our data, a temporal-symmetry model (Pradel 1996) was used that

contained parameters for finite rate of population change (λ_t), annual survival (ϕ_t), and capture probability (p_t) and treated λ_t as a random effect (Franklin et al. 2004; Blakesley et al. 2010). Blakesley et al. (2010) used mark-recapture data from 1990–2005 on the EDSA, but they omitted the first 2 and last estimates of λ_t , which may have been confounded with p_t when the parameters were modeled with a categorical time covariate (i.e., a different parameter estimate for each year). We used data from only 1993–2010 in our analyses to maintain congruence with our occupancy modeling. Our top models did not include any categorical time covariates, so we did not omit any λ_t estimates from our results.

We also used a functional form of Pradel's temporal-symmetry model that contained parameters for recruitment (f_t), ϕ_t , and p_t , and treated all parameters as fixed effects. Although treating λ_t as a random effect allows the partitioning of process variance (i.e., variation in λ_t due to covariate effects) from sampling variance (i.e., variation in λ_t due to random sampling; Burnham & White 2002), we wished to maintain an approach consistent with our occupancy modeling. An additional benefit of our approach was the explicit modeling of both mechanisms (recruitment and survival) responsible for population change. For comparison with Blakesley et al. (2010), we also conducted a random-effects analysis with their methods (see Supporting Information).

We used MARK (version 6.1) to compare competing models with AIC_c and obtain model-averaged parameter estimates on the basis of ω_i . MARK provided annual estimates of finite rates of population change ($\hat{\lambda}_t$), which were derived from $\hat{f}_t$ and $\hat{\phi}_t$ (Pradel 1996). We then calculated $\hat{\lambda}$, Δ_t , and their variances as above (see Occupancy Modeling above).

As with the occupancy modeling, we conducted the mark-recapture modeling in 2 stages. First, we used the fully parameterized model (f_t, ϕ_t, p_t) to model p_t . In this case, p refers to the probability of recapturing a marked individual that was still alive during a given year, whereas p in the occupancy modeling referred to the probability of detecting an owl(s) at an occupied territory during a given survey. We developed 12 models containing covariates that we hypothesized could affect p (Supporting Information). Walk-in effort represented the amount of time spent conducting diurnal surveys in a given year. Relatively greater walk-in effort is positively correlated with p on the EDSA for survival analyses (Blakesley et al. 2010). Blakesley et al. (2010) also found that a bird's sex affected p on the EDSA. Finally, we included time trends (linear, quadratic, and log linear) because observer proficiency may have improved as our study progressed.

In the second modeling stage, we used the best structure for p_t and compared models in which f_t and ϕ_t varied temporally in 5 ways: constant (.), different in each year (t), linear trend (T), quadratic trend (TT), and log-linear trend (lnT). We considered all possible combinations of

Table 1. Top-ranked models for multiseason occupancy analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993–2010.

Model ^a	No. parameters	AIC ^b	ΔAIC^c	ω_i^d
$\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	8	3081.93	0.00	0.108
$\psi_1, \gamma_{\cdot}, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	8	3082.60	0.67	0.077
$\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	9	3082.82	0.89	0.069
$\psi_1, \gamma_{\ln T}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	9	3083.44	1.51	0.051
$\psi_1, \gamma_T, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	9	3083.50	1.57	0.049
$\psi_1, \gamma_{\cdot}, \varepsilon_{TT}, p_{T, \text{initial} + \text{repro}}$	9	3083.65	1.72	0.046
$\psi_1, \gamma_{\cdot}, \varepsilon_T, p_{TT, \text{initial} + \text{repro}}$	9	3083.74	1.81	0.044
$\psi_1, \gamma_{\ln T}, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	9	3084.04	2.11	0.038
$\psi_1, \gamma_T, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	9	3084.15	2.22	0.036
$\psi_1, \gamma_{\cdot}, \varepsilon_{TT}, p_{TT, \text{initial} + \text{repro}}$	10	3084.32	2.39	0.033
$\psi_1, \gamma_{\ln T}, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	10	3084.41	2.48	0.031
$\psi_1, \gamma_T, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	10	3084.46	2.53	0.030
$\psi_1, \gamma_{TT}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}$	10	3084.66	2.73	0.028
$\psi_1, \gamma_{\cdot}, \varepsilon_T, p_t, \text{initial} + \text{repro}$	24	3085.03	3.10	0.023
$\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_t, \text{initial} + \text{repro}$	24	3085.05	3.12	0.023
$\psi_1, \gamma_{TT}, \varepsilon_T, p_{T, \text{initial} + \text{repro}}$	10	3085.10	3.17	0.022
$\psi_1, \gamma_{\ln T}, \varepsilon_{TT}, p_{T, \text{initial} + \text{repro}}$	10	3085.20	3.27	0.021
$\psi_1, \gamma_{\ln T}, \varepsilon_T, p_{TT, \text{initial} + \text{repro}}$	10	3085.25	3.32	0.021
$\psi_1, \gamma_T, \varepsilon_{TT}, p_{T, \text{initial} + \text{repro}}$	10	3085.26	3.33	0.020
$\psi_1, \gamma_T, \varepsilon_T, p_{TT, \text{initial} + \text{repro}}$	10	3085.34	3.41	0.020
$\psi_1, \gamma_{TT}, \varepsilon_{\ln T}, p_{TT, \text{initial} + \text{repro}}$	11	3085.62	3.69	0.017

^aModel variables are defined in Methods.^bAkaike's information criterion.^cDistance in AIC units from the model with the lowest AIC value.^dAkaike weight.

temporal trends for f_t and φ_t . As with the occupancy modeling, we did not include additional biological covariates because our goal was to obtain the best estimate of temporal trends in population size, not to test biological hypotheses related to individual survival or recruitment.

Results

Territory Occupancy

We located 45 owl territories from 1993–2010, and owls had been detected at least once at all sites by 1997. Reproduction by owls was observed at 39 of 45 territories at least once during the study, which indicated we had identified biologically relevant territories. At least 1 owl was detected at 40 of 45 (90.0%) territories in 1993, but at only 26 of 45 (57.8%) territories surveyed in 2010. Thus, naïve territory occupancy estimates, which did not account for imperfect detection, indicated occupancy declined by 31% (14/45) during our study.

In the first modeling stage, model $\{\psi_1, \gamma_t, \varepsilon_t, p_{t, \text{initial} + \text{repro}}\}$ had 100.0% of the Akaike weight among the 16 candidate models. Therefore, we used $p_{t, \text{initial} + \text{repro}}$ in all second-stage models, of which $\{\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}\}$ was the top-ranked model (Table 1). However, considerable uncertainty existed regarding which model best fit the data as the top 7 models were

within 2.0 AIC units of each other (Burnham & Anderson 2002). Parameter estimates from model $\{\psi_1, \gamma_{\cdot}, \varepsilon_{\ln T}, p_{T, \text{initial} + \text{repro}}\}$ indicated that within-year detection probability of owls was higher on surveys following the initial detection of an owl at a territory ($\hat{\beta}_{\text{initial}} = 1.20$ [SE 0.11]) and higher for nesting owls ($\hat{\beta}_{\text{repro}} = 1.63$ [SE 0.14]). Annual detection probabilities were generally high, particularly for nesting owls (Supporting Information).

Due to model-selection uncertainty, we obtained model-averaged estimates for $\hat{\gamma}_t$, $\hat{\varepsilon}_t$, and $\hat{\psi}_t$ with the 21 models that had >80% of the Akaike weight (Fig. 1). We used the top 80% because all models outside of this set had low support ($\omega_i \leq 0.02$). When a model contained a temporal covariate for either $\hat{\gamma}_t$ or $\hat{\varepsilon}_t$, the indicated trend was always negative for $\hat{\gamma}_t$ and positive for $\hat{\varepsilon}_t$. Thus, territory extinction increased over time ($\hat{\varepsilon}_{1993} = 0.019$ [SE 0.012]; $\hat{\varepsilon}_{2009} = 0.134$ [SE 0.043]), whereas territory colonization decreased over time ($\hat{\gamma}_{1993} = 0.323$ [SE 0.124]; $\hat{\gamma}_{2009} = 0.242$, SE = 0.058). As a result, territory occupancy declined during the study ($\hat{\psi}_{1993} = 0.957$ [SE 0.045]; $\hat{\psi}_{2010} = 0.671$ [SE 0.069]). The model-averaged estimates of ψ corresponded well with the naïve estimates of occupancy, despite a decline in the annual estimates of p during the study (Fig. 1). The estimated and naïve occupancy estimates did not diverge because p remained relatively high throughout our study, and we conducted sufficient surveys at a territory each year (average number of surveys per territory = 3.9) to detect owls reliably.

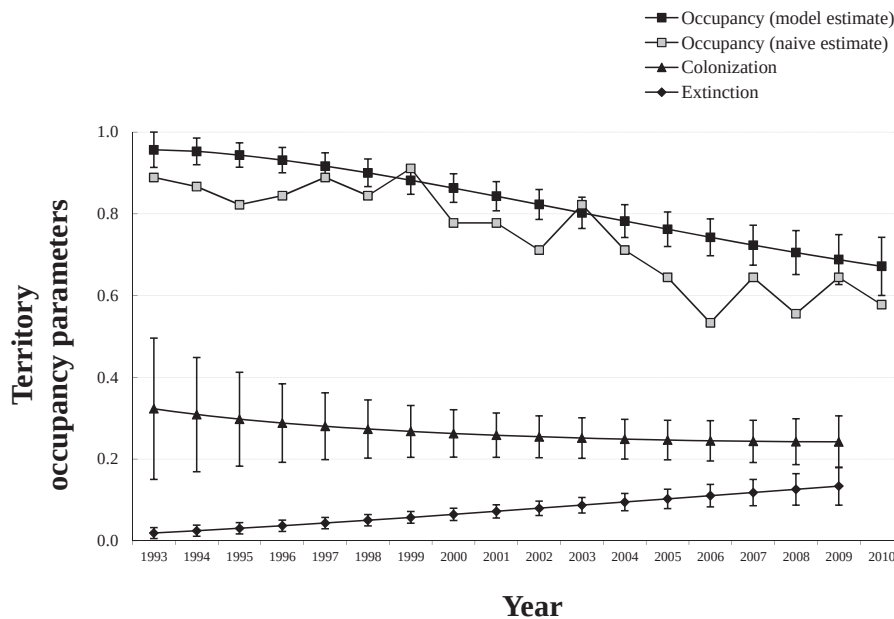


Figure 1. Annual estimates (SE) of territory extinction, colonization, and occupancy at California Spotted Owl (*Strix occidentalis occidentalis*) territories in the central Sierra Nevada, 1993–2010.

Table 2. Top-ranked temporal-symmetry models with recruitment and survival for mark-recapture analysis of a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993–2010.

Model ^a	No. parameters	AIC _c ^b	ΔAIC _c ^c	ω _i ^d
$\varphi, f, p_{\text{sex}} + \text{effort}$	5	2326.29	0.00	0.186
$\varphi, f_{\text{inT}}, p_{\text{sex}} + \text{effort}$	6	2326.86	0.57	0.139
$\varphi, f_T, p_{\text{sex}} + \text{effort}$	6	2327.56	1.27	0.099
$\varphi, f_{\text{TT}}, p_{\text{sex}} + \text{effort}$	7	2327.60	1.31	0.096
$\varphi_{\text{inT}}, f, p_{\text{sex}} + \text{effort}$	6	2328.25	1.96	0.070
$\varphi_T, f, p_{\text{sex}} + \text{effort}$	6	2328.30	2.01	0.068
$\varphi_T, f_{\text{inT}}, p_{\text{sex}} + \text{effort}$	7	2328.88	2.59	0.051
$\varphi_{\text{inT}}, f_{\text{inT}}, p_{\text{sex}} + \text{effort}$	7	2328.89	2.60	0.051
$\varphi_T, f_T, p_{\text{sex}} + \text{effort}$	7	2329.58	3.29	0.036
$\varphi_{\text{inT}}, f_T, p_{\text{sex}} + \text{effort}$	7	2329.59	3.30	0.036
$\varphi_T, f_{\text{TT}}, p_{\text{sex}} + \text{effort}$	8	2329.60	3.31	0.035
$\varphi_{\text{inT}}, f_{\text{TT}}, p_{\text{sex}} + \text{effort}$	8	2329.61	3.32	0.035
$\varphi_{\text{TT}}, f, p_{\text{sex}} + \text{effort}$	7	2330.26	3.97	0.025

^aModel variables are defined in Methods.

^bAkaike's information criterion adjusted for small sample size.

^cDistance in AIC_c units from the model with the lowest AIC_c value.

^dAkaike weight.

Mark-Recapture Abundance

In the first modeling stage, model $\{\varphi_t, f_t, p_{\text{sex}} + \text{effort}\}$ was the top-ranked model and had 35.7% of the Akaike weight among the 12 candidate models, so we used $p_{\text{sex}} + \text{effort}$ for detection probability in all second-stage models. In the second modeling stage, model $\{\varphi, f, p_{\text{sex}} + \text{effort}\}$ was the top-ranked model (Table 2). Parameter estimates from model $\{\varphi, f, p_{\text{sex}} + \text{effort}\}$ indicated that φ and f were constant during our study period and that p was higher for male owls ($\hat{\beta}_{\text{sex}} = 0.54$ [SE 0.25]) and positively correlated with annual walk-in survey effort ($\hat{\beta}_{\text{effort}} = 1.46$ [SE 0.67]). However, the top 6 models were within 2.0 AIC units of each other.

Due to model-selection uncertainty, we obtained model-averaged estimates for $\hat{\varphi}_t$, $\hat{f}_t$, and $\hat{\lambda}_t$ with the 14 models that had $\geq 95.0\%$ of the Akaike weight (Fig. 2). The top 4 models specified that φ was constant; when a model contained a temporal covariate for $\hat{\varphi}_t$, the trend was weakly negative. The top model specified that f was constant; when a model contained a temporal covariate for $\hat{f}_t$, the trend was negative. Thus, survival was nearly constant over time ($\hat{\varphi}_{1993} = 0.816$ [SE = 0.020]; $\hat{\varphi}_{2009} = 0.815$ [SE 0.019]), whereas recruitment decreased slightly ($\hat{f}_{1993} = 0.195$ [SE 0.032]; $\hat{f}_{2009} = 0.160$ [SE 0.023]). As a result, the finite rate of population change slightly declined during the study ($\hat{\lambda}_{1993} = 1.011$ [SE 0.035]; $\hat{\lambda}_{2009} = 0.975$ [SE 0.024]).

Occupancy versus Abundance

The realized change in occupancy ($\Delta_t = 0.702$, 95% CI 0.552–0.852) (Fig. 3) and the geometric mean of annual change in occupancy ($\hat{\lambda} = 0.979$, 95% CI 0.967–0.992) both suggested that territory occupancy declined from 1993–2010. Changes in occupancy within our study area should reflect changes in abundance unless the average number of owls detected at a territory also changed over time (i.e., more or fewer single owls). Thus, we performed a linear regression of the number of owls detected per territory versus year, and the slope was not significantly different from 0.0 ($\beta = -0.004$, $F_{1,16} = 1.13$, $p = 0.30$).

The realized change in population size ($\Delta_t = 0.725$, 95% CI 0.445–1.004) (Fig. 3) and the geometric mean of the finite rate of population change ($\hat{\lambda} = 0.981$, 95% CI 0.959–1.004) also suggested that population size declined from 1993–2010, but the 95% CI slightly

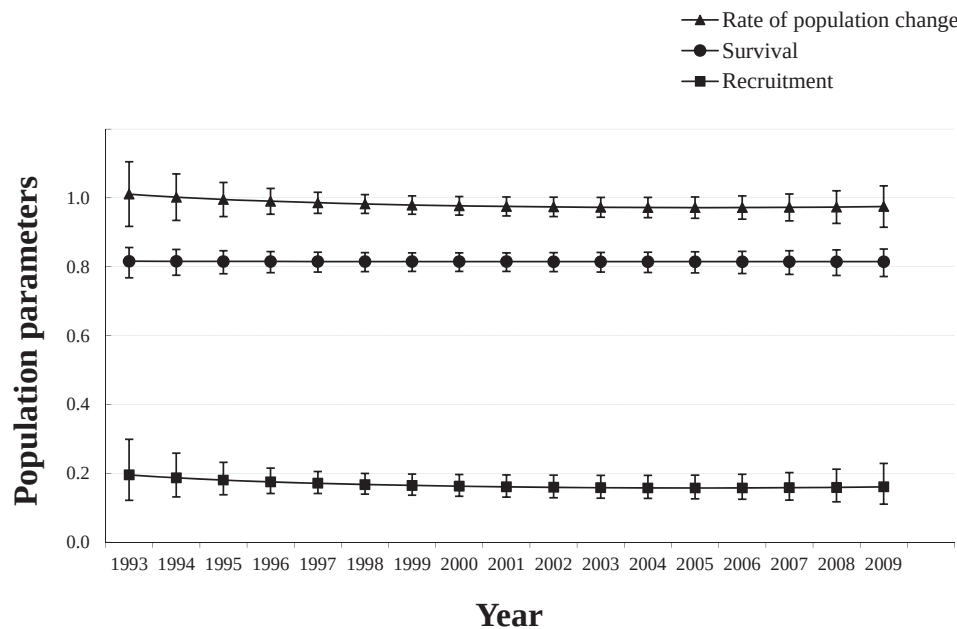


Figure 2. Annual estimates (SE) of survival, recruitment, and finite rate of population change for a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993-2009.

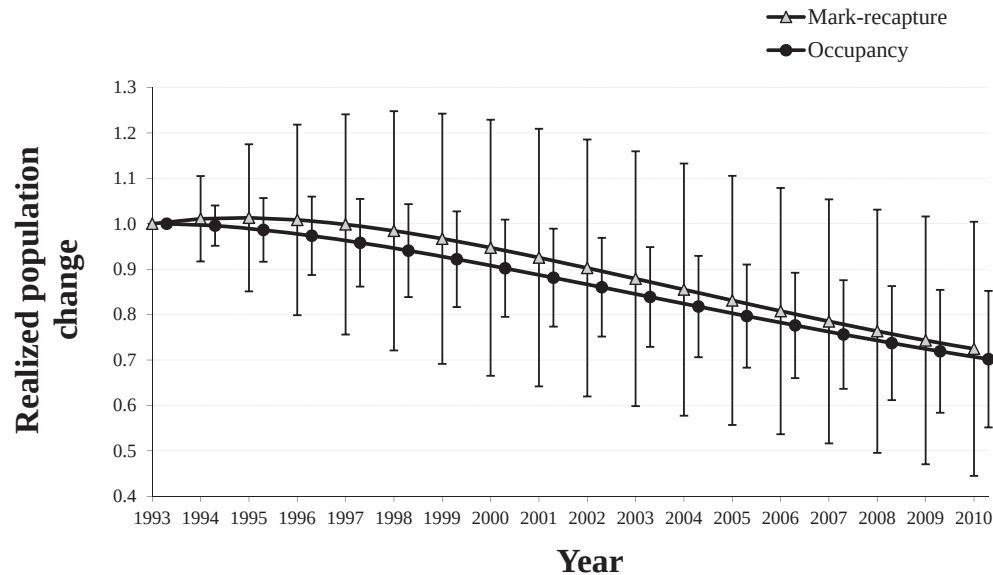


Figure 3. Realized population change (95% CI) with both occupancy and mark-recapture data for a California Spotted Owl (*Strix occidentalis occidentalis*) population in the central Sierra Nevada, 1993-2010.

overlapped 1.0 for both parameters. The realized change in territory occupancy closely matched the realized population change estimated from mark-recapture data, although the realized population change estimates were less precise (Fig. 3).

Discussion

The realized change in population we estimated on the basis of occupancy closely matched the realized population change estimated from mark-recapture data. This

result suggests occupancy monitoring may offer an accurate, cost-effective means to monitor the population trends of territorial species over large spatial extents. The relation between occupancy and abundance may be less strong for nonterritorial species (e.g., semicolonial; Estrada & Arroyo 2012), so we encourage assessments of the occupancy-abundance relation for such species. Occupancy models that incorporate observed counts of individuals and imperfect detection should be well suited for such applications (Royle et al. 2005).

We obtained more-precise parameter estimates with occupancy modeling relative to mark-recapture

modeling. The determination of the effective sample size in occupancy studies has not been fully resolved (J. Nichols, personal communication). However, we apparently obtained a larger sample size with our occupancy data because the robust-design occupancy model accommodated multiple surveys (i.e., data points) at a territory each year, whereas we used a mark-recapture model that used a single datum each year for the marked individuals in our population. Robust-design models that accommodate missing observations are available for mark-recapture data (Pollock 1982), but we believe a site-based occupancy approach offers greater flexibility. For example, if the entire study area is not surveyed during each secondary sampling period, it is unclear how one would generally determine which individuals were not sampled during that period. Alternatively, the size of the study area can be increased to add more individuals, but this again requires substantial survey effort for species with large home ranges. In contrast, additional sampling units can be more easily added with occupancy surveys because the sampling unit is the site (whether defined as quadrats, territories, etc.), not the individual.

For the occupancy modeling, territory extinction increased over time, and colonization rates were insufficient to maintain occupancy at its initial level. Annual territory extinction was low during our study, but its effects were significant because most territories were occupied at the study's onset and colonization rates were also low. Territories may not have been colonized because habitat alteration during the study (e.g., logging, high-intensity wildfire) may have affected the quality of vacant owl territories (Seamans & Gutiérrez 2007). In addition, the mark-recapture modeling showed a declining trend in individual recruitment, so the population may have produced an insufficient number of owls to colonize vacant territories and maintain occupancy at its initial level.

We identified 2 factors that greatly affected the detection probability (p) in our occupancy analysis. First, p increased after the initial detection of owls at a territory during a given year (see Riddle et al. 2010). Owl demographic studies are designed to capture birds (either by banding unmarked birds or resighting marked birds) and to determine reproductive activity (Franklin et al. 1996), so observers intensify their efforts to locate birds after initial detection. This phenomenon suggests that future occupancy analyses for studies originally designed to collect mark-recapture data should include a within-year, initial-detection effect in the model structure. Second, we found that nesting spotted owls were more likely to be detected, which confirmed the results of prior analyses (Nichols et al. 2007; MacKenzie et al. 2009). Our results also supported the need to model detection probability appropriately during occupancy analyses to reduce bias in site-occupancy estimates (Mackenzie et al. 2006).

Our results suggested that occupancy data can provide reliable information on wildlife population trends,

as evidenced by the concurrent declines in territory occupancy and population size of California Spotted Owls. Therefore, managers may be justified in using less costly, occupancy-based study designs to monitor spotted owls and other species of management concern over large geographic areas. Our occupancy models also provided more precise parameter estimates than our mark-recapture models because we conducted multiple surveys at each territory per primary sampling period. A robust-design mark-recapture model could have been used, but it was unclear to us how one would determine whether individuals were sampled during a defined secondary sampling period. We caution, however, that occupancy data may be more suitable for inferring the population status of territorial species than those with clumped spatial distributions, unless data collection also includes counts of individual organisms (in addition to the simple detection or nondetection of the target species) and researchers use occupancy models that incorporate such data (Royle et al. 2005).

We encourage future research that incorporates ecological covariates (e.g., habitat quality, habitat change) to elucidate site-occupancy dynamics and inform management decisions that may affect the California Spotted Owl. For example, managers need information on how timber harvest affects territory extinction and colonization, reproductive output, and individual survival (U.S. Forest Service 2004). We also recognize that mark-recapture studies provide important demographic information not provided by occupancy studies, which may allow the identification of life-history stages that are limiting a population. Thus, the choice of study design will depend on the specific research or management objectives for a given wildlife population.

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Supporting Information

The methods and results for our random-effects mark-recapture modeling for which we used the methods of Blakesley et al. (2010) (Appendix S1), our a priori models for detection probability (occupancy modeling) and capture probability (mark-recapture modeling) (Appendix S2), and the annual detection probabilities for our occupancy modeling (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Effects of forest management on California Spotted Owls: implications for reducing wildfire risk in fire-prone forests

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Abstract. Management of many North American forests is challenged by the need to balance the potentially competing objectives of reducing risks posed by high-severity wildfires and protecting threatened species. In the Sierra Nevada, California, concern about high-severity fires has increased in recent decades but uncertainty exists over the effects of fuel-reduction treatments on species associated with older forests, such as the California Spotted Owl (*Strix occidentalis occidentalis*). Here, we assessed the effects of forest conditions, fuel reductions, and wildfire on a declining population of Spotted Owls in the central Sierra Nevada using 20 years of demographic data collected at 74 Spotted Owl territories. Adult survival and territory colonization probabilities were relatively high, while territory extinction probability was relatively low, especially in territories that had relatively large amounts of high canopy cover ($\geq 70\%$) forest. Reproduction was negatively associated with the area of medium-intensity timber harvests characteristic of proposed fuel treatments. Our results also suggested that the amount of edge between older forests and shrub/sapling vegetation and increased habitat heterogeneity may positively influence demographic rates of Spotted Owls. Finally, high-severity fire negatively influenced the probability of territory colonization. Despite correlations between owl demographic rates and several habitat variables, life stage simulation (sensitivity) analyses indicated that the amount of forest with high canopy cover was the primary driver of population growth and equilibrium occupancy at the scale of individual territories. Greater than 90% of medium-intensity harvests converted high-canopy-cover forests into lower-canopy-cover vegetation classes, suggesting that landscape-scale fuel treatments in such stands could have short-term negative impacts on populations of California Spotted Owls. Moreover, high-canopy-cover forests declined by an average of 7.4% across territories during our study, suggesting that habitat loss could have contributed to declines in abundance and territory occupancy. We recommend that managers consider the existing amount and spatial distribution of high-canopy forest before implementing fuel treatments within an owl territory, and that treatments be accompanied by a rigorous monitoring program.

Key words: California Spotted Owl; fire severity; forest management; fuels reduction; high-canopy-cover forest; Sierra Nevada, California, USA; *Strix occidentalis occidentalis*; timber harvest; wildfire.

INTRODUCTION

Forest managers in North America are challenged by the need to balance the potentially competing objectives of reducing wildfire risk and protecting threatened species. For millennia, low- to moderate-severity wildfires occurred at frequent (often less than 20-year) intervals in many western forests. These fires naturally removed fuels such as woody debris, shrubs, and small trees, and shaped the ecology of these forests (Agee 1993, Noss et al. 2006). However, decades of wildfire suppression have disrupted historic fire regimes, in-

creased the amount of surface and ladder fuels, and have led to more frequent high-severity wildfires that now threaten ecological and human communities (Westerling et al. 2006). In addition, warmer and drier conditions associated with climate change may lead to further increases in fire activity over the next century (Westerling and Bryant 2008, Liu et al. 2013). As a result, policy makers and forest managers have proposed landscape-scale forest treatments to remove surface and ladder fuels and reduce the risk of high-severity fires in many western forests (e.g., USFS 2004).

Proposed fuel-reduction measures pose a potential risk to wildlife species associated with older forests because they change forest structure in ways that may negatively affect the species' ability to survive and

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reproduce. Species such as the Spotted Owl (*Strix occidentalis*), fisher (*Pekania pennanti*), and American marten (*Martes americana*) have already declined because of habitat loss and fragmentation resulting from more than a century of timber harvest (Gutiérrez 1994, Zielinski et al. 2005). Although fuels management may provide long-term benefits to such species by reducing future habitat loss from high-severity fires (Finney 2001, Ager et al. 2007, Finney et al. 2007, Collins et al. 2011), regulations protecting sensitive species often constrain the placement and number of potential fuel treatments (Collins et al. 2010). Thus, there is an urgent need to understand the effects of fuel-reduction treatments on old-forest-associated species so that fire risk can be managed while maintaining viable populations of these species (Zielinski et al. 2013). Doing so, however, is challenging because many of these species are rare and long-lived such that impacts may not be immediately apparent. Thus, long-term studies are needed to provide sufficient statistical power to discriminate between the effects of forest management and other sources of variation in demographic rates.

A high-profile example of the attempt to balance wildfire risk and species conservation is the management of public forests and Spotted Owls in the Sierra Nevada, California, USA. As with other western forests, the area burned by high-severity fires in the Sierra Nevada has increased over the past several decades (Miller et al. 2009). However, the implementation of landscape-scale fuel treatments in the Sierra Nevada (USFS 2004) has been contentious because of the potential for these fuel treatments to negatively affect the Spotted Owl and other sensitive species. For example, site occupancy of California Spotted Owls declined following the alteration of >20 ha of habitat within territories (Seamans and Gutiérrez 2007a). However, Seamans and Gutiérrez (2007a) did not attribute habitat changes to specific causes (e.g., fire, different types of logging) or assess the relationship between these events and reproduction, survival, or fitness. Thus, considerable uncertainty remains about the impact of forest management on California Spotted Owls.

We assessed the effects of timber harvest, wildfire, and vegetation conditions on a declining population of California Spotted Owls in the central Sierra Nevada, California, from 1993 to 2012. Specifically, we assessed the effects of forest treatments and vegetation conditions on reproduction, survival, and territory occupancy of California Spotted Owls and used these vital rates to determine the sensitivity of population growth and occupancy to changes in vegetation conditions due to wildfire or timber harvest. Our objectives were to understand the potential direct, short-term impacts of management actions intended to reduce wildfire risk on Spotted Owls, and to gain insight into the causes of an approximate 30% decline in abundance on our study area over the past two decades (Tempel and Gutiérrez 2013). Moreover, our study is particularly timely

because of heightened public concern following the 2013 fire season in the Sierra Nevada, which included one of the largest wildfires in California history (Rim Fire) and a wildfire that burned part of our study area (American Fire).

MATERIAL AND METHODS

Study area

Our study area was located in the central Sierra Nevada, California, between the North and South Forks of the American River. Within this area, we had a 345-km² Density Study Area (DSA) that we completely surveyed for Spotted Owls each year from 1993 to 2012, regardless of land ownership or past occupancy by owls. About 60% of the DSA was National Forest, and the remainder was privately owned land. In 1997 we established a Regional Study Area (RSA) surrounding the DSA. The RSA consisted of historical (previously known) owl territories and territories that we began surveying during 1997–1999. We then conducted annual surveys within owl territories on the RSA from 1997 to 2012, but we did not completely survey the landscape between these territories. In 2007, we established the 248-km² Last Chance Study Area (LCSA) as part of the Sierra Nevada Adaptive Management Project, 2013 (SNAMP).⁵ The LCSA was adjacent to the northern boundary of the DSA and was also completely surveyed for Spotted Owls each year from 2007 to 2012, regardless of land ownership or past occupancy by owls. We detected no Barred Owls (*Strix varia*) during our study, although we did detect two Barred × Spotted Owl hybrids that were not included in our assessment.

The study area consisted of mountainous terrain bisected by steep river canyons with elevations ranging from 300 to 2500 m. The study area had a mediterranean climate with cool, wet winters and hot, dry summers. Sierran mixed-conifer forest was the principal vegetation type and had a canopy dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*). California black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflora*), and big-leaf maple (*Acer macrophyllum*) were common understory species. Forests dominated by red fir (*A. magnifica*) and lodgepole pine (*P. contorta*) occurred at the highest elevations. Montane chaparral and black oak woodlands were vegetation types that were locally distributed at lower and middle elevations. The area has experienced a complex history of timber harvests over the past century, which added to the spatial complexity of vegetation conditions.

Spotted Owl surveys

Each year we conducted nighttime surveys from April through August to locate individuals by imitating vocalizations of Spotted Owls for a minimum of 10

⁵ <http://snamp.cnr.berkeley.edu>

TABLE 1. Description of vegetation classes used to characterize forest conditions used by Spotted Owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, California, USA.

Class	Description	dbh (cm)	Canopy cover (%)
1	Hardwood forest		>10 hardwood; <10 conifer
2	Shrubs and/or saplings	<15.2	
3	Pole conifer forest	15.2–30.4	
4	Medium-sized conifer forest with low canopy cover	30.5–60.9	30–69
5	Medium-sized conifer forest with high canopy cover	30.5–60.9	≥70
6	Large-sized conifer forest with low canopy cover	≥61.0	30–69
7	Large-sized conifer forest with high canopy cover	≥61.0	≥70
8	Water or barren rock		
9	Medium/large-sized, conifer forest with very low canopy cover	≥30.5	<30

minutes at call stations spaced ~0.8 km apart, or while walking routes that connected multiple call stations. If owls were detected, we conducted walk-in surveys at dawn or dusk in an attempt to identify owls and locate nests and roosts. We attempted to capture and band all Spotted Owls following the methods of Franklin et al. (1996). We fitted captured owls with a U.S. Geologic Survey (USGS) locking aluminum band on one leg and a unique color band and tab combination on the other leg. We determined sex of individuals by the pitch of calls and behavior (Forsman et al. 1984). We identified four age classes based on plumage characteristics: juvenile, first-year subadult, second-year subadult, and adult (≥3 years old) (Moen et al. 1991).

We estimated reproduction of Spotted Owls (i.e., the number of young produced per pair per year) by feeding live mice to owls (Franklin et al. 1996). Reproducing owls usually take offered prey to their nest or young, whereas nonreproducing owls usually eat or cache the mice. We inferred that owl pairs were nonreproductive if: (1) an owl took two or more mice and cached the last mouse without bringing a mouse to a nest or young; (2) an owl ate or cached four or more mice without bringing a mouse to a nest or young; (3) an owl ate two mice and ignored a third mouse for >1 hour; (4) a female owl was captured prior to 1 June and did not have a brood patch; or (5) a female owl was observed roosting for ≥60 minutes before 1 June, which suggested that the female was not incubating eggs or brooding. The number of young fledged from successful nests was determined by observing the delivery of offered mice from parents to young and by counting young during visual searches of the nest stand.

We determined site occupancy following the protocol of Tempel and Gutiérrez (2013). We divided the survey season each year into 10 bimonthly sampling periods (i.e., 1–15 April, 16–30 April, 1–15 May, 16–31 May, and so forth). We identified 74 owl territories using the criterion that reproduction must have been observed at least once at that location during our study. We considered the detection of at least one owl at a territory to indicate site occupancy. We eliminated nocturnal detections >400 m from the territory core area (i.e., areas frequently used by nesting and roosting owls at a territory; Berigan et al. 2012) to minimize the inclusion

of false positive detections of non-territorial floaters or residents straying from nearby territories.

Vegetation and forest treatment mapping

We interpreted aerial photographs to map vegetation cover types and changes in cover type that resulted from forest management, succession, and wildfire within all 74 owl territories during 1993–2012. Our vegetation map represented a spatial and temporal expansion of a similar map developed for our study area that also relied upon aerial photo interpretation, but was limited to a subset of territories and years (Chatfield 2005, Seamans and Gutiérrez 2007a). We mapped cover types within a 1128 m radius (400-ha) circle around each owl territory center; this radius was equal to half of the mean nearest neighbor distance during our study. We did not know if territorial owls used the entire 400 ha, but owls responded to our vocal surveys within these areas, and these areas encompassed all known nest locations on our study area (Seamans and Gutiérrez 2007a). We estimated a single center for each owl territory as the geometric mean of the most informative owl location(s) from each year that the territory was occupied. We used a nest location if one was located that year, but if we did not find a nest, we used the mean location of all roost trees located that year.

Vegetation cover was assigned to one of nine possible classes based on species composition, canopy cover, and the size class of dominant trees (Table 1; Appendix A). We used vegetation classes based upon the California Wildlife Habitat Relationships system (CWHR; Mayer and Laudenslayer 1988). As noted, we used a cover map developed by Chatfield (2005) as our base map, which had an overall accuracy (i.e., correct classification of cover types) of 83% based on randomly sampled vegetation plots. We updated this map for each year of our study using National Agriculture Imagery Program images, USGS 1-m digital orthophoto quarter quads (DOQQs), and geo-rectified aerial photographs (1:15 840 scale) obtained for the following years: 1993, 1996–1998, 2000, 2005, 2009, and 2010–2012. We drew polygons around relatively homogenous vegetation classes visible on the images using a minimum polygon size of ~1 ha. When we could not reliably assign a year to a visible change in cover type between available

images, we assumed that the change occurred at the midpoint between image years (see Fig. 1 as an example of the vegetation cover map for a single owl territory).

We identified the timing, location, and type of timber harvests from the U.S. Forest Service (USFS) Activity and Tracking System (FACTS; database *available online*),⁶ the California Department of Forestry and Fire Protection (CDFFP) Timber Harvest Plans (database *available online*),⁷ and information provided by private landowners. These databases contained 16 different timber harvest practices that we pooled into three broad categories for analytical purposes: low-intensity, medium-intensity, and high-intensity timber harvest (Appendix B). The classification scheme was based on the expected change in forest structure and was developed after consultation with three local forest managers who were naïve to the objectives of our study. We confirmed or modified the year and boundary of all treatments in the databases by visually examining the imagery and obtaining supplementary information from field visits, the USFS, and private landowners. We acquired fire perimeter data from the CDFFP Fire and Resource Assessment Program (*available online*).⁸

We did not specifically test for effects on Spotted Owls of Forest Service-implemented fuel-reduction treatments as proposed in USFS (2004) because implementation of these treatments was relatively recent (only 11 owl territories were affected by these treatments after 2007). However, these recent fuel-reduction treatments had effects on forest structure similar to those of other treatments in the medium-intensity category, most of which also occurred on USFS land. Prior to 2004, USFS timber harvests were governed by an “interim” management plan designed to maintain viable Spotted Owl populations (USFS 1993). Similar to the 2004 plan, the 1993 interim plan was designed to protect known owl nest stands from any significant modification, to protect large trees (≥ 76.2 cm dbh), to retain at least 40% canopy cover, and to reduce the threat of stand-destroying fires. The primary change implemented by the 2004 plan was a greater emphasis placed on the removal of understory fuels. Thus, we identified the occurrence of understory treatments through conversations with USFS and private timber company personnel and visual interpretation of aerial photos, and further categorized these treatments as “medium-intensity with understory removal.”

We extracted spatial data relevant to Spotted Owl ecology (see *Methods: A priori model development and selection*) from the cover maps with ArcGIS 10.0 (ESRI, Redlands, California, USA) using Patch Analyst 5.1.0.0 (Rempel et al. 2012) for subsequent use in demographic analysis. To calculate the amount of edge between vegetation classes, we used Patch Grid after first

converting vector data to raster data at a 30-m scale (Rempel et al. 2012). All other spatial variables were calculated directly from the vector maps. All habitat and timber harvest variables that we extracted from our vegetation maps were time-varying and could change annually because of natural disturbance, timber harvest, or regrowth. We expected that reproduction, survival, and occupancy at a territory would be impacted by timber harvest and wildfire in previous years, as well as the current year. Thus, we calculated harvest and wildfire covariates over three temporal scales: 3 years, 6 years, and 9 years. For example, at the 6-year time scale, the area of a specific disturbance type was the sum of those disturbances that occurred in the previous five years and the current year.

A priori model development and selection

We modeled putative relationships between vegetation classes and four vital rates (reproduction, survival, territory colonization, and territory extinction) by evaluating the level of support for competing, *a priori* models. We used Akaike's information criterion (AIC) values to rank competing models (Burnham and Anderson 2002). When evaluating support for covariate effects within a given model, we assessed whether the 95% confidence interval of the associated parameter estimate overlapped zero. We conducted the modeling in three steps to reduce the number of candidate models and thus reduce the likelihood of finding spurious relationships (Table 2). In the first step, we evaluated covariates that represented the amount of potential owl nesting and roosting habitat within territories. In the second step, we used the covariates from the top-ranked model from the first step and included additional covariates for potential owl foraging habitat, amount of private land, and the spatial distribution of forest cover types. In the third step, we used the covariates from the top-ranked model in the second step and included additional covariates that represented different types of forest disturbance. By using this hierarchical approach, we were able to control for existing habitat conditions within each territory when assessing the impacts of forest disturbance. For steps 1 and 2 of our modeling, we used the entire 20-year data set. For step 3, we used the covariates from the most parsimonious models from step 2, but then used reduced data sets for the three temporal scales because we lacked timber harvest data for years prior to 1993. None of the covariates that we used were highly correlated with each other ($r > 0.60$).

Previous studies of our study population revealed that high canopy cover and large trees were important components of nesting and roosting conditions used by Spotted Owls (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). Therefore, in step 1 of our analysis we evaluated support for the combined areas of vegetation classes 5 and 7 (57; model 1.1) and the combined areas of vegetation classes 6 and 7 (67; model 1.4). Vegetation

⁶ www.fs.usda.gov/main/r5/landmanagement/gis

⁷ ftp.fire.ca.gov/forest/

⁸ <http://frap.fire.ca.gov/data/frapgisdata-subset.php>

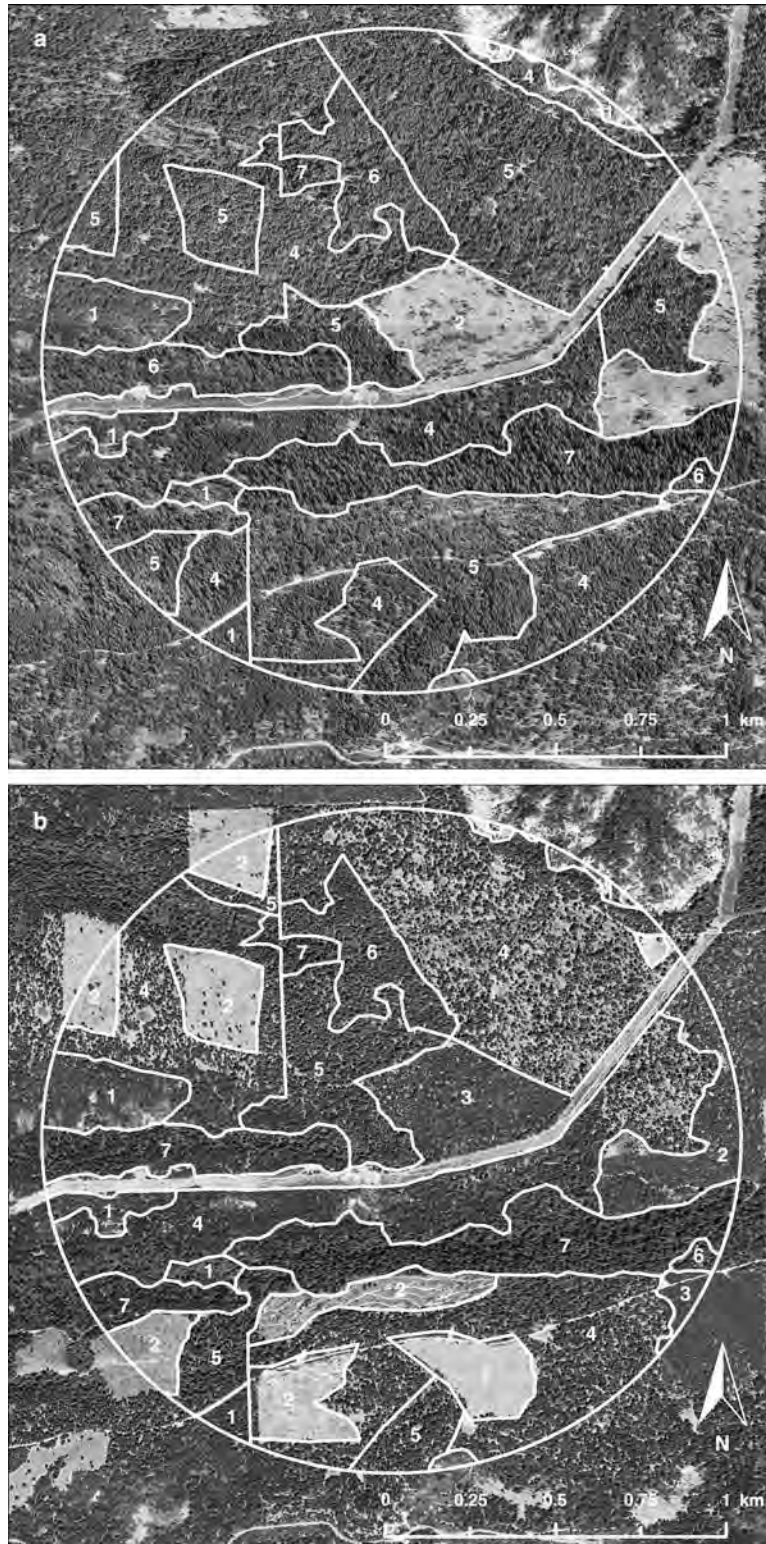


FIG. 1. Example of a vegetation cover map based on aerial photographs taken in 1993 (a) and 2012 (b) for a California Spotted Owl (*Strix occidentalis occidentalis*) territory on our study area in the central Sierra Nevada, California, USA. The territory is delineated by a circular boundary that encompasses 400 ha. See Table 1 for definitions of the numbered vegetation classes.

TABLE 2. List of a priori models for three-step modeling of reproduction, survival, and territory occupancy of Spotted Owls in the central Sierra Nevada, California, USA.

Model	Covariates	Description
Step 1		
1.1	57	linear relationship with area (ha) of classes 5 + 7
1.2	log(57)	log-linear relationship with area (ha) of classes 5 + 7
1.3	57 + (57) ²	quadratic relationship with area (ha) of classes 5 + 7
1.4	67	linear relationship with area (ha) of classes 6 + 7
1.5	log(67)	log-linear relationship with area (ha) of classes 6 + 7
1.6	67 + (67) ²	quadratic relationship with area (ha) of classes 6 + 7
Step 2		
2.1	[step 1]† + hardwoods	[step 1] + area (ha) of hardwoods
2.2	[step 1] + edge	[step 1] + edge (km) between vegetation class 2 and classes 4, 5, 6, and 7
2.3	[step 1] + private	[step 1] + area (ha) of private land
2.4	[step 1] + habitat diversity	[step 1] + habitat diversity (Shannon-Wiener)‡
2.5	[step 1] + mean patch size	[step 1] + mean habitat patch size (ha)‡
Step 3		
3.1	[step 2]§ + high	[step 2] + area (ha) of high-intensity harvests
3.2	[step 2] + fire	[step 2] + area (ha) of wildfire
3.3	[step 2] + understory	[step 2] + area (ha) of medium-intensity harvests with understory removal
3.4	[step 2] + medium	[step 2] + area (ha) of all medium-intensity harvests
3.5	[step 2] + low	[step 2] + area (ha) of low-intensity harvests
3.6	[step 2] + [treatment] + interaction between habitat and treatment	[step 2] + variables from best model among 3.1–3.6 + interaction with step 1 habitat

Note: We used the same models for all three time scales that we considered (3, 6, and 9 years); vegetation classes are defined in Table 1.

† The variables from the top model in step 1.

‡ Habitat diversity and mean patch size were calculated using either 57 or 67, depending on which habitat variable (if any) was in the best step 1 model. Combined area of vegetation classes 5 and 7 includes the amount of forest with high ($\geq 70\%$) canopy cover and a dominant tree size of ≥ 30.5 cm dbh; combined area of vegetation classes 6 and 7 includes the amount of forest dominated by large trees ≥ 61.0 cm dbh with a lower threshold ($\geq 30\%$) for canopy cover.

§ Variables from the top model in step 2.

classes 5 and 7 represented the amount of forest with high ($\geq 70\%$) canopy cover and a dominant tree size of ≥ 30.5 cm diameter at breast height (dbh). In addition to providing nesting and roosting conditions, this forest type provides habitat for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel 1995), which were the primary prey item of Spotted Owls on our study area (R. J. Gutiérrez, unpublished data). Vegetation classes 6 and 7 represented the amount of forest dominated by large trees (≥ 61.0 cm dbh) with a lower threshold ($\geq 30\%$) for canopy cover. The current management plan for national forests in the Sierra Nevada (USFS 2004) contains harvest limits on both canopy cover (minimum 40–50% postharvest) and tree size (< 76.2 cm dbh). Although these two covariates (57, 67) were correlated ($r = 0.60$), we chose to retain both covariates in our analyses to test whether high canopy cover or large trees were more important components of owl habitat. We also considered log-linear (models 1.2, 1.5) and quadratic (models 1.3, 1.6) relationships because such relationships between habitat and Spotted Owl vital rates have been detected in other regions (Franklin et al. 2000, Dugger et al. 2005, Forsman et al. 2011). We included a covariate for age (a subadult is 1 or 2 years old, an adult is at least 3 years old) when modeling survival and reproduction, and a covariate for sex when modeling survival, because age and sex have been shown to be important predictors of these vital

rates for Spotted Owls (Blakesley et al. 2010). Finally, we included a null model without explanatory covariates in which each vital rate had a constant value over time.

In step 2 of our analysis, we hypothesized that hardwood forests (vegetation class 1; model 2.1) may support greater densities of dusky-footed woodrats (*Neotoma fuscipes*) than other forest types (Sakai and Noon 1993, Innes et al. 2007); woodrats are an important prey item for Spotted Owls on our study area, especially at lower elevations (unpublished data). We posited that the amount of edge between shrubs or saplings (vegetation class 2) and forests dominated by trees ≥ 30.5 cm (vegetation classes 4, 5, 6, and 7; model 2.2) may have positively affected Spotted Owl vital rates because the presence of brush fields adjacent to older forest may increase the availability of woodrats to owls (Sakai and Noon 1997). We hypothesized that the area of private land (model 2.3) may negatively affect Spotted Owl vital rates because data from a radiotelemetry study conducted in our study area during 2006–2007 suggested that owls use private lands less than expected, possibly owing to a history of more intensive timber harvests on private land (Williams et al. 2014). Finally, we hypothesized that the spatial arrangement of owl habitat may affect owl vital rates (Franklin et al. 2000). For example, high interspersed of different forest cover types within a territory may allow owls to more easily meet all of their life history requirements (nesting,

roosting, foraging). We first examined the correlation between several potential territory spatial metrics (mean distance between patches, mean patch size, number of patches, diversity) and found that most were correlated with each other or with habitat covariates from step 1 ($r > 0.60$). Thus, we chose to use two metrics that were not highly correlated with each other or with the step 1 covariates: the Shannon-Wiener diversity index (model 2.4) and the mean size of owl habitat patches (model 2.5). We calculated these metrics for the owl habitat type (57 or 67) found in the best model from step 1. We log-transformed all step 2 covariates (except for the Shannon-Wiener diversity index) for our analyses because their distributions were right-skewed.

In step 3 of our analysis, we introduced covariates that represented the potential effects of forest disturbances. Disturbances generally consisted of timber harvest, but also included wildfires that occurred within 12 owl territories during our study. We expected all types of disturbance to negatively impact vital rates of Spotted Owls, and ranked them in order of the expected magnitude of their effects as follows: high-intensity harvests, wildfire, medium-intensity harvests with understory removal, all medium-intensity harvests, and low-intensity harvests (models 3.1–3.5). We ranked wildfire second because most of the acreage burned on our study area was the result of a single fire in 2001 that was predominantly a stand-replacing fire and impacted eight territories to varying degrees. We then sequentially added the disturbance covariates to the best model from step 2 in order of their expected impact and retained the covariate in the model if it reduced the model's AIC value. Finally, we considered a model (model 3.6) in which the amount of habitat (57 or 67) interacted with the disturbance covariate(s) from the best model among models 3.1–3.5. We considered this a test of the hypothesis that territories containing relatively large amounts of Spotted Owl habitat would be more resilient to disturbance (Seamans and Gutiérrez 2007a). All step 3 covariates were right-skewed, so we added 1 to their values and log-transformed them for our analyses.

Statistical modeling

Reproduction.—We used mixed-model analysis of variance (PROC MIXED in SAS 9.3; Littell et al. 2006) to test the a priori hypotheses described previously with respect to reproduction. In these analyses, we treated reproduction (i.e., the number of young fledged per territory per year) as the dependent variable, habitat covariates and female age (subadult or adult) as fixed effects, and territory identity and year (1993–2012) as random effects. We considered territory to be a random blocking factor because reproduction within a territory may not be independent among years. We treated reproduction as a normally distributed variable because McDonald and White (2010) found that analysis of variance procedures based on a normal distribution performed well for small count data similar to ours.

Moreover, before examining a priori habitat models, we used restricted maximum likelihood estimation to model the following potential variance–covariance structures within territories across years: compound symmetric, first-order autoregressive, heterogeneous first-order autoregressive, and log-linear (Littell et al. 2006). Once we identified the best variance–covariance structure (i.e., lowest AIC value), we used full maximum likelihood estimation to model the influence of the fixed effects on reproduction according to the framework just described. We considered female age a factor in all models, based on differences in reproduction between subadults and adults in previous studies (Blakesley et al. 2010).

Survival.—We used the Cormack-Jolly-Seber open-population model (CJS; Cormack 1964, Jolly 1965, Seber 1965) implemented in the R package *marked* (Laake et al. 2013) to test the a priori hypotheses previously described with respect to apparent survival of Spotted Owls. Apparent survival refers to the inability to differentiate between true mortality and permanent emigration from the study area. Although capture histories were developed based on the capture and resighting of individual Spotted Owls, our goal was to make inferences based on the habitat occupied by an owl, which varied by territory. Thus, we modified the capture histories used for the temporal analyses to reflect movement among territories (sensu Franklin et al. 2000). If an individual was not resighted for one or more years and was then resighted on a new territory, we removed the portion of its capture history pertaining to the original territory. We did this to avoid making assumptions about the owl's location during the intervening period. As a result, we used partial capture histories for 14 of the 350 individuals in our data set.

No methods exist for estimating overdispersion ($\hat{c}$) in CJS models containing individual covariates (Jeff Laake, *personal communication*), so instead we used Program MARK to estimate $\hat{c}$ for our most highly parameterized model without covariates, $\phi(\text{age} \times \text{sex} \times \text{year})$ and $p(\text{age} \times \text{sex} \times \text{year})$. We found no evidence for a lack of model fit ($\hat{c} = 0.998$). Prior to modeling survival rates, we first examined a priori model structures for the probability of recapture (p). We examined three covariates that may influence recapture probabilities: age (subadult or adult), sex, and survey effort (the amount of time spent conducting walk-in surveys each year) (Blakesley et al. 2010). Using the best model structure for p , we then followed the framework described previously to model the influence of habitat and forest disturbance on apparent survival.

Occupancy.—We used a multi-season occupancy model with parameters for local extinction (ϵ_t) and local colonization (γ_t) of Spotted Owl territories (MacKenzie et al. 2003). We separately modeled the extinction and colonization processes using Program PRESENCE v. 5.9 (Hines 2006). When modeling extinction, we specified a full time structure for colonization (i.e.,

different parameter estimates for each year), and vice versa when modeling colonization. The primary sampling periods were each year of the study, and the secondary sampling periods were the 10 bimonthly intervals within each year. Two critical assumptions of this model were: (1) occupancy status at each territory did not change during the survey season (i.e., no permanent emigration); and (2) detections at each territory were independent (MacKenzie et al. 2006). Because nearly all of the owls on our study area were marked, we could determine when individuals moved among territories during the survey season. Such movements only occurred on 10 occasions during our study, and we only considered one of the territories to be occupied in these situations (i.e., where the individual was most frequently detected). In addition, we excluded nocturnal detections >400 m from a territorial core area to help ensure independence of detections at territories. Finally, we interpreted occupancy as the proportion of territories used by owls during a breeding season because some territories may not have been continuously occupied throughout the entire season (MacKenzie et al. 2006).

We first examined a priori model structures for detection probabilities (p). For the occupancy analyses, p represented the probability of detecting an owl during a survey when the territory was occupied. Note that for the mark-recapture analyses, p represented the probability of recapturing an individual during a given year. We modeled within-year p using two covariates, *initial* and *repro* (Tempel and Gutiérrez 2013). *Initial* specified a different p for all survey occasions subsequent to the first detection at a territory each year, and *repro* indicated whether owls attempted to nest at a territory that year. We then modeled annual p with the following temporal effects: linear, log-linear, quadratic, different for each year, and constant. We selected the model with the best-fitting time structure and then introduced covariates for vegetation class (57 and 67) relative to p and initial occupancy probability (ψ_1). Using the best model structure, we then followed the framework described previously to model the relationships between vegetation class and forest disturbance on territory extinction and colonization.

Sensitivity analyses

Life stage simulation.—We conducted life stage simulation analyses (LSA) to assess which covariates had the greatest influence on annual population growth rate (λ) of Spotted Owls by estimating the amount of variation in λ explained by each covariate that appeared in the top-ranked models of reproduction and survival (Wisdom et al. 2000). We used a stage-based, post-breeding census Lefkovich matrix model parameterized with reproductive and survival rates to represent changes in female population size:

$$\begin{bmatrix} N_{J,t+1} \\ N_{S1,t+1} \\ N_{S2,t+1} \\ N_{A,t+1} \end{bmatrix} = \begin{bmatrix} 0 & \phi_{S,t}b_{S,t} & \phi_{S,t}b_{A,t} & \phi_{A,t}b_{A,t} \\ \phi_{J,t} & 0 & 0 & 0 \\ 0 & \phi_{S,t} & 0 & 0 \\ 0 & 0 & \phi_{S,t} & \phi_{A,t} \end{bmatrix} \begin{bmatrix} N_{J,t} \\ N_{S1,t} \\ N_{S2,t} \\ N_{A,t} \end{bmatrix} \quad (1)$$

where $N_{J,t}$, $N_{S1,t}$, $N_{S2,t}$, and $N_{A,t}$ were the number of juvenile, first-year subadult, second-year subadult, and adult females at time t , respectively; $\phi_{J,t}$, $\phi_{S,t}$, and $\phi_{A,t}$ were the apparent survival rates of juvenile, subadult, and adult females from time t to $t + 1$, respectively; and $b_{S,t}$ and $b_{A,t}$ were the fecundity rates for subadult and adult females at time t , respectively. Fecundity was the number of female offspring produced per female in the population. We assumed a 1:1 sex ratio of offspring and divided the reproductive rate from our reproduction model by two. We estimated λ as the dominant eigenvalue of the matrix.

We expressed apparent survival and fecundity as functions of covariates and set the beta coefficients for all covariate effects equal to their estimated values from the top-ranked models for apparent survival and fecundity (Table 3). As an example, apparent survival was estimated as

$$\text{logit}(\phi) = \beta_0 + \beta_1 \times \text{sex} + \beta_2 \times \text{age} + \beta_3 \times \log(57) + \beta_4 \times \text{edge} \quad (2)$$

where sex is 0 for females and 1 for males, and age is 0 for subadults and 1 for adults. Thus, apparent survival for non-juvenile females was estimated as

$$\text{logit}(\phi) = -1.010 + 0.452 \times \text{age} + 1.004 \times \log(57) + 0.763 \times \text{edge}. \quad (3)$$

We allowed the vegetation covariates to vary between the minimum and maximum values observed within any territory during the 20-year study period (range for area of 57 is 0–332.8 ha; range for edge is 0–28.5 km). In addition, we lacked reliable estimates of juvenile survival for our study area, so we used the reported estimate from an insular population of California Spotted Owls ($\phi_{J,t} = 0.368$; LaHaye et al. 2004). We ran additional simulations in which we allowed juvenile survival to range from 0.318 to 0.418, and the results were nearly identical. We used SAS 9.3 (SAS Institute, Cary, North Carolina, USA) to conduct 1000 simulations in which we randomly generated sets of vegetation class covariate values from uniform probability distributions, estimated λ for each simulation, and regressed λ against each vegetation covariate for all 1000 simulations. The percentage of variation in λ that was explained by each vegetation covariate was a measure of the sensitivity of λ to changes in the vegetation covariate (Wisdom et al. 2000).

Occupancy.—Analogous to the LSA, we assessed which vegetation covariates had the greatest influence on the equilibrium territory occupancy (ψ_{Eq}) by estimating the variation in ψ_{Eq} explained by each covariate that appeared in our best-fitting dynamic

TABLE 3. Model results for analyses of California Spotted Owl reproduction (number of young fledged), apparent survival, territory extinction, and territory colonization at a 6-year time scale in the central Sierra Nevada, 1993–2012.

Model covariates	<i>k</i>	AIC	ΔAIC	<i>w_i</i>
Reproduction				
Female age + hardwoods + medium	8	1205.1	0.00	0.29
Female age + hardwoods	7	1205.6	0.50	0.23
Female age + hardwoods + high	8	1206.0	0.90	0.19
Female age + hardwoods + fire	8	1207.1	2.00	0.11
Female age + hardwoods + low	8	1207.4	2.30	0.09
Female age + hardwoods + understory	8	1207.5	2.40	0.09
Adult survival				
Sex + age + log(57) + edge	9	1311.11	0.00	0.32
Sex + age + log(57) + edge + medium	10	1312.82	1.71	0.14
Sex + age + log(57) + edge + understory	10	1313.07	1.96	0.12
Sex + age + log(57) + edge + high	10	1313.07	1.96	0.12
Sex + age + log(57) + edge + low	10	1313.10	1.99	0.12
Sex + age + log(57) + edge + fire	10	1313.11	2.00	0.12
Sex + age + log(57) + edge + medium + medium × log(57)	11	1314.39	3.28	0.06
Territory extinction				
57 + diversity(57) + high	39	3808.93	0.00	0.30
57 + diversity(57) + high + medium	40	3809.63	0.70	0.21
57 + diversity(57) + high + fire	40	3810.34	1.41	0.15
57 + diversity(57) + high + understory	40	3810.80	1.87	0.12
57 + diversity(57) + high + low	40	3810.85	1.92	0.11
57 + diversity(57) + high + high × 57	40	3810.92	1.99	0.11
57 + diversity(57)	38	3815.70	6.77	0.01
Territory colonization				
log(57) + diversity(57) + fire	39	3800.63	0.00	0.32
log(57) + diversity(57) + fire + medium	40	3802.25	1.62	0.14
log(57) + diversity(57) + fire + understory	40	3802.28	1.65	0.14
log(57) + diversity(57) + fire + low	40	3802.38	1.75	0.14
log(57) + diversity(57) + fire + fire × log(57)	40	3802.63	2.00	0.12
log(57) + diversity(57)	38	3803.02	2.39	0.10
log(57) + diversity(57) + high	39	3804.94	4.31	0.04

Notes: Shown are values for *k*, the number of model parameters; AIC, Akaike's information criterion; ΔAIC, the difference in AIC value from the top-ranked model; and *w_i*, AIC weight. See Table 2 for covariate definitions. Combined vegetation classes 5 and 7 (57) and classes 6 and 7 (67) are as defined in Table 2.

occupancy models. If local extinction (ϵ) and local colonization (γ) rates are constant, ψ_{Eq} can be calculated as $\gamma/(\gamma + \epsilon)$ (MacKenzie et al. 2006). This equation was equivalent to a mainland–island metapopulation model with no rescue effect (Hanski 1999), where each territory was a “subpopulation” within a larger population of Spotted Owl territories. Although owl territories were not strictly subpopulations, they represented breeding units within our study area because we defined them as locations where reproduction was observed at least once. The proportion of occupied territories probably never reached equilibrium during our study, so the actual values of ψ_{Eq} should be interpreted with caution. Nevertheless, we believe that our approach provided general insight into the importance of habitat and forest disturbance to occupancy dynamics of Spotted Owls.

We again set the beta coefficients for all covariate effects equal to their estimated values from the top-ranked models and allowed the vegetation covariates (except for the amount of wildfire, which we will discuss) to vary between their minimum and maximum observed values. As with the LSA, we used SAS 9.3 to conduct 1000 simulations, determined ψ_{Eq} for each simulation, and regressed ψ_{Eq} against each vegetation covariate for all 1000 simulations.

We handled the wildfire covariate, which appeared in the territory colonization model, in a more spatially explicit manner. The effect of wildfire on territory colonization was strongly negative due to a high-severity fire that occurred on our study area in 2001 and completely burned two territories, which subsequently were never colonized by owls. However, most owl territories were unaffected by wildfire because fire occurred within only 12 territories during our study. Therefore, we defined two types of territories, burned and unburned. For each simulation, we randomly varied the number of territories that burned from 1 to 12. For burned territories, we then randomly varied the amount of wildfire from 0 to 400 ha. We separately calculated γ and ψ_{Eq} for burned and unburned territories and calculated an overall ψ_{Eq} for the 74 territories as a weighted average of ψ_{Eq} . We regressed ψ_{Eq} against the average amount of wildfire in all 74 territories; for example, if 100 ha of wildfire occurred in six territories during a simulation, then the average amount of wildfire per territory was 8.1 ha (600/74). In addition, we conducted 1000 additional simulations in which we varied the number of burned territories from 1 to 24 to represent a scenario of increased wildfire activity.

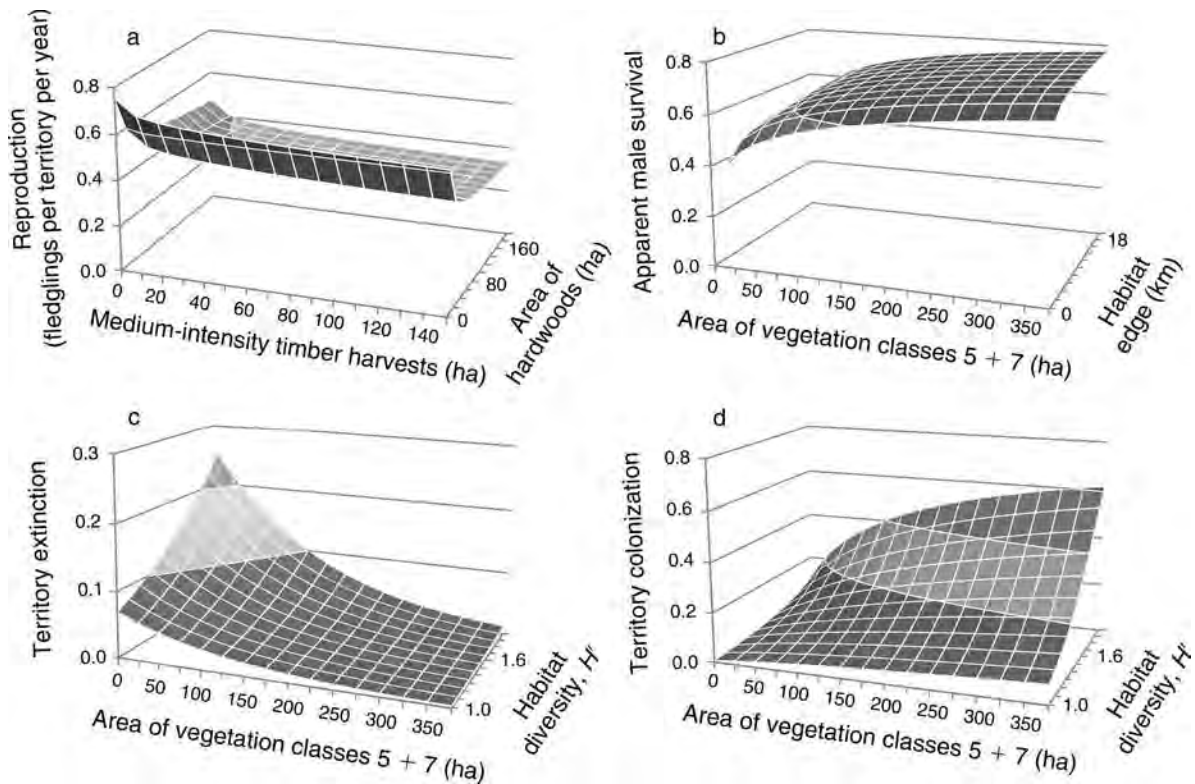


FIG. 2. Vital rates of California Spotted Owls in the central Sierra Nevada, California, 1993–2012, as a function of habitat, timber harvest, and wildfire covariates. We show (a) reproduction for adult females (number of young fledged per territory per year) vs. the total area of medium-intensity timber harvests in the previous 6 years and the area of hardwood forests within owl territories; (b) apparent survival for adult males vs. the total area of vegetation classes 5 and 7 and the amount of habitat edge within owl territories; (c) territory extinction (the probability that a territory occupied in year t becomes unoccupied in year $t + 1$); and (d) territory colonization (the probability that a territory not occupied in year t becomes occupied in year $t + 1$) as a function of the total area of classes 5 and 7 and habitat diversity (Shannon-Wiener index).

RESULTS

The results from the reproduction, survival, and occupancy analyses were similar for the three temporal scales (3, 6, and 9 years) used to calculate the timber harvest and wildfire covariates. Thus, we only present results for models containing timber harvest and wildfire covariates using the 6-year time frame, and we used this time frame for the sensitivity analyses as well. We present results for the 3- and 9-year time frames in Appendix C.

Reproduction

We assessed reproduction on 676 occasions at 70 territories, excluding territories with fewer than three reproductive observations and cases in which territories were occupied by a single owl. There were, on average, 0.612 ± 0.032 young fledged per territory per year (mean $\pm$ SE), and we detected 0, 1, 2, and 3 young on 62.1%, 14.8%, 22.8%, and 0.30% of the sampling occasions, respectively. The autoregressive variance-covariance structure was supported over the compound-symmetric ($\Delta\text{AIC} = 7.6$) or default ($\Delta\text{AIC} = 13.9$) variance-covariance structures. This structure indicated that reproduction in consecutive years was negatively corre-

lated ($\text{ARH1} = -0.148$, $\text{SE} = 0.048$) and was used in all subsequent modeling of fixed effects. The random year and territory effects were either statistically significant or nearly statistically significant (for year, $Z = 2.74$, $P = 0.003$; for territory, $Z = 1.28$, $P = 0.100$), so we retained both random effects when modeling fixed effects.

None of the vegetation covariates considered in step 1 (linear and nonlinear forms of 57 and 67) lowered the AIC value when added to a model containing only female age (Appendix C). The top-ranked model from step 2 included covariates for the area of hardwood forest within a territory and female age, and was 2.90 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 contained a covariate for the area of medium-intensity timber harvests, but this model was only 0.50 AIC units lower than the best model from step 2 (Table 3). This model suggested a negative influence of medium-intensity (subscript “med”) timber harvests on reproduction of Spotted Owls, but we found only weak support for this effect based on the degree to which the 95% CI of the beta coefficient overlapped zero ($\beta_{\text{med}} = -0.065$, 95% CI = -0.145 to 0.016 ; Fig. 2a). In addition, adult females (subscript “ad”) had higher

reproduction than subadults ($\beta_{ad} = 0.335$, 95% CI = 0.136–0.533), and reproduction was negatively related to the area of hardwood (“hw”) forests ($\beta_{hw} = -0.123$, 95% CI = -0.219 to -0.027) (Fig. 2a).

Survival

We estimated apparent survival using 350 individual capture histories. The best structure for recapture probability contained covariates for age, sex, and survey effort. Recapture probability was higher for adults ($\beta_{ad} = 1.320$, 95% CI = 0.522–2.119) and males ($\beta_{male} = 0.571$, 95% CI = 0.121–1.022) and was positively correlated with annual survey effort (“eff”) ($\beta_{eff} = 1.607$, 95% CI = 0.342–2.872). We used this structure for recapture probability in all subsequent modeling of survival. Real values of recapture probability estimates were high. When annual survey effort was set equal to its mean value, recapture probability was estimated to be 0.92, 0.87, 0.75, and 0.63 for adult males, adult females, subadult males, and subadult females, respectively.

The top-ranked survival model in step 1 (Appendix C) contained covariates for sex, age, and the logarithm of the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 also contained a covariate for the amount of habitat edge within a territory, and was 7.14 AIC units lower than the second-ranked model (Appendix C). None of the step 3 covariates (timber harvest, wildfire) lowered the AIC value when added to the best model from step 2. The second-ranked overall model ($\Delta AIC = 1.71$) contained a covariate for the area of medium-intensity timber harvests (Table 3), but this model was poorly supported, given that the maximum possible ΔAIC is 2 when an uninformative parameter is added (Arnold 2010). In the top-ranked model, adults ($\beta_{ad} = 0.452$, 95% CI = 0.016–0.889) and males ($\beta_{male} = 0.304$, 95% CI = 0.034–0.575) had higher survival rates than subadults and females, respectively. Survival was positively correlated with the area of 57 ($\beta_{\log(57)} = 1.004$, 95% CI = -0.337 to 2.345) (Fig. 2b) and the amount of edge ($\beta_{edge} = 0.763$, 95% CI = -0.104 to 1.629) (Fig. 2b), but the 95% CI for the beta coefficients overlapped zero. If we set the habitat covariates equal to their mean value for all territories, apparent survival was estimated to be 0.73, 0.66, 0.63, and 0.56 for adult males, adult females, subadult males, and subadult females, respectively.

Occupancy

We estimated territory extinction and colonization probabilities using 4907 survey occasions. The best model for detection probability (p) indicated that p was different for each year. Within years, p was higher at territories with reproducing owls ($\beta_{repr} = 1.566$, 95% CI = 1.339–1.794), at territories containing more forest dominated by large trees ($\beta_{67} = 0.017$, 95% CI = 0.000–0.033), and on surveys subsequent to the initial (“init”) detection of owls at a territory ($\beta_{init} = 1.185$, 95% CI = 1.011–1.359). The probability of initial occupancy (ψ_1) was not dependent on the amount of vegetation classes

57 or 67 within a territory (i.e., ψ_1 was constant). We used this structure for detection and initial occupancy probabilities for all subsequent modeling of territory extinction and colonization. Real values of detection probability estimates were high. When the area of forest with large trees was set equal to its mean value for all territories, detection probability was estimated to be 0.94, 0.83, 0.77, and 0.50 at territories with reproducing owls after the initial detection, territories with reproducing owls before the initial detection, territories with nonreproducing owls after the initial detection, and territories with nonreproducing owls before the initial detection, respectively.

Territory extinction.—The top-ranked model from step 1 (Appendix C) contained a covariate for the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 included a covariate for habitat diversity in addition to the area of 57 and was 4.28 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 also included the area of high-intensity timber harvests. In this model, territory extinction was negatively correlated with the area of 57 ($\beta_{57} = -0.117$, 95% CI = -0.189 to -0.044), such that occupied territories with greater amounts of 57 were less likely to become extinct (Fig. 2c). Surprisingly, territory extinction was also negatively correlated with the area of high-intensity timber harvests ($\beta_{high} = -0.776$, 95% CI = -1.327 to -0.224). Finally, territory extinction was positively correlated with habitat diversity ($\beta_{div} = 1.509$, 95% CI = 0.148–2.871) (Fig. 2c).

Territory colonization.—The top-ranked model from step 1 (Appendix C) contained a covariate for the logarithm of the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 contained an additional covariate for habitat diversity and was 1.57 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 included the area of wildfire that occurred within a territory. In this model, wildfire had a strong negative effect on territory colonization ($\beta_{fire} = -24.057$), but the standard error was unestimable because of the small number of territories that experienced fire. However, the value for β_{fire} was consistent across all of the models. Territory colonization was positively correlated with the area of 57 ($\beta_{\log(57)} = 1.299$, 95% CI = -0.857 to 3.456) (Fig. 2d) and habitat diversity ($\beta_{div} = 2.985$, 95% CI = -0.222 to 6.191) (Fig. 2d), but the beta coefficients had 95% CI's that overlapped zero, suggesting that these effects were relatively weak.

Sensitivity analyses

Life stage simulation.—Estimates of apparent survival from our simulations ($\hat{\phi}_A = 0.68$, 95% CI = 0.54–0.76; $\hat{\phi}_S = 0.58$, 95% CI = 0.42–0.67) were lower than those previously reported for this population (Blakesley et al. 2010) because we removed part of the capture histories for 14 individuals that relocated to different

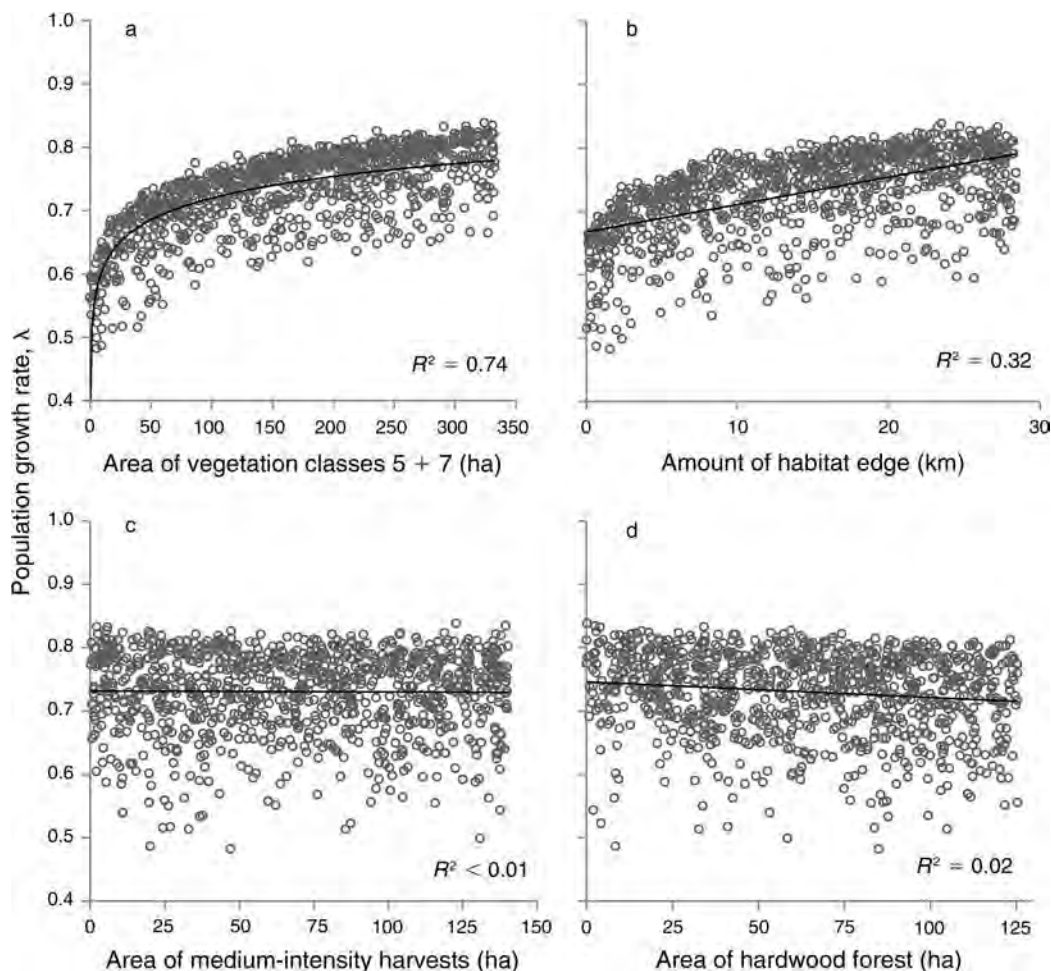


FIG. 3. Results of a life stage simulation analysis that we used to assess the sensitivity of annual population growth rate (λ) of California Spotted Owls to changes in forest vegetation conditions within owl territories. We generated 1000 λ values by randomly drawing (a) area of vegetation classes 5 and 7; (b) amount of habitat edge; (c) area of medium-intensity timber harvests; and (d) area of hardwood forest from a uniform distribution. Panel (a) is a best-fit logarithmic regression, and all other panels are best-fit linear regressions.

territories after a “missing” interval of one or more years (see *Methods: Sensitivity analyses*). Estimates of fecundity from our simulations were higher for adults ($\hat{b}_A = 0.22$ female offspring per female, 95% CI = 0.18–0.28) than for subadults ($\hat{b}_S = 0.05$ female offspring per female, 95% CI = 0.02–0.11), a pattern that has been previously reported for this study population (Blakesley et al. 2010).

Population growth rate was most sensitive (positive correlations) to the area of 57 and habitat edge, the two covariates that also best explained variation in apparent survival. We noted that population growth rate and the area of 57 were clearly related in a nonlinear fashion, so we calculated R^2 using a logarithmic relationship for this covariate; we specified a linear relationship for all other covariates. Population growth rate was positively correlated with the area of 57 ($R^2 = 0.74$; Fig. 3a) and habitat edge ($R^2 = 0.32$; Fig. 3b). In contrast, population growth rate was not sensitive to either of the covariates

used to model reproduction (for area of medium-intensity harvests, $R^2 < 0.01$; for area of hardwood forests, $R^2 = 0.02$; Fig. 3c, d). Population growth rate was always less than 1.0 ($\hat{\lambda} = 0.73$, 95% CI = 0.57–0.82), but we expected our matrix model to underestimate λ in the presence of immigration (Peery et al. 2006). Additionally, as we have noted, our apparent survival estimates were biased low. Nonetheless, changes in population growth rate allowed us to evaluate the relative importance of each covariate.

Occupancy.—Estimates of territory colonization from our simulations were strongly dependent upon the occurrence of wildfire during the previous six years ($\hat{\gamma}$ without fire = 0.21, 95% CI = 0.04–0.52; $\hat{\gamma}$ with fire = 0.00, 95% CI = 0.00–0.00) because we only observed three postfire colonization events at burned territories in the following six years. However, fire did not negatively affect territory occupancy in all cases. For example, the largest and most intense fire occurred on our study area

in 2001 and impacted nine owl territories. Five of these territories remained occupied every year after the fire, and thus, postfire colonization could not occur at these sites. Estimates of territory extinction were low ($\hat{\epsilon} = 0.03$, 95% CI = 0.00–0.12), which reflected the strong site fidelity displayed by Spotted Owls (e.g., Blakesley et al. 2005, Seamans and Gutiérrez 2007a).

Equilibrium occupancy was most sensitive (positive correlation) to the area of 57 within a territory. We again noted a nonlinear relationship between equilibrium occupancy and the area of 57 and calculated R^2 using a logarithmic relationship for this covariate ($R^2 = 0.87$; Fig. 4a). Equilibrium occupancy was not sensitive to changes in habitat diversity ($R^2 = 0.02$; Fig. 4b) or high-intensity timber harvests ($R^2 = 0.01$; Fig. 4c). Equilibrium occupancy was weakly negatively correlated with wildfire when it occurred at the same frequency as during our study ($R^2 = 0.02$; Fig. 4d). However, when we doubled the frequency of wildfire to represent a future scenario of increased fire activity, we found a stronger negative association between the area burned and equilibrium occupancy ($R^2 = 0.11$; Fig. 4e). As a result, equilibrium occupancy was higher under the scenario with fewer fires ($\hat{\psi} = 0.78$, 95% CI = 0.37–0.96) than the scenario with more fires ($\hat{\psi} = 0.72$, 95% CI = 0.36–0.94).

DISCUSSION

We characterized associations between territory-scale changes in forest conditions and demographic rates in a declining population of California Spotted Owls to assess the potential consequences of implementing landscape-scale fuel treatments in the Sierra Nevada. Although the correlative nature of our study posed constraints on inferences, we used 20 years of data on owl demography, forest treatments, and detailed changes in forest conditions. Our study differed from most previous, long-term Spotted Owl studies in that we quantified habitat within owl territories on an annual basis, rather than assuming that habitat was static over time. Thus, we believe that the relationships that we detected can help to guide forest management intended to balance reductions in high-severity fires with the needs of a key old-forest-associated species in the Sierra Nevada, as well as provide insight into mechanisms responsible for observed declines in California Spotted Owls in this region.

The amount of forest with high (>70%) canopy cover dominated by medium- or large-sized trees was the most important predictor of variation in demographic rates; this variable occurred in the top-ranked models for survival, territory extinction, and territory colonization rates, and explained far more variation in population growth rate and equilibrium occupancy than other covariates based on our simulations. This result is consistent with previous studies of Northern and California Spotted Owls that found a strong correlation between the area of high-canopy-cover forest and adult

survival, and in some cases, reproduction and occupancy of territories (Franklin et al. 2000, Blakesley et al. 2005, Dugger et al. 2005, Seamans and Gutiérrez 2007a). We also found that forests with large trees and a lower threshold of canopy cover (>30%) were not a significant predictor of owl vital rates. This finding suggested that high canopy cover was a more important habitat component than large trees, although forests containing both were probably the highest quality habitat. The specific reasons for why high-canopy-cover forests are important for California Spotted Owls are unknown, but prey availability, predator avoidance, or microclimate may all be important factors (Verner et al. 1992). Nevertheless, consistent positive associations between demographic rates of Spotted Owls and forest with high canopy cover across studies and subspecies indicate the importance of these forest conditions for Spotted Owl populations.

The positive association between owl demographic rates and high-canopy-cover forest, coupled with the average loss of 10.6 ha (7.4%) of high-canopy-cover forest within territories on the DSA from 1993–2012 (Fig. 5a), suggests that habitat loss may have been at least partially responsible for the observed ~30% decline in abundance and territory occupancy in our study population (Tempel and Gutiérrez 2013). We were unable to assess the potential lag effects associated with habitat change prior to 1993, when more stringent harvesting guidelines were implemented on public land (USFS 1993); thus, observed declines could also reflect the historic legacy of timber harvesting. Nevertheless, many factors not considered here such as predation, prey availability, and disease, also could have contributed to population declines. Associations between high-canopy-cover forest and both population growth and equilibrium occupancy were nonlinear such that further loss of habitat could lead to relatively rapid declines in abundance and occupancy (Figs. 3a and 4a). For example, 26 owl territories currently contain between 100 and 150 ha of high-canopy-cover forest (Fig. 5b). If the average amount of high-canopy-cover forest within territories were reduced from 150 to 100 ha, the estimated decrease in population growth rate ($\lambda_{150\text{ha}} = 0.740$, $\lambda_{100\text{ha}} = 0.720$) would lead to a significant difference in realized population change when extrapolated over long time periods. We expected our estimates of population growth rate to be biased low, but the importance of forest with high canopy cover nevertheless can be assessed by relative changes in population growth rate.

As predicted, medium-intensity timber harvests characteristic of proposed fuel treatments were negatively related to reproduction of Spotted Owls in our study. Reproduction appeared sensitive to modest amounts of medium-intensity harvests, and was predicted to decline from 0.54 to 0.45 when 20 ha were treated (assuming the mean area of hardwoods in territories, 60 ha). Greater areas harvested in this manner only resulted in slightly

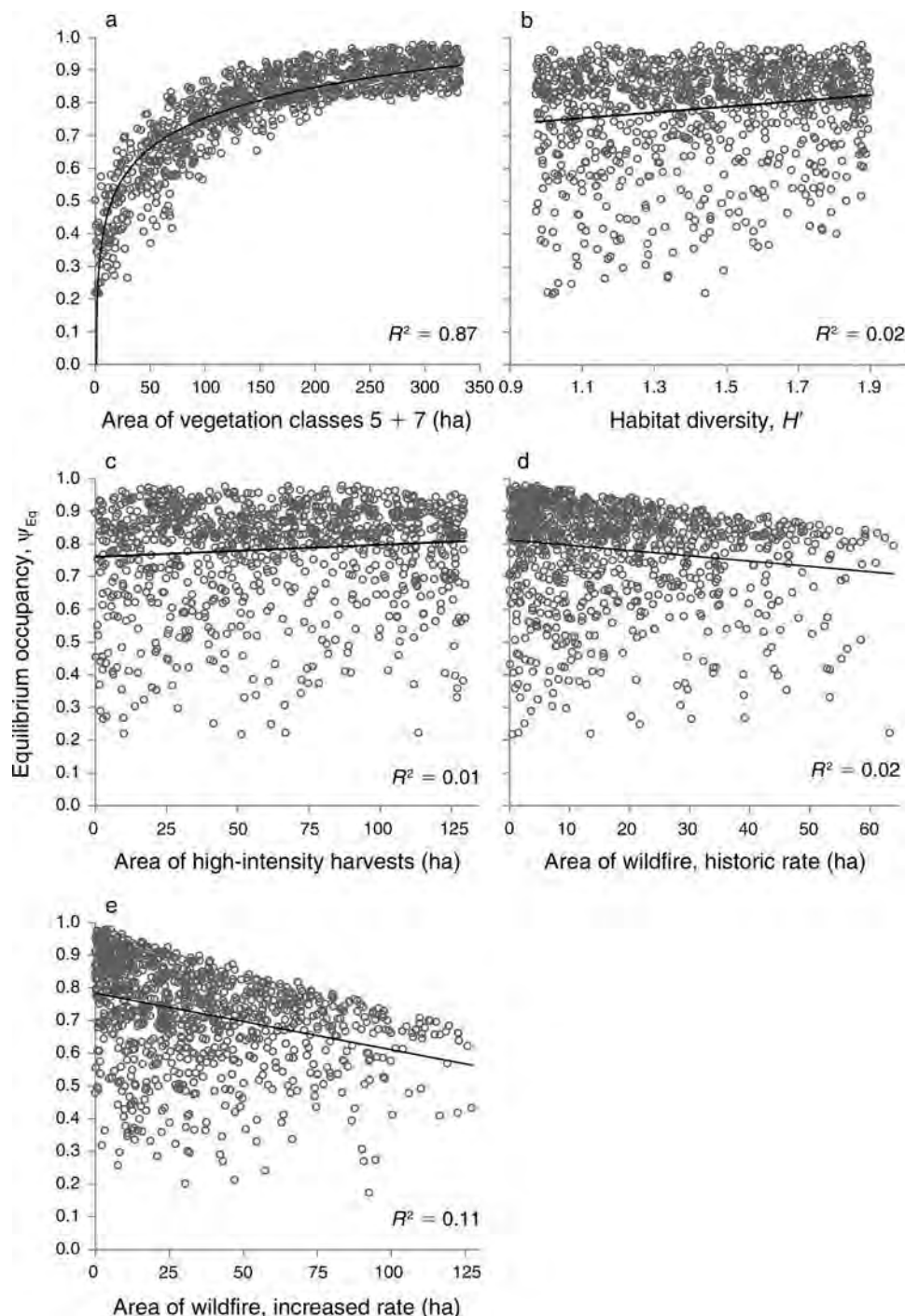


FIG. 4. Assessment of the sensitivity of equilibrium occupancy (ψ_{Eq}) of California Spotted Owl territories to changes in forest vegetation conditions within owl territories. We generated 1000 ψ_{Eq} values by randomly drawing: (a) area of vegetation classes 5 and 7; (b) habitat diversity (Shannon-Wiener index); and (c) area of high-intensity timber harvests from a uniform distribution. Panels (d) and (e) were generated under two different wildfire scenarios: a maximum of 12 territories burned (the observed number during our study) and a maximum of 24 territories burned (representing the potential for increased fire frequency in the future), respectively. Panel (a) is a best-fit logarithmic regression, and all other panels are best-fit linear regressions.

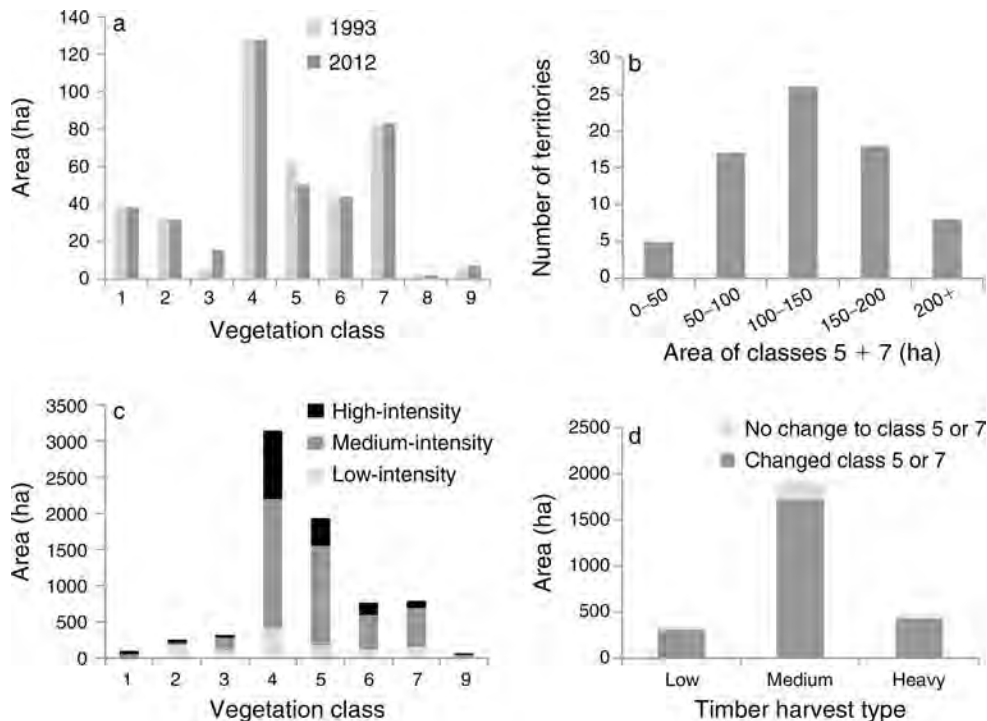


FIG. 5. Vegetation conditions within California Spotted Owl territories on our study area in the central Sierra Nevada, California, as represented by (a) the area of each vegetation class in owl territories on the Density Study Area in 1993 and 2012; (b) the number of owl territories containing different areas of vegetation classes 5 and 7 in 2012; (c) the area of low-, medium-, and high-intensity timber harvests that occurred in each vegetation class from 1993–2012 (class 8, water or barren rock, was omitted here as no timber harvest was possible); and (d) the area of low-, medium-, and high-intensity timber harvests occurring in vegetation classes 5 and 7 that did or did not result in a change in vegetation class from 1993 to 2012.

larger declines in reproduction (Fig. 2a). The mechanism linking medium-intensity timber harvests to declines in reproduction is not entirely clear, but the thinning practices characteristic of medium-intensity harvests typically reduce the vertical forest structure and understory complexity that are believed to be important characteristics of foraging conditions used by Spotted Owls (Verner et al. 1992). Although we detected an overall effect of medium-intensity timber harvests on reproduction, we did not detect an effect of understory removal independent of modifications to the overstory for medium-intensity harvests. Understory removal is generally an important component of fuel-reduction strategies, but we caution that medium-intensity harvesting with understory treatments occurred on only 5.2% of the total area within owl territories, which could have limited our power to detect effects.

Unlike reproduction, we did not detect a relationship between the area of medium-intensity harvests and apparent survival or territory occupancy. The absence of an association is perhaps not surprising, given the Spotted Owl's "bet-hedging" life history strategy in which individuals have evolved long life spans and forgo reproduction when environmental conditions are unfavorable without compromising lifetime reproductive success (Seamans and Gutiérrez 2007b). In addition, only

42.8% of medium-intensity harvests occurred in forests with high canopy cover; thus, over half of these harvests occurred in habitats that might be less important to Spotted Owls (Fig. 5c). When medium-intensity harvests were implemented within high-canopy-cover forests, they reduced the canopy sufficiently for mapped polygons to be reclassified into a lower-canopy-cover vegetation class in 90.1% of these treated areas (Fig. 5d). As we described previously, such changes were associated with reductions in survival and territory colonization rates, as well as increases in territory extinction rates. As a result, we believe that the most appropriate inference about the influence of medium-intensity harvesting practices is that they appear to reduce reproductive potential, and when implemented in forests with high canopy cover, are likely to reduce survival and territory occupancy as well.

Contrary to our prediction, the probability of a territory going extinct was reduced in proportion to the area harvested with high-intensity practices such as clear-cutting and shelterwood harvest. In principle, harvesting prescriptions creating small gaps might promote brushy habitat suitable for prey species such as woodrats and increase prey availability for Spotted Owls along the edges of forested habitats (Sakai and Noon 1997). Similarly, we found that owl survival and population growth were positively associated with the

amount of habitat edge between shrubs/saplings and forests dominated by trees ≥ 30.5 cm dbh, so the juxtaposition of owl and prey habitat could be important, as suggested by Franklin et al. (2000). Nevertheless, these associations are largely speculative without direct evidence of foraging by owls and elevated prey availability along ecotones. Moreover, high-intensity treatments occurred on only 5.4% of the total area within our owl territories and larger scale implementation of heavy harvesting could have adverse impacts on Spotted Owls. Finally, flying squirrels are the most important prey by biomass within our study area (R. J. Gutiérrez, *unpublished data*), and intensive harvesting practices are believed to negatively impact this species (Waters and Zabel 1995, Manning et al. 2012). Thus, while detailed studies of prey availability and Spotted Owl foraging near brush habitat are merited, we believe it would be premature to implement such timber-harvesting practices as a tool for managing prey availability for California Spotted Owls.

Although our results suggested that fuel treatments can have negative and direct impacts on Spotted Owl habitat quality in the short term, comprehensive assessments must consider the potential long-term benefits of reduced wildfire risk. Long-term benefits will depend on both the risk that fire poses to Spotted Owls and the extent to which fuel treatments reduce high-severity fires. We detected a large decline in territory colonization following wildfire, but not all burned territories were negatively affected by fire. Several burned territories remained occupied in all years after a fire (see *Results: Sensitivity analyses*); as a result, colonization could not occur, by definition. Thus, while our results were somewhat consistent with other studies that detected adverse impacts of high-severity fires on Spotted Owls, particularly when coupled with salvage logging (Clark et al. 2013, Lee et al. 2013), the effect of wildfire on Spotted Owls and their habitat is undoubtedly complex (Bond et al. 2009, 2013). Nonetheless, because equilibrium occupancy declined more under a scenario of increased fire activity (Fig. 4e), which is projected under some climate change scenarios (Liu et al. 2013), we believe a valid need exists to reduce the risk of wildfire to Spotted Owls. Previous modeling efforts indicated that the benefits of reducing habitat loss from high-severity fires outweighed the impacts of fuel treatments on forest conditions used by Spotted Owls (Lee and Irwin 2005, Ager et al. 2007). However, these studies were either conducted for Northern Spotted Owls in another physiographic province (Ager et al. 2007) or did not assess the immediate effects of fuel treatments on California Spotted Owl demographic rates using empirical data (Lee and Irwin 2005). Thus, additional research is needed to determine the long-term trade-offs between direct reductions in owl habitat from fuel treatments vs. habitat loss from increased fire frequency or severity.

We suggest the following caveats from our study when considering the impact to Spotted Owls from forest fuel

treatments and wildfire. First, our study was observational, not experimental, and thus observed relationships between covariates and owl demographic rates were correlative and not directly attributable to cause and effect. Second, a broad range of timber harvests occurred within owl territories during our study, which may have confounded our ability to assess specific management practices (e.g., fuel-reduction treatments following current management prescriptions; USFS 2004). Nevertheless, proposed fuel-reduction treatments have effects on forest structure similar to those in our medium-intensity timber harvest category (Appendix B). Third, we used aerial photos to compile our vegetation map, which required us to subjectively categorize vegetation classes into relatively coarse bins. Thus, we were unable to assess the potential effects of small (e.g., 10%) reductions in canopy cover that did not result in changes in vegetation class. Our mapping approach also precluded the inclusion of potentially important habitat elements such as large, residual trees and understory structure. Large trees are known to be important components of nesting and roosting conditions used by Spotted Owls (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997), and the high-canopy-cover forest that we found to be highly correlated with owl demographic rates included vegetation class 7 (trees with dbh ≥ 76.2 cm). Finally, the potential effects of habitat, forest treatments, and wildfire within owl territories were probably confounded with differences in individual quality, which can be an important source of variation in avian demographic rates (e.g., Goodburn 1991, Espie et al. 2004, Sergio et al. 2009). Despite these caveats, we identified several reasonable predictors of Spotted Owl demographic parameters supported by prior knowledge of Spotted Owl environmental requirements that we believe can contribute to forest management.

Conclusions

Our results suggest that reductions in the area of high-canopy-cover forest resulting from either logging or high-severity wildfire could reduce the viability of California Spotted Owl populations and may be contributing to ongoing declines in abundance and territory occupancy (Conner et al. 2013, Tempel and Gutiérrez 2013). Nevertheless, our results also suggest that fuel treatments that occur in forests with lower canopy cover ($< 70\%$) or do not significantly reduce canopy in high-canopy-cover forests are less likely to have adverse impacts on Spotted Owls. While such a constraint may seem restrictive because fuel-reduction treatments necessarily target dense, fire-prone stands, we note that 50.7% of all medium-intensity harvests implemented from 1993 to 2012 occurred in medium-sized forest with low canopy cover (vegetation class 4 = 40.1%) or large-sized forest with low canopy cover (vegetation class 6 = 10.6%; Fig. 5c). Moreover, fuel treatments in dense stands can emphasize thinning from below while maintaining sufficient canopy cover and some vertical stand structure (Verner et al. 1992).

Zielinski et al. (2013) recently concluded that it may be possible to implement fuel-reduction treatments that achieve fire-reduction goals without affecting occupancy by fishers, another species associated with older forests in the Sierra Nevada. However, they did not distinguish among different types of timber harvest, nor did they assess where timber harvests occurred with respect to preexisting vegetation types. We recommend that landscape-scale fuel treatments intended to reduce fire risk in the Sierra Nevada proceed with caution to reduce the chance of impacting old-forest-associated species, particularly in high-canopy-cover forests. Specifically, we recommend that fuel treatments focus on ladder fuels and reduction in tree density while maintaining relatively high canopy cover. Given the uncertain relationship between timber harvest and demography of Spotted Owls, we suggest that landscape-scale fuel treatments be accompanied by a rigorous monitoring program.

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SUPPLEMENTAL MATERIAL

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Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species

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Abstract. Fuels-reduction treatments are commonly implemented in the western U.S. to reduce the risk of high-severity fire, but they may have negative short-term impacts on species associated with older forests. Therefore, we modeled the effects of a completed fuels-reduction project on fire behavior and California Spotted Owl (*Strix occidentalis occidentalis*) habitat and demography in the Sierra Nevada to assess the potential short- and long-term trade-offs. We combined field-collected vegetation data and LiDAR data to develop detailed maps of forest structure needed to parameterize our fire and forest-growth models. We simulated wildfires under extreme weather conditions (both with and without fuels treatments), then simulated forest growth 30 years into the future under four combinations of treatment and fire: treated with fire, untreated with fire, treated without fire, and untreated without fire. We compared spotted owl habitat and population parameters under the four scenarios using a habitat suitability index developed from canopy cover and large-tree measurements at nest sites and from previously derived statistical relationships between forest structure and fitness (λ) and equilibrium occupancy at the territory scale. Treatments had a positive effect on owl nesting habitat and demographic rates up to 30 years after simulated fire, but they had a persistently negative effect throughout the 30-year period in the absence of fire. We conclude that fuels-reduction treatments in the Sierra Nevada may provide long-term benefits to spotted owls if fire occurs under extreme weather conditions, but can have long-term negative effects on owls if fire does not occur. However, we only simulated one fire under the treated and untreated scenarios and therefore had no measures of variation and uncertainty. In addition, the net benefits of fuels treatments on spotted owl habitat and demography depends on the future probability that fire will occur under similar weather and ignition conditions, and such probabilities remain difficult to quantify. Therefore, we recommend a landscape approach that restricts timber harvest within territory core areas of use (~125 ha in size) that contain critical owl nesting and roosting habitat and locates fuels treatments in the surrounding areas to reduce the potential for high-severity fire in territory core areas.

Key words: California Spotted Owl; fuels treatment; habitat; Sierra Nevada; *Strix occidentalis occidentalis*; territory fitness; territory occupancy; wildfire.

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INTRODUCTION

The management of fire-adapted forests in the western U.S. is increasingly challenged by the need to consider the ecological impacts of wildfire and fuels-reduction treatments intended to modify wildfire behavior (Stephens et al. 2013). Historic fire regimes in many of these forests were characterized by fires burning at intervals of less than 20 years and having primarily low- and moderate-severity fire effects but interspersed with some areas of high-severity effects (Agee 1993, Skinner and Chang 1996), and some high-severity fire apparently occurred with regularity (Collins and Stephens 2010, Hanson and Odion 2014). This type of fire regime resulted in highly heterogeneous landscapes in which vegetation conditions were governed by complex interactions between topography, site productivity, and disturbance (Collins et al. 2015, Stephens et al. 2015). However, decades of fire exclusion have disrupted historic fire regimes, altered forest structure and landscape vegetation patterns, increased forest fuel loads, and led to increases in the frequency of large fires (Westerling et al. 2006), as well as increases in proportions and patch sizes of high-severity fire (Miller et al. 2009, Miller and Safford 2012). In addition, further increases in fire activity are expected under most climate change scenarios (Westerling and Bryant 2008, Liu et al. 2013). High-severity fire effects (defined by >75% mortality of overstory trees) can impact ecosystem processes such as erosion rates, stream sedimentation, and carbon sequestration (Benavides-Solorio and MacDonald 2001, Breshears and Allen 2002), as well as modify forest structure and wildlife habitat. While some wildlife species become more abundant after high-severity fire (Smucker et al. 2005, Fontaine and Kennedy 2012), other species, particularly those associated with older forests, may be negatively impacted by habitat loss resulting from large patches of high-severity fire (e.g., Lee et al. 2013). Old-forest species with large home ranges are typically rare and preventing their

populations from reaching critically small sizes is widely regarded as an important policy objective (e.g., National Forest Management Act of 1976), in part because meeting the habitat needs of such species might protect broader old-forest communities (Temple 1997).

To reduce the potential for large patches of high-severity fire, forest managers are implementing fuels-reduction treatments in many western U.S. forests (e.g., USFS 2004). Fuels-reduction treatments primarily remove duff, downed wood, shrubs, and smaller trees (i.e., surface and ladder fuels), and fire models suggest that these treatments can reduce potential fire spread and intensity across landscapes (Ager et al. 2007, Finney et al. 2007). However, these treatments also reduce canopy cover and vertical forest structure, which could have negative short-term impacts on old-forest-associated species such as the spotted owl (*Strix occidentalis*). Hypothetically, such short-term negative impacts would be outweighed by the longer-term benefits from reductions in the amount of habitat lost during future wildfires, as has been suggested by previous simulations (Ager et al. 2007, Roloff et al. 2012). Similarly, the current management plan for the national forests in the Sierra Nevada posits that fuels-reduction treatments will result in long-term increases in the amount of suitable California Spotted Owl (*S. o. occidentalis*) habitat while acknowledging the potential for short-term negative impacts (USFS 2004). Indeed, a recent study found that fuels-reduction treatments can negatively impact spotted owl populations over shorter time frames (<10 years) if they reduce the amount of high-canopy-cover ($\geq 70\%$) forest dominated by trees ≥ 30.5 cm diameter at breast height (dbh) within owl territories (Tempel et al. 2014a). However, whether short-term impacts of fuels treatments to spotted owls and their habitat in the Sierra Nevada will be offset by long-term gains resulting from reductions in high-severity fire is unknown.

Here, we used fire and forest-growth models to simulate how fuels treatments might alter the

effects of fire on spotted owl habitat and demographic rates at the “fireshed” scale over a 30-year period in the Sierra Nevada. Firesheds are contiguous areas with similar fire histories and have been identified by the U.S. Forest Service as useful landscape units for fuels-treatment planning and effective fire suppression (Bahro et al. 2007, North et al. 2015). Firesheds are commonly delineated by sub-watershed boundaries and range in size from ~3,200 to 16,200 ha within the Sierra Nevada (North et al. 2015). We chose this spatial scale because of its management relevance (i.e., project planning) and because our field-based vegetation sampling would not have been feasible at larger spatial scales. In contrast to previous studies that relied upon simulated treatments (Ager et al. 2007, Roloff et al. 2012; but see Stephens et al. 2014), our study involved actual fuels-reduction treatments implemented by the U.S. Forest Service and was intended to assess the efficacy of existing management guidelines governing forest management at a bio-regional scale. We intensively sampled the vegetation within field plots before and after the implemented treatments and coupled this fine-scale vegetation data with LiDAR data to quantify changes in forest structure and parameterize fire and forest-growth models. Finally, we linked spotted owl demographic rates to changes in vegetation conditions resulting from fuels treatments and wildfire using data from a long-term demography study, as few previous studies have simulated the short- versus long-term trade-offs of fuel treatments on wildlife population dynamics (however, see Scheller et al. 2011). We specifically considered two demographic parameters at the scale of an owl territory: (1) fitness, which we defined as the population growth rate (λ) conferred on resident owls by habitat conditions within the territory (Franklin et al. 2000); and (2) equilibrium occupancy, which is the level at which occupancy probability at a territory will stabilize when colonization and extinction probabilities remain constant (MacKenzie et al. 2006).

We hypothesized that fuels treatments would result in a short-term loss of owl habitat, but in the event of simulated wildfire, these treatments would result in a long-term increase in owl habitat (relative to the untreated landscape) by reducing owl habitat loss to fire. Thus, if a fire

was simulated under extreme weather conditions shortly after treatment implementation, we predicted the treatments to reduce the amount of habitat lost during the fire and to result in greater habitat amounts 30 years post-fire because forest growth would be insufficient to compensate for the loss of overstory trees during this timeframe. If no fire was simulated after treatment implementation, we expected that the amount of habitat would initially decline, but that similar amounts would be present on treated and untreated landscapes after 30 years because of forest regrowth (Collins et al. 2011). Because owl demographic rates are strongly and positively correlated with the amount of high-canopy-cover ($\geq 70\%$) forest within owl territories (Tempel et al. 2014a), we predicted that owl demographic rates would follow similar patterns as habitat amount. Thus, we hypothesized that fuels treatments would reduce territory fitness and occupancy in the short-term, but result in higher fitness and occupancy after 30 years in the event of simulated fire.

MATERIALS AND METHODS

Study area

Our 13,482-ha Last Chance Study Area (LCSA) was located within the Tahoe National Forest in the central Sierra Nevada, California (Fig. 1). Elevations ranged from 600 to 2,200 m. The vegetation was primarily mixed-conifer forest dominated by white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and California black oak (*Quercus kelloggii*), with lesser amounts of other forest types and montane chaparral. The LCSA had a Mediterranean climate with an average of 1,182 mm of precipitation, most of which fell as snow, from 1990 to 2008 (Hell Hole Remote Automated Weather Station). The historic fire regime in this region mainly consisted of frequent, low-to moderate-severity fire occurring every 5–15 years (Stephens and Collins 2004).

As part of the experimental design for SNAMP, the study area was composed of a central treatment fireshed (4,293 ha) and two adjacent watersheds to the north and south that together served as a control ‘fireshed’ (5,658 ha; Fig. 1). We further expanded the study area by an

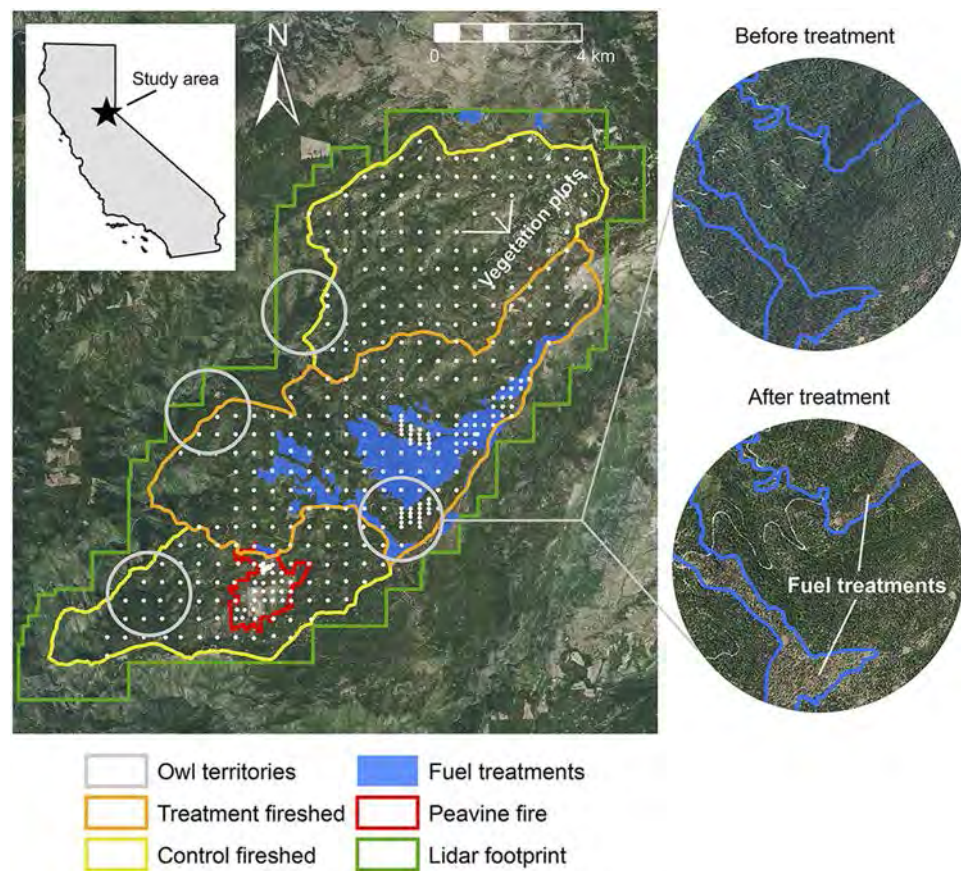


Fig. 1. Map of the Last Chance Study Area in the central Sierra Nevada, California, showing the delineation of treatment and control firesheds, the locations of four California Spotted Owl (*Strix occidentalis occidentalis*) territories used in our demographic analyses, fuel treatments conducted in 2011–2012, the plot network for ground-based sampling of forest vegetation before and after the fuel treatments, and an aerial overview of part of the treated area before and after the fuel treatments.

additional 3,531 ha of untreated landscape covered by the LiDAR footprint to incorporate additional owl territories (Fig. 1). Fuels-reduction treatments were implemented within the treatment fireshed by the U.S. Forest Service during 2011–2012 as part of the Sierra Nevada Adaptive Management Project (SNAMP; Sierra Nevada Adaptive Management Project 2014). The fuels treatments, also known as Strategically Placed Landscape Area Treatments (SPLATs), followed the guidelines specified in the 2004 management plan for national forests in the Sierra Nevada (USFS 2004). The management plan specified that no trees ≥ 76.2 cm can be harvested, at least 40% canopy cover must be retained, and at least 40% of a stand's basal area must be retained.

Treatments were implemented on 942 ha (7.0% of the total study area) as follows: 561 ha of mechanical thinning (tractor and cable), 247 ha of prescribed fire, and 134 ha of mastication of shrubs and small trees. Although no treatments were implemented in the control fireshed, the 2008 Peavine Fire burned 268 ha within the southern unit of the control fireshed (Fig. 1). Collins et al. (2011) modeled treatments and hazardous fire potential in the same study area, but focused on the treatment fireshed only.

Development of vegetation map

We developed a pre-treatment vegetation map using a combination of LiDAR, high-resolution digital color-infrared (CIR) aerial imagery, and an

intensive network of field plots. First, we used LiDAR and CIR data to create an initial polygon-based map where the polygons represented areas of homogeneous vegetation in terms of species, vertical structure, basal area, and canopy cover. The mean polygon size was 9.4 ha (range = 0.9–72.6 ha). We collected the LiDAR and CIR data before the fuels-reduction treatments, and we sampled vegetation at the field plots before and after treatment. We then used the field-plot data to impute detailed attributes (e.g., tree lists and fuels models) for each polygon. Thus, we derived two different maps (with and without treatment), which we used in fire and forest-growth modeling. We used field-plot data to assess the accuracy of the pre-treatment and post-treatment maps in terms of canopy cover and large tree density, which were the variables we used to identify spotted owl habitat (see *Materials and methods: Assessing effects of fuels treatments and fire on spotted owl habitat*). We found that values for percent canopy cover and large tree density were similar for field plots and their associated map polygon, although on average the field plot values were slightly lower than the map values. For percent canopy cover, the average difference for the pre-treatment map was –5.42% canopy cover (SE = 1.12), and for the post-treatment map the average difference was –2.05% canopy cover (SE = 1.21; Appendix A). For large tree density, the average difference for the pre-treatment map was –7.05 large trees per hectare (SE = 1.51), and for the post-treatment map the average difference was –4.30 large trees per hectare (SE = 1.55; Appendix A).

We contracted with the National Center for Airborne LiDAR Mapping (National Center for Airborne Laser Mapping 2011) to collect small-footprint, multiple-return airborne LiDAR data with a point density of 6–10 points/m² in September 2008, and we obtained 1 × 1 m² resolution CIR data collected by the National Agriculture Imagery Program (NAIP) in 2005. After initial processing of the LiDAR and CIR data, we used an object-based segmentation approach to delineate polygons of homogeneous vegetation types. We then applied an unsupervised classification strategy to label the different vegetation types based on the Bayesian Information Criterion algorithm, which is used to automatically determine the optimized number

of vegetation groups. We identified 8 vegetation types on our study area—low shrub, high shrub, open true fir, pine forest, cedar forest, young mixed-conifer forest, and mature mixed-conifer forest. The dominant vegetation type on the study area was mixed-conifer forest (56% mature, 19% young); the other forest types were present in lesser amounts (13% cedar, 7% pine, 4% open true fir). Chaparral (low and high shrubs) covered only 1% of the study area. Post-treatment LiDAR was collected in 2013 and was used to delineate actual treatment areas based on a change-detection algorithm to identify where forest structure noticeably changed between the two LiDAR acquisitions. This approach was employed because there can be inconsistencies between agency-generated treatment polygons and actual treatment extent on the ground.

We sampled forest vegetation at field plots that were spaced at 500-m intervals across the LCSA, except the southwest corner of the LCSA where extreme topography precluded sampling (Fig. 1). We sampled more intensively at 125- and 250-m spacing around instrument locations for a separate hydrological study. In August 2008, we also intensively sampled the area burned by the Peavine Fire. In total, we sampled 408 plots in 2007–2008 (pre-treatment) and 369 plots in 2013 (post-treatment). We briefly summarize the vegetation sampling here, but refer the reader to Collins et al. (2011) for greater detail. We sampled within 0.05-ha circular plots and recorded information on individual trees using three different sampling intensities based on tree size: (1) throughout the entire plot for trees ≥19.5 cm dbh; (2) within a random one-third of the plot (167 m²) for trees 5.0–19.4 cm dbh; and (3) along a random belt transect (76 m²) for trees <5.0 cm dbh. We recorded tree species, vigor, crown position, dbh, total height, and height to live crown base (live trees only) for all trees in the upper two size classes, and species and dbh for trees in the smallest size class. In addition, we sampled downed wood, litter, duff fuels, and woody shrub cover on three randomly chosen transects within each plot. We used the line-intercept method to sample downed woody fuels (van Wagner 1968, Brown 1974), and we recorded percent cover and average height for woody shrubs intersecting each transect.

We then used the field-plot data to impute

detailed vegetation attributes for each polygon of the vegetation map for use in the fire and forest-growth modeling. We developed an imputation procedure to assign three field plots to each map polygon based on their similarity in “gradient space” (Ohmann and Gregory 2002). We performed a multivariate analysis of the plot data to define the gradient space. The definition of the gradient nearest neighbors for each polygon (*sensu* Ohmann and Gregory 2002) included topographic variables (e.g., slope, aspect, elevation), canopy structure (percent canopy cover and an index of large tree density), and vegetation type. To maintain some of the fine-scale heterogeneity observed in the field, we identified all plots in the 95th percentile in terms of nearest neighbor distance for each stand and then randomly assigned three of those plots to the stand. Our pre-treatment map represented conditions after the Peavine Fire occurred (see *Materials and methods: Study area*) because we collected the remotely sensed data and sampled additional field plots within the burned area after the fire. The treatment scenario differed from the no treatment scenario in what field-plot data were used to impute vegetation attributes for polygons where treatments occurred. For the treatment scenario, we used post-treatment tree lists from treated plots ($n = 49$) for polygons that experienced noticeable structural change based on LiDAR change detection or were confirmed on-the-ground to have been burned by prescribed fire.

Modeling forest dynamics and fire

We considered four scenarios when modeling forest dynamics and wildfire: (1) with treatments and with fire; (2) without treatments and with fire; (3) with treatments and without fire; and (4) without treatments and without fire. For the “with fire” scenarios, we used FARSITE (Finney 1998) to simulate a single fire for both the treated and untreated landscape based on the weather conditions during the 2001 Star Fire, which burned 6,817 ha, including 314 ha on the northeast edge of our study area (Fig. 2). Approximately 39% of this fire burned at high severity (www.mtbs.gov; accessed on 4 February 2015). FARSITE is a spatially explicit fire-growth model that uses several topographic, forest-structure, and fuel-model map layers to project

fire behavior parameters over a complex landscape. Topographic inputs such as slope, aspect, and elevation were obtained from the LiDAR-derived surface elevation model at 30-m resolution. We derived forest structure map layers for canopy cover, canopy bulk density, canopy base height, and canopy height using the imputation procedure previously described. We calculated fuel-model assignments using a selection logic based on surface fuels and forest structure measured at the plots (Collins et al. 2011, 2013). This approach has proven sufficient at assigning fuel models based on actual fuel loads rather than relying on the Forest Vegetation Simulator (FVS; Dixon 2002), which has been shown to use fuel models that underestimate fire behavior (Collins et al. 2013). This approach for assigning fuel models was different for treated and untreated stands. For untreated stands, we used a regression tree analysis with several response variables representing surface fuels: shrub cover, litter, 1- to 100-hour woody fuels, and 1000-hour woody fuels. Forest structure and stand vegetation classification were used as independent variables. Model fits were moderate ($R^2 = 0.3$ – 0.6), but given the known variability in surface fuels in mixed-conifer forests (Lydersen et al. 2015), we deemed the assignments to be sufficient in describing the generalized fuel conditions represented by surface fuel models (Collins et al. 2011, 2013). For treated stands, post-treatment fuel models were based on treatment type and post-treatment fuel measurements. Prescribed-burn plots were assigned a moderate-load timber-litter fuel model (Scott and Burgan 2005). We assigned a low-load, timber-understory model to initial post-treatment masticated stands based on observed fire behavior from Knapp et al. (2011). There were two types of tree-harvest treatments: thinning and cable logging. Prescriptions for the cable-logging units indicated that the slash was to remain on site, so we used a moderate-load, timber-slash model followed by timber-understory models. Thinning treatments used whole-tree removal in which slash typically was removed, so we used the same selection logic for these treatments that we used for untreated stands.

We obtained weather information from the Duncan Remote Automatic Weather Station, limited to the active burning period of the Star

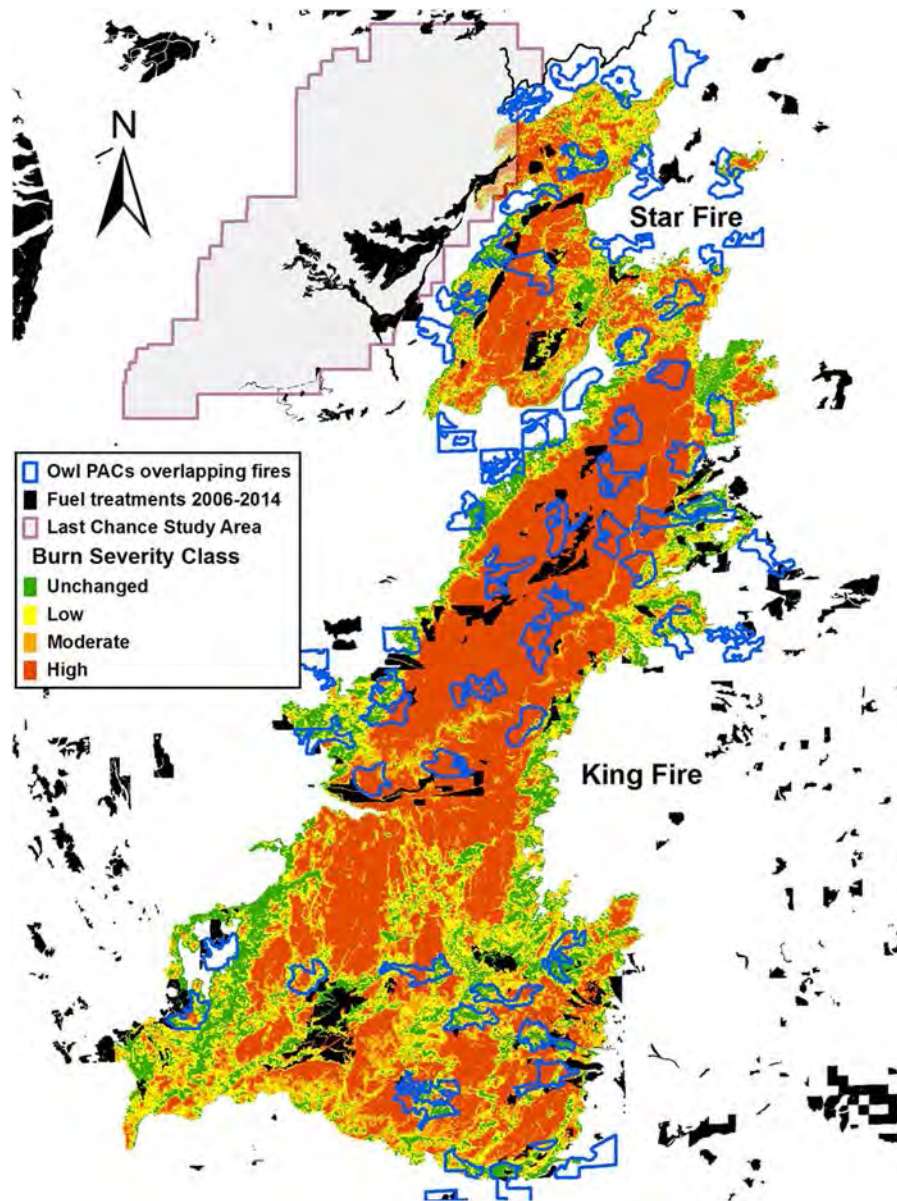


Fig. 2. Burn-severity map of the 2001 Star Fire and 2014 King Fire that burned near the Last Chance Study Area in the central Sierra Nevada, California. The burn-severity maps were created by the U.S. Forest Service (USFS) as detailed in Finco et al. (2012). We also show the spotted owl Protected Activity Centers (PACs) that were affected by these fires, and fuels-reduction treatments that were implemented by the USFS from 2006 to 2014.

Fire (August–September 2001), which served as the basis of our fire modeling. Moisture content for live and dead woody fuels and live herbaceous fuels used in the model were equivalent to 97th percentile weather conditions. Winds were generally easterly in the morning, switching to southwest to west during the day, with an

average of 8 km h^{-1} (range = $0\text{--}15 \text{ km h}^{-1}$). Our ignition location was established in the northeast corner of the study area where the Star Fire perimeter overlapped our study area boundary. There were other wildfires that burned into the study area (2008 Peavine Fire, 2013 American Fire), but the 2001 Star Fire location and the

conditions it burned under yielded the highest potential to burn a large portion of our study area, and in doing so impact more known owl sites. The simulation duration was set to allow the fire perimeter to expand through the entire study area.

We used the tree list databases associated with the 2008 pre-treatment field plots when simulating fire under the “no treatment” scenario, and we used the 2013 post-treatment field plots when simulating fire under the “treatment” scenario. Stand average flame lengths and proportion burned by fire type (surface fire, conditional crown fire, and active crown fire) were calculated for both scenarios and used as inputs for fire effects simulation using the keyword SIMFIRE in FVS with the Fire and Fuels Extension (FFE; Reinhardt and Crookston 2003).

For all four scenarios, we then simulated 30 years of forest growth on the study area in 10-year time steps using FVS with FFE. The simulations were performed using the integrated platform ArcFuels (Ager et al. 2006, Vaillant et al. 2011), which runs FVS-FFE to produce the forest structure inputs needed for FARSITE. We used the western Sierra variant of FVS to simulate forest dynamics over the simulation periods. Because this variant does not include a “full-establishment model,” users must set parameters for tree regeneration by identifying number, species, and frequency of establishment. Following the methods of Collins et al. (2011, 2013), we used a random-number generator, within defined bounds, to set the number of seedlings at each time step in FVS while regulating height-growth rates to simulate realistic conditions in a mixed-conifer forest.

Assessing effects of fuels treatments and fire on spotted owl habitat

We identified canopy cover and large trees as the most important predictors of spotted owl habitat because nest locations were characterized by greater amounts of these elements in the central Sierra Nevada (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997, Williams et al. 2011). To determine a biologically meaningful definition of a large tree, we examined 101 spotted owl nest trees on the nearby Eldorado Demography Study Area (EDSA). The size distribution of these nest trees was not significantly different from a

normal distribution at $\alpha = 0.05$ (Shapiro-Wilk test, $p = 0.052$), so we estimated the standard deviation of the 101 nest tree diameters and used the 10% quantile value of a normal distribution to identify the minimum size of a large tree as 71.3 cm dbh. Thus, 90% of owl nest trees on our study area were expected to be ≥ 71.3 cm dbh. We then performed a logistic regression (Hosmer et al. 2013) of owl nesting habitat as a function of canopy cover and large tree density using data collected by Bond et al. (2004) within 0.02-ha plots at 25 nest trees and 36 random locations within potentially suitable owl nesting habitat on the EDSA (Fig. 3). We identified the following logistic regression equation for canopy cover (CC; percent) and large tree density (LT; ha^{-1}) using SAS (SAS Institute, Cary, North Carolina, USA):

$$\begin{aligned} \text{logit}(\text{Pr}[\text{nesting habitat}]) = & -4.141 \\ & + 0.026 \times \text{CC} \\ & + 0.052 \times \text{LT}. \quad (1) \end{aligned}$$

The parameter estimate for large tree density was statistically significant at $\alpha = 0.05$ ($p < 0.01$, Wald chi-squared test statistic [Q_W] = 8.71, $\text{df} = 1$), but the parameter estimate for canopy cover was not ($p = 0.19$, $Q_W = 1.72$, $\text{df} = 1$). However, we elected to include CC in the model given that canopy cover is known to be an important component of spotted owl nesting habitat (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997).

We used Eq. 1 to estimate the probability that each forest stand (i.e., map polygon) on our study area contained suitable owl nesting habitat under each of the four treatment/wildfire scenarios at four points in simulated time (years 0, 10, 20, and 30). Using the values for canopy cover and large tree density from each map polygon, we calculated the probability that the polygon contained suitable nesting habitat and obtained an average probability (weighted by the area of each map polygon) for the entire study area, which we refer to hereafter as the habitat suitability index. We also obtained separate habitat suitability indices for the control and treatment fireshed within the study area (see *Materials and methods: Study area*) because we expected the direct and indirect (i.e., through modification of fire behavior) effects of fuels treatments to be more pronounced near the treatments.

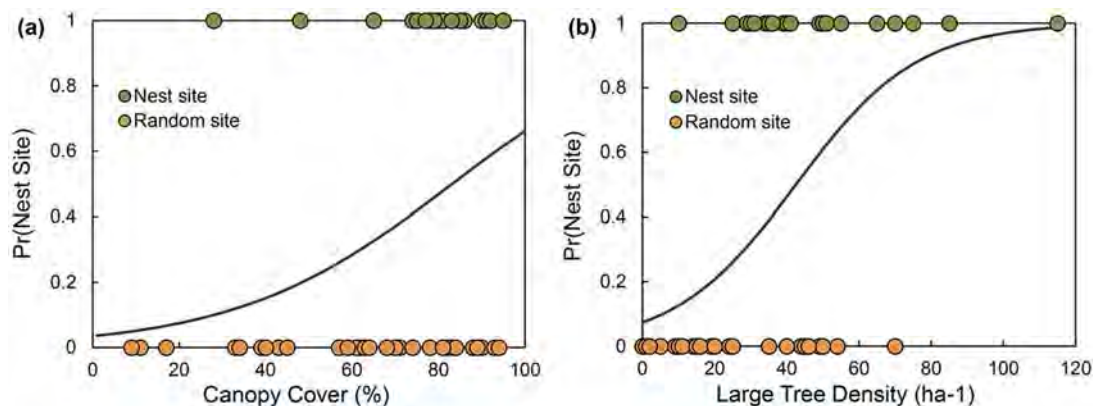


Fig. 3. Comparison of (a) canopy cover (percent) and (b) large tree density (≥ 71.3 cm dbh; ha^{-1}) for 25 California Spotted Owl (*Strix occidentalis occidentalis*) nest locations and 36 random locations in potentially suitable owl nesting habitat on the Eldorado National Forest in the central Sierra Nevada, California. These data were used to develop a logistic regression model to estimate the probability of forest being suitable as spotted owl nesting habitat; best-fit logistic regression lines are shown on each graph.

Assessing effects of fuels treatments and fire on spotted owl demography

Under each of the four treatment/wildfire scenarios, we projected how changes in owl habitat were expected to affect fitness and equilibrium occupancy (ψ_{Eq}) at the spatial scale of a spotted owl territory. We defined an owl territory as the area contained within a 1,128-m radius (400-ha) circle around each owl territory center; this radius was equal to one-half the mean nearest neighbor distance between owl territory centers on the EDSA (Tempel et al. 2014a). We estimated the territory center as the geometric mean of the most informative owl location(s) from each year that the territory was occupied. We used a nest location if one was located that year; otherwise we used the mean of the roost locations for that year. We located nests and roost sites during surveys conducted annually from 2007 to 2013 during the spotted owl breeding season (April–August; see Tempel et al. [2014a]), and we found no barred owls (*Strix varia*) on our study area. We limited this analysis to four spotted owl territories that were largely within our study area ($\geq 80\%$ of the 400-ha territory). Three of the territories were occupied by an owl pair every year from 2007 to 2013, and the other was occupied in all but one of those years. For the demographic analyses, we defined owl habitat as high-canopy-cover forest dominated

by trees ≥ 30.5 cm dbh because previous analyses showed that this vegetation type had a strong positive relation with λ and ψ_{Eq} (Tempel et al. 2014a). On the 2008 pre-treatment map, forest stands with $\geq 70\%$ canopy cover always contained a substantial number of trees ≥ 30.5 cm dbh (mean density = 55.8 ha^{-1} , range = 16.0 – 130.7 ha^{-1}), so we considered all of these stands to be dominated by trees ≥ 30.5 cm dbh. Although our inferences were limited by the small sample size of four territories, the amount of high-canopy-cover forest within these territories (mean = 154 ha, range = 102–207 ha) was typical of the amount found in 70 other territories near our study area (mean = 132 ha; Tempel et al. 2014a).

To assess how changes in the amount of high-canopy-cover forest impacted fitness and ψ_{Eq} at each of the four territories, we used the habitat maps developed under each scenario at four points in simulated time (years 0, 10, 20, and 30) to quantify the proportion of each territory consisting of high-canopy-cover forest. We estimated territory fitness and equilibrium occupancy following the methods of Tempel et al. (2014a). For fitness, where we used a stage-based, Lefkovich matrix model parameterized with fecundity and survival rates to represent changes in the female population size

$$\begin{bmatrix} N_{J,t+1} \\ N_{S1,t+1} \\ N_{S2,t+1} \\ N_{A,t+1} \end{bmatrix} = \begin{bmatrix} 0 & \varphi_{S,t}b_{S,t} & \varphi_{S,t}b_{A,t} & \varphi_{A,t}b_{A,t} \\ \varphi_{J,t} & 0 & 0 & 0 \\ 0 & \varphi_{S,t} & 0 & 0 \\ 0 & 0 & \varphi_{S,t} & \varphi_{A,t} \end{bmatrix} \begin{bmatrix} N_{J,t} \\ N_{S1,t} \\ N_{S2,t} \\ N_{A,t} \end{bmatrix}$$

where $N_{J,t}$, $N_{S1,t}$, $N_{S2,t}$ and $N_{A,t}$ were the number of juvenile, first-year subadult, second-year subadult, and adult females at time t , respectively; $\varphi_{J,t}$, $\varphi_{S,t}$ and $\varphi_{A,t}$ were the apparent survival rates of juvenile, subadult, and adult females from time t to $t + 1$, respectively; and $b_{S,t}$ and $b_{A,t}$ were the fecundity rates for subadult and adult females at time t , respectively. Fecundity was the number of female offspring produced per female in the population, assuming a 50:50 sex ratio for fledged owls. Based on previous analyses in Tempel et al. (2014a), we estimated survival at each territory as a function of female age and the logarithm of the hectares of high-canopy-cover forest (HCF)

$$\logit(\varphi) = -0.005 + 0.557 \times \text{age} + 0.497 \times \log([HCF/10] + 1) \quad (2)$$

where $\text{age} = 0$ for subadults and 1 for adults, and we divided the amount of HCF by 10 to facilitate model fitting. However, we estimated fecundity solely as a function of female age because high-canopy-cover forest was not a significant predictor of reproductive output,

$$b = 0.153 + 0.178 \times \text{age} \quad (3)$$

where $\text{age} = 0$ for subadults and 1 for adults. Using the territory-specific estimates of survival and fecundity, we then computed a territory-specific fitness (i.e., λ) as the dominant eigenvalue of the matrix. As noted in Tempel et al. (2014a), we expected our estimates of fitness to be biased low because (1) we did not incorporate immigration into the projection matrix, and (2) if an individual was not resighted for one or more years and was then resighted on a new territory, we removed the portion of its capture history at the original territory (which lowered the estimates of annual survival) to avoid making assumptions about the owl's location during the intervening period. Nevertheless, differences in fitness allowed us to evaluate the relative simulated effects of fuels treatments and wildfire.

We calculated equilibrium occupancy (ψ_{Eq}) from the territory extinction (ε) and colonization (γ) rates at each territory where $\psi_{Eq} = \gamma/(\gamma + \varepsilon)$

(MacKenzie et al. 2006). Again, based on previous analyses in Tempel et al. (2014a), we estimated extinction probability at each territory as a linear function of the hectares of HCF

$$\logit(\varepsilon) = -1.944 - 0.058 \times (HCF/10), \quad (4)$$

and we estimated colonization as a function of the logarithm of the hectares of HCF

$$\logit(\gamma) = -3.528 + 2.149 \times \log([HCF/10] + 1). \quad (5)$$

As we did when estimating survival, we divided the amount of HCF by 10 to facilitate model fitting.

RESULTS

Effects of fuels treatments on forest structure

We compared pre- and post-treatment measurements at 49 field plots located within the fuels-treatment network (Table 1). Fuels treatments reduced the mean canopy and woody shrub cover by ~10% and reduced mean total tree density from 540.8 to 263.6 trees/ha. Mean large tree density increased slightly from 20.8 to 22.8 trees/ha, perhaps because of tree growth during the five years that elapsed between pre- and post-treatment measurements. Fuels treatments decreased the amount of 1–1000 hour woody fuels from 31.5 to 24.9 Mg/ha, whereas duff fuels increased from 64.2 to 67.2 Mg/ha.

Fire modeling

The simulated fire spread across nearly all of the study area for both scenarios (with and without treatment) because of the prevailing winds (Fig. 4). Fuels treatments reduced the intensity of the fire, as evidenced by the predicted flame lengths, with the greatest reductions occurring within treated areas. Overall, when fire occurred on the untreated landscape, 70.2%, 16.6%, 9.3%, and 3.9% of the study area experienced flame lengths of <2, 2–4, 4–8, and >8 m, respectively. In contrast, when fire occurred on the treated landscape, 76.2%, 14.3%, 6.8%, and 2.7% of the study area burned at these flame lengths. Collins et al. (2011) noted that flame lengths >2 m often corresponded to areas with crown fire initiation (i.e., torching). Differences in fire behavior between the two scenarios (i.e., a greater proportion of the fire

Table 1. Comparison of pre- and post-treatment canopy cover (percent), total tree density (ha^{-1}), large tree density (≥ 71.3 cm dbh; ha^{-1}), shrub cover (percent), duff fuels (Mg/ha), and woody fuels (1–1000 hour; Mg/ha) at 49 field plots located within a fuels-treatment network on the Last Chance Study Area in the central Sierra Nevada, California. Standard errors are shown in parentheses.

Vegetation attribute	Pre-treatment	Post-treatment
Canopy cover	56.6 (3.2)	45.8 (2.7)
Total tree density	540.8 (31.6)	263.6 (21.1)
Large tree density	20.8 (4.4)	22.8 (4.6)
Shrub cover	31.6 (4.0)	22.2 (3.3)
Duff fuels	64.2 (5.4)	67.2 (5.6)
Woody fuels	31.5 (4.9)	24.9 (4.1)

burned at <2 m after fuels treatments) also generally held true for the land encompassed by the four owl territories. Interestingly, the one territory where this pattern did not hold true was at the territory located within the fuels-treatment network (the territory in the southeastern part of the study area; Fig. 4) where 29.3% of the

territory burned at flame lengths >2 m under the treatment scenario compared to 19.7% under the no treatment scenario. This result may have been influenced by differences in the direction of fire spread and time-of-day that the territory burned, which would influence burning conditions via fuel moisture, relative humidity, and air temperature.

Effects of fuels treatments and fire on spotted owl habitat

When we applied Eq. 1 to the habitat maps under the four treatment/wildfire scenarios, we found that fuels treatments had a persistent, slightly negative effect on the owl habitat suitability index for the entire study area when no wildfire occurred (Fig. 5). Implementing fuels treatments immediately decreased the habitat suitability index (0.25 for 2008 pre-treatment map compared to 0.23 for 2013 post-treatment map), and this small difference was still present after 30 years of simulated forest growth (0.37 without treatment versus 0.36 with treatment). Conversely, we found that fuels treatments had a

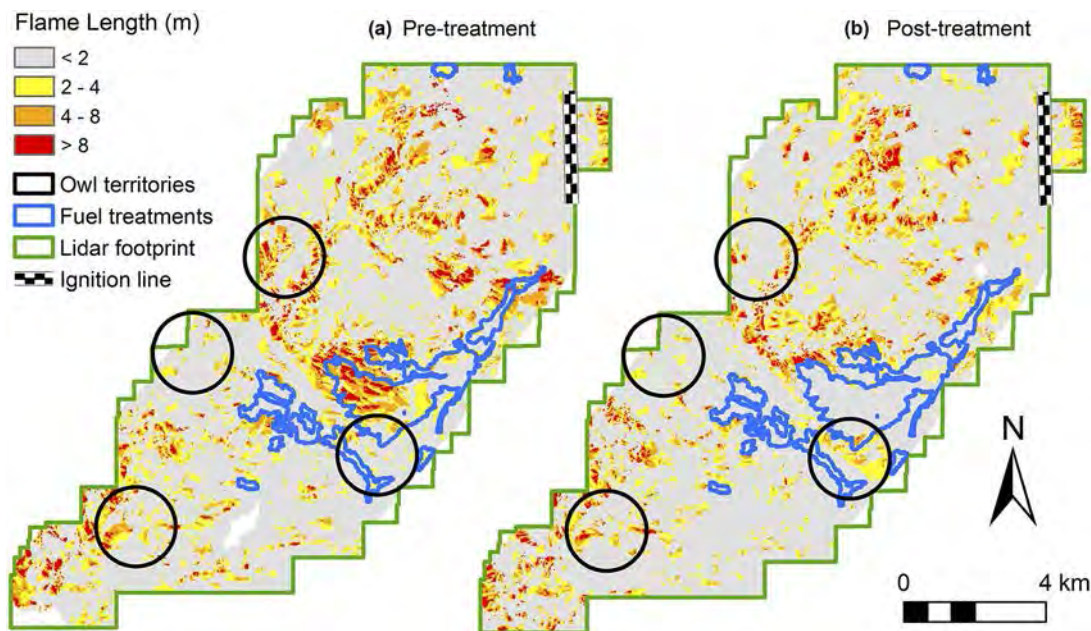


Fig. 4. Flame lengths (m) of simulated fires on the Last Chance Study Area under two scenarios: (a) on an untreated landscape; and (b) after implementation of fuels treatments. We show the location of treatment polygons in (a) for ease of comparison, but treatments were not implemented in (a). Four California Spotted Owl (*Strix occidentalis occidentalis*) territories within the study area are also shown. Fire occurred in all areas within the “ < 2 m” category (gray shading).

persistent, slightly positive effect on the owl habitat suitability index for the entire study area after wildfire was simulated (Fig. 5). After 30 years of simulated forest growth following fire, the habitat suitability index under the treatment scenario was 0.20 compared to 0.17 under the no treatment scenario. The results were very similar when we summarized habitat suitability indices separately for the control and treatment fireshed (Appendix B).

Effects of fuels treatments and fire on spotted owl demography

We estimated that fuels treatments had a slight, persistent negative effect on fitness at four spotted owl territories within our study area when no wildfire occurred (Fig. 6). The mean fitness of owls at the four territories using the 2013 post-treatment map was 0.825 (SE = 0.012) compared to 0.839 (SE = 0.007) using the 2008 pre-treatment map. This difference was still present after 30 years of simulated forest growth (fitness with treatments = 0.850, SE = 0.008; fitness with no treatments = 0.856, SE = 0.005). In contrast, the simulations suggested that fuels treatments had a larger positive effect on

territory fitness after wildfire (Fig. 6). Thirty years after the occurrence of fire, the simulations projected the mean territory fitness with treatments to be 0.796 (SE = 0.009) versus 0.776 (SE = 0.008) with no treatments.

The general patterns for equilibrium occupancy were similar to those for territory fitness, but there was greater variation in ψ_{Eq} under the different scenarios (Fig. 6). Fuels treatments again had a slight negative effect if fire did not occur, but they had a larger positive effect if simulated fire did occur. When fire did not occur, the projected mean equilibrium occupancy for the four territories after 30 years was 0.883 (SE = 0.037) with fuels treatments and 0.911 (SE = 0.023) with no fuels treatments. In contrast, the projected mean equilibrium occupancy 30 years after fire was 0.577 (SE = 0.053) with treatments compared to 0.468 (SE = 0.042) with no treatments.

DISCUSSION

Several studies have investigated the short-term and long-term impacts of fuel treatments on habitat availability for old-forest species using various treatment simulations (Lee and Irwin 2005, Ager et al. 2007, Thompson et al. 2011, Roloff et al. 2012), but ours was unique in several respects. First, we simulated the effects of actual (as opposed to hypothetical) fuels treatments that reflected an actual implementation of a region-wide strategy to reduce landscape-level fire spread and intensity on U.S. Forest Service lands, while conserving key forest structural attributes associated with old-forest species (i.e., large trees, high canopy cover; USFS 2004). Second, we combined field-collected vegetation data and LiDAR data to develop a detailed map of forest structure used to parameterize our fire and forest-growth models. The LiDAR data provided information on vertical structure that was unattainable with other sources of remotely sensed data (Lefsky et al. 2002) and allowed us to determine the actual extent of treatments. While the full potential of LiDAR data was not demonstrated here (e.g., the mapping of individual trees; Li et al. 2012, Jakubowski et al. 2013), the LiDAR data were critical in developing a more detailed and accurate vegetation map for use in fire modeling than what could have been

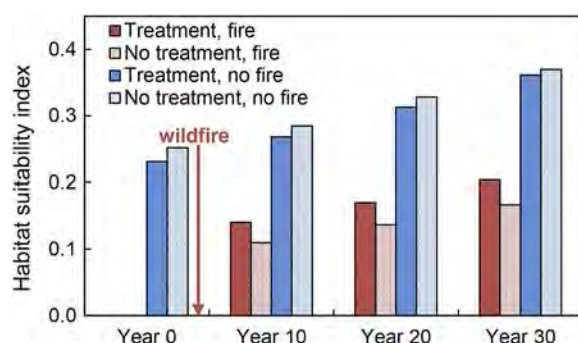


Fig. 5. California Spotted Owl (*Strix occidentalis*) habitat suitability index for a 13,482-ha study area in the Sierra Nevada under four scenarios: (1) no fuel treatments and no wildfire; (2) fuel treatments and no wildfire; (3) no fuel treatments and wildfire; and (4) fuel treatments and wildfire. Year 0 for the “no treatment” scenarios was 2008, and year 0 for the “treatment” scenarios was 2013 (i.e., after fuels treatments were implemented). Simulated fires occurred in year 0 for both the “no treatment” and “treatment” scenarios, and post-fire effects were first assessed in year 10.

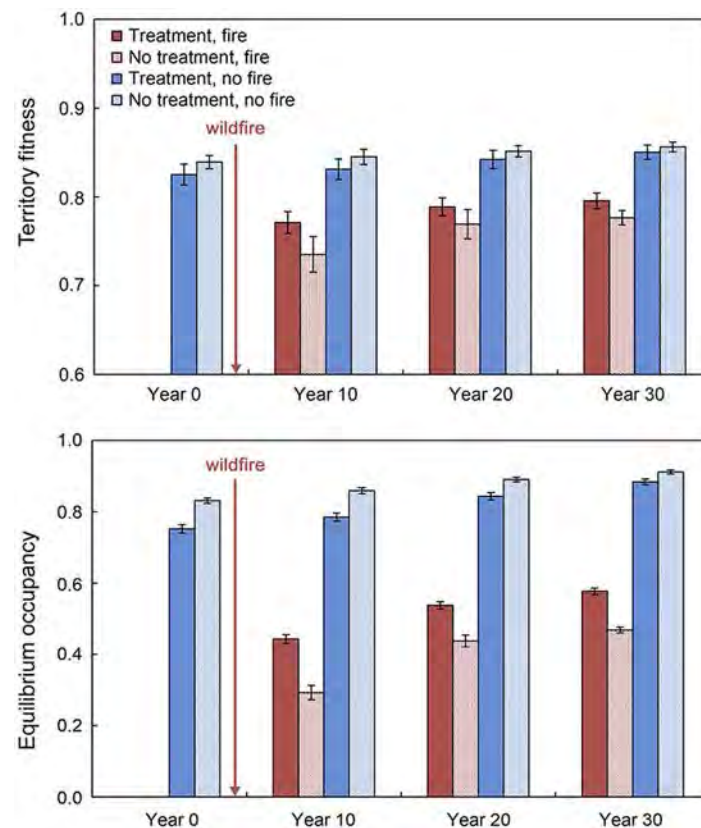


Fig. 6. The average territory fitness and equilibrium occupancy with standard errors at four California Spotted Owl (*Strix occidentalis occidentalis*) territories on a 13,482-ha study area in the Sierra Nevada under four scenarios: (1) no fuel treatments and no wildfire; (2) fuel treatments and no wildfire; (3) no fuel treatments and wildfire; and (4) fuel treatments and wildfire. Year 0 for the “no treatment” scenarios was 2008, and year 0 for the “treatment” scenarios was 2013 (i.e., after fuels treatments were implemented). Simulated fires occurred in year 0 for both the “no treatment” and “treatment” scenarios, and post-fire effects were first assessed in year 10.

solely achieved with lower-resolution satellite or optical imagery. Finally, in addition to projecting changes in habitat over time, we linked vegetation conditions under the different scenarios to territory fitness and occupancy within our study area using previously modeled relationships between forest structure and owl demography (Tempel et al. 2014a). For these reasons, we believe our study provided a rigorous simulation of the effects of fuels-reduction treatments on an old-forest species that has regional-scale implications for forest management.

We modeled the behavior of a fire (both with and without fuels treatments) parameterized using actual conditions during the 2001 Star Fire; this fire burned large areas at high severity (2,677 of 6,817 total ha; Fig. 2). We then simulated forest

growth 30 years into the future under four landscape scenarios: treated/fire, untreated/fire, treated/no fire, and untreated/no fire. As predicted, we projected that fuels-reduction treatments had a negative short-term impact on spotted owl habitat and demographic rates in the absence of fire, but contrary to our expectations, a very slight negative effect was still evident after 30 years. Conversely, treatments had a projected long-term positive effect on owls up to 30 years later when we simulated a fire that burned 30% of our study area at high severity (i.e., >2 m flame length). Thus, our findings were in general agreement with previous modeling efforts for the Northern Spotted Owl (*S. o. caurina*) in the Pacific Northwest where treated landscapes contained more owl habitat after simulated fire than

untreated landscapes, either immediately afterwards (Ager et al. 2007) or up to 75 years later (Roloff et al. 2012).

The observed differences in owl habitat and demographic rates under the different scenarios were modest. For example, the habitat suitability index on our study area 30 years after simulated fire was 0.20 and 0.17 for the treated and untreated landscapes, respectively. Within the four owl territories 30 years after fire, we estimated the mean territory fitness to be 0.796 and 0.776 for the treated and untreated landscapes, respectively. Only 7% of the study area was treated because we expanded our study area to include additional owl territories (Fig. 1), but previous fire modeling studies suggested that at least 20% of the landscape should be treated to significantly reduce fire spread and intensity (e.g., Ager et al. 2007, Finney et al. 2007, Moghaddas et al. 2010). Thus, our finding of fairly modest differences in predicted flame lengths outside of the “treatment” fireshed for the treated and untreated scenarios (Fig. 4) was likely related to the low overall proportion of the study area treated. Based on the original study design, 18% of the area (i.e., the treatment fireshed) was treated, which was shown to be effective at reducing hazardous fire potential across the treatment fireshed (Collins et al. 2011). Although the projected effects on owl fitness are relatively small, even small reductions in annual growth rates (a function of fitness parameters) can translate into large population declines over longer time periods (Tempel et al. 2014b). For example, if the annual growth rate is 1.00, then the population size remains unchanged after 30 years. In contrast, if the annual growth rate is 0.98, then population size would decline by 45% after 30 years. Importantly, California Spotted Owl populations have already declined by up to 50% throughout the Sierra Nevada in the past 20 years (Conner et al. 2013, Tempel et al. 2014b), and any further declines could jeopardize their long-term persistence.

We linked spotted owl demography to fuels treatments and fire behavior via their effects on high-canopy-cover forests because relationships between owl territory fitness/occupancy and this forest type have been well-established in the Sierra Nevada (Blakesley et al. 2005, Tempel et al. 2014a). Moreover, previous studies have shown

that large (>50 ha) areas of high-severity fire within owl territories may reduce territory occupancy (Lee et al. 2013). In addition, territory extinction has been positively correlated with the combined area of early-seral forests, high-severity burn, and post-fire salvage logging within owl territories (Clark et al. 2013). As such, a reasonable ecological basis exists for inferring that simplification or elimination of high-canopy-cover forests by fuels treatments or high-severity fire will adversely affect spotted owl populations. However, the effects of wildfire on spotted owls are undoubtedly complex and owls may benefit from the presence of a mosaic of habitat types promoted by mixed-severity fire, and particularly from shrub patches and early-seral forests that harbor diverse prey assemblages (Roberts et al. 2015). For example, Bond et al. (2009) found that spotted owls in the southern Sierra Nevada selectively foraged in burned areas, even those that burned at high severity. We further note that not all previous studies of spotted owls have found reduced occupancy rates in burned areas relative to unburned areas (Roberts et al. 2011, Lee et al. 2012). Therefore, to the extent that low- or moderate-severity fire may benefit owls, the modeled declines in territory fitness and occupancy in our fire scenarios might be overestimated, and by extension the long-term (30-year) benefits of fuels reduction treatments overly optimistic. Clearly, additional empirical work is needed to assess the complex effects of wildfire on spotted owls, particularly longer-term studies of marked individuals in landscapes that have experienced a range of fire severities (with and without existing fuel treatment networks on the landscape) and that are not confounded by the effects of salvage logging.

Other Sierra Nevada species of conservation concern have similar habitat needs as the spotted owl (i.e., mature forests with high canopy cover), particularly the Pacific fisher (*Pekania pennanti*) and Northern Goshawk (*Accipiter gentilis*; Greenwald et al. 2005, Davis et al. 2007). Thus, similar forest-management trade-offs may exist for these species such that fuels-reduction treatments may reduce available habitat in the short-term but result in greater, long-term habitat amounts if fire occurs. Indeed, Thompson et al. (2011) performed an analogous study to ours, in which they modeled fire and forest growth under

treatment and no treatment scenarios and assessed fisher habitat suitability in the southern Sierra Nevada. They projected that fuels treatments had slight negative effects on fisher habitat in the absence of fire, but provided significant positive benefits up to 37 years after simulated fire. Truex and Zielinski (2013) suggested that less fisher resting habitat was present immediately after mechanical fuels treatments were implemented in the Sierra Nevada. However, fishers consistently used areas in the southern Sierra Nevada where some timber harvest had occurred, so it may be possible to implement fuels-reduction treatments at an extent and rate that achieves fire-hazard-reduction goals (Zielinski et al. 2013). Therefore, we believe that our results, although specific to the spotted owl, have broader applicability to other species of management concern in the Sierra Nevada that selectively use forests characterized by large trees and high canopy cover.

We note, however, several caveats from our study when assessing the long-term effects of fuels treatments and wildfire on spotted owls. First, our projections were based on a single simulated fire for each treatment scenario (with and without treatment), and additional fire simulations may have suggested alternative fire patterns with differing effects on the components of owl habitat that we considered (canopy cover, large tree density). We used FARSITE to simulate a single fire in order to obtain specific predictions on how fire would impact forest structure via tree mortality, as opposed to probabilistic predictions on fire occurrence at a specific location (e.g., Ager et al. 2007). By having spatially explicit predictions of fire effects on forest structure, we were able to track the impacts of fire on owl habitat and make more direct assessments of owl demography over time. Second, our simulation was conducted at the relatively fine spatial scale of the fireshed (10s of km²) because of its management relevance (North et al. 2015) and the difficulty of collecting detailed vegetation data for improved parameterization of fire models at larger spatial scales. However, conducting simulations such as ours at a larger spatial scale would increase the sample size of owl territories used to assess the potential effects of fire and fuels treatments on spotted owls. Future studies should carefully weigh the

trade-off between collecting more accurate vegetation data at smaller spatial scales, and therefore deriving more accurate inputs for fire modeling, and increasing the number of owl territories by using larger spatial scales. Third, both of our simulated fires exhibited burn patterns that were substantially different than the burn patterns of the 2001 Star Fire that we attempted to simulate and the large 2014 King Fire (39,545 ha) that burned near our study area (cf. Figs. 2 and 4). Whereas our simulations resulted in relatively small, evenly distributed patches of high-severity fire, the Star Fire and King Fire burned large, contiguous areas at high severity. Indeed, our past experience suggests that existing fire models are generally incapable of replicating the burn patterns seen in the most extreme real fires. Thus, improved fire models are needed to more reliably assess how fuels treatments modify fire behavior and effects on forest structure especially under extreme conditions. Fourth, we did not simulate post-fire salvage logging (which often occurs after fires) on the habitat suitability of burned areas, and post-fire salvage logging has been shown to negatively affect spotted owl occupancy rates (Clark et al. 2013, Lee et al. 2013). Finally, the net effect of fuels treatments on spotted owls depends upon the true, but unknown, probability that high-severity fire effects will occur within individual owl territories. If individual territories have a low probability of experiencing high-severity fire effects, a relatively small portion of the owl population would accrue the long-term benefits of fuels reductions, whereas a greater portion of the population would experience the unfavorable short-term impacts. However, it is difficult to estimate spatially explicit, future probabilities for specific fire behaviors (e.g., crown-fire initiation) on specific areas of the landscape, and it is thus difficult to quantify trade-offs associated with fuel treatments on large spatial scales and in absolute terms (Finney 2005). We note, however, that the area burned by high-severity fire in the Sierra Nevada has increased in the past 30 years (Miller et al. 2009, Miller and Safford 2012) and may increase further in upcoming years because of climate change (Westerling and Bryant 2008, Liu et al. 2013). In addition, several fires on or near our study area have burned large areas of the

landscape in the last 15 years (2001 Star Fire [6,817 ha], 2013 American Fire [11,305 ha], 2014 King Fire [39,545 ha]) and provide circumstantial evidence that a significant probability of large-scale, high-severity fire effects can be expected, at least in this region of the north-central Sierra Nevada. All three of these fires were human-ignited, which further complicates the estimation of future fire probabilities. In sum, future research on the short- versus long-term benefits of fuels treatments would benefit from a greater understanding of the probability of fire under various climate change scenarios, and linking replicated fire and forest-growth simulations to spotted owl population dynamics at landscape scales using spatially explicit population models.

In conclusion, our results suggest that fuels-reduction treatments, as currently implemented by the U.S. Forest Service in the Sierra Nevada, have the potential to provide long-term (30-year) benefits to spotted owls in the event of fire under extreme weather conditions, but can have long-term negative effects on owls if fire does not occur. Furthermore, major uncertainties remain (e.g., What is the future probability that high-severity fire effects will occur within individual owl territories?). In conjunction with the observed population declines in the last 20 years (Conner et al. 2013, Tempel et al. 2014b), we believe these uncertainties warrant an informed approach to landscape fuels management that explicitly balances the seemingly conflicting goals of providing habitat for owls and reducing hazardous fire potential. Specifically, we recommend that the U.S. Forest Service continue its current policy that restricts timber harvest within spotted owl Protected Activity Centers (PACs), which contain ~125 ha of the best habitat that owls use for nesting and roosting over long time periods (up to 24 years; Berigan et al. 2012). Furthermore, fuels-treatment arrangements should be designed to limit the potential for high-severity fire to spread into PACs.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A and B are available online: <http://dx.doi.org/10.1890/ES15-00234.1.sm>

Wildfire and California Spotted Owl Habitat in the Sierra Nevada



*John J. Keane, Ross A. Gerrard, Lief R. Gallagher, Thomas E. Munton and
Paula A. Shaklee*

Pacific Southwest Research Station, USDA Forest Service

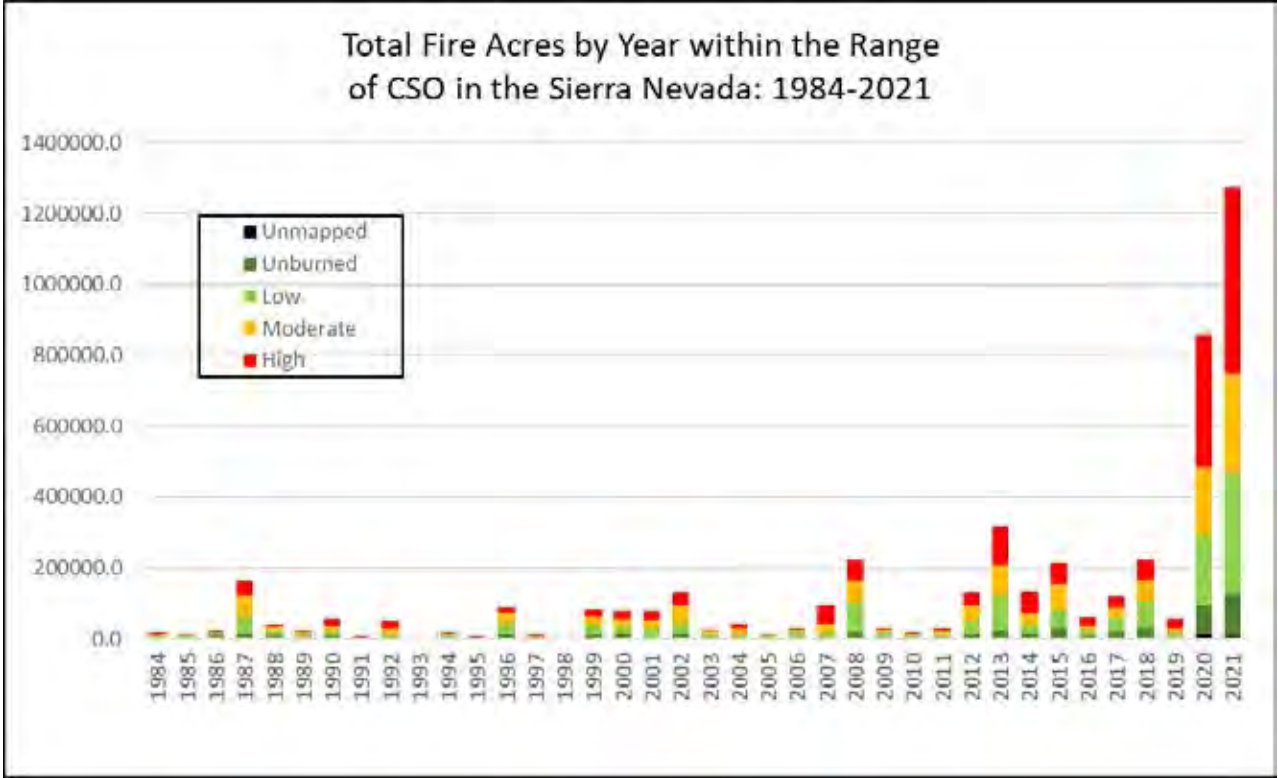
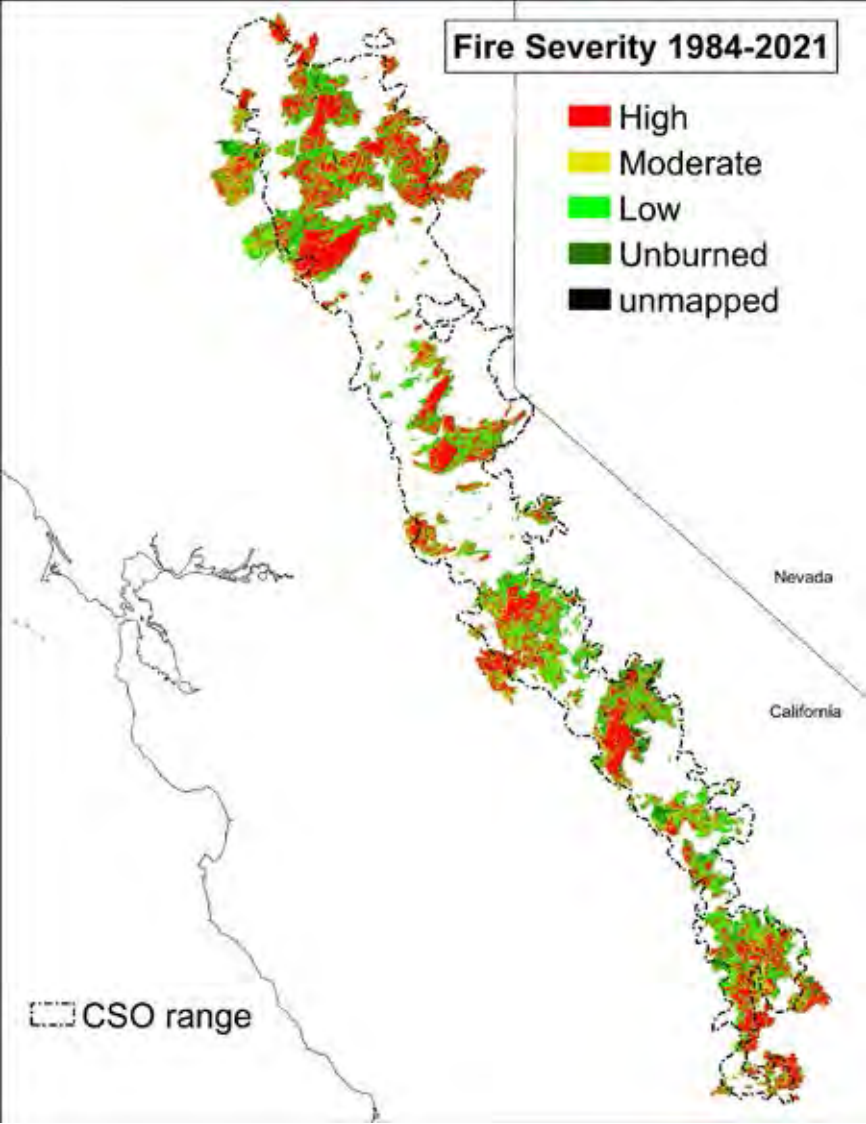
Overview

- Wildfire patterns and trends across the Sierra Nevada: 1984-2021.
- Effects of wildfire on California spotted owl protected activity centers: 1993-2021.
- Effects of wildfire on California spotted owl habitat: 2012-2021.
- Impacts of the Creek, North Complex, Caldor and Dixie Fires on California spotted owl protected activity centers and territories: 2020-2021.



Tom Munton

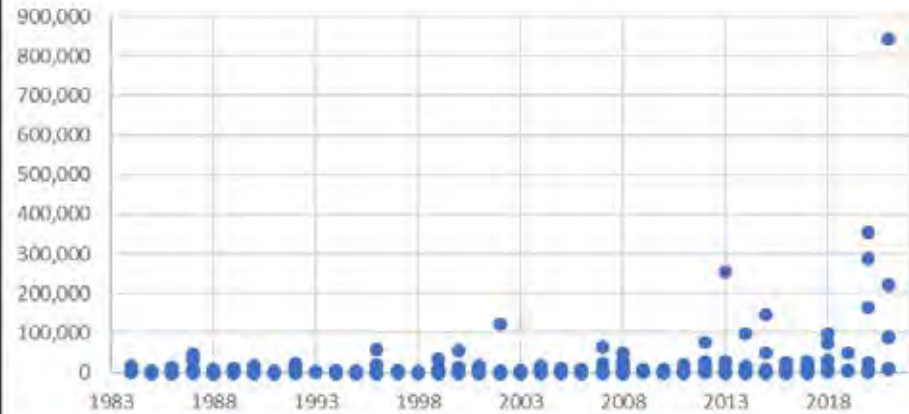
Fire within California Spotted Owl Range in the Sierra Nevada: 1984-2021



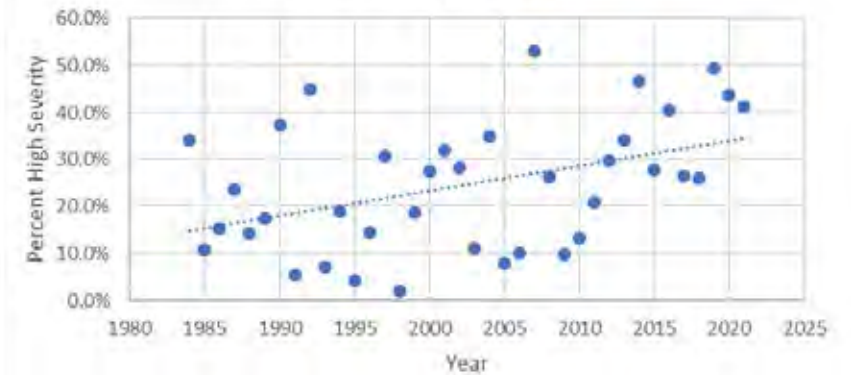
Time Period	Acres Burned	Percent of Total Acres	Acres of High Severity	Percent Of High Severity Acres
1984-2019	2,679,044	55.7%	784,820	46.6%
2020-2021	2,131,593	44.3%	898,929	53.4%
Total	4,810,637		1,683,750	35.0%

Characteristics of Fires within California Spotted Owl Range in the Sierra Nevada: 1984-2021

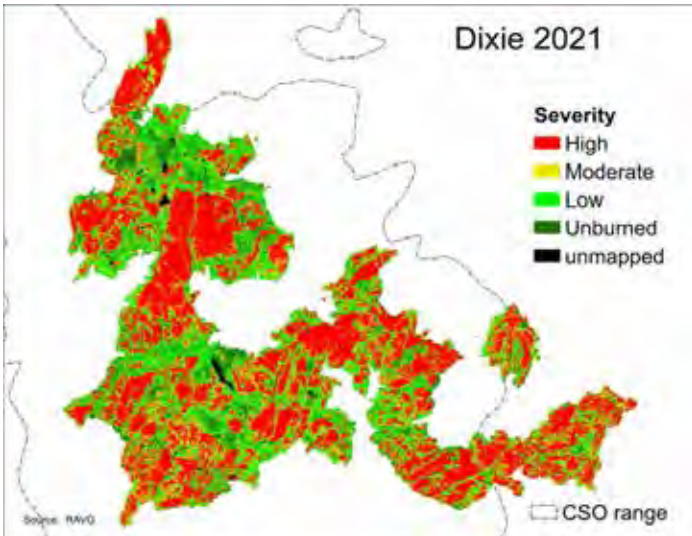
Fire Size (acres) within Range of the California Spotted Owl, Sierra Nevada, CA: 1984-2021



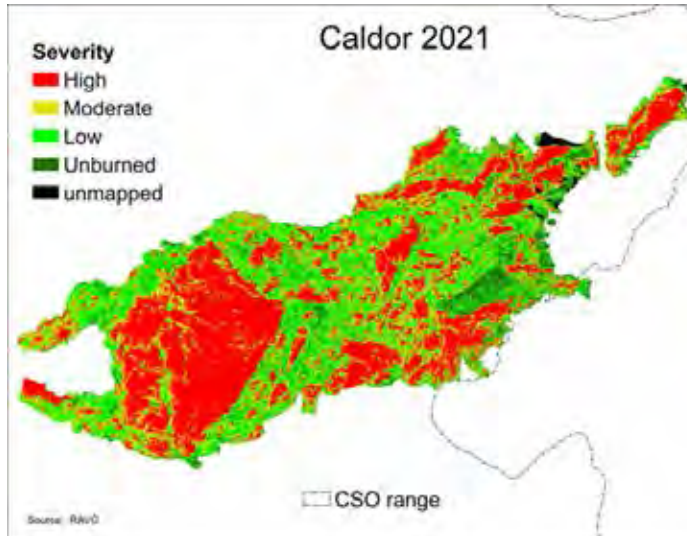
Percent of Annual Fire Acres that Burned at High Severity: 1984-2021



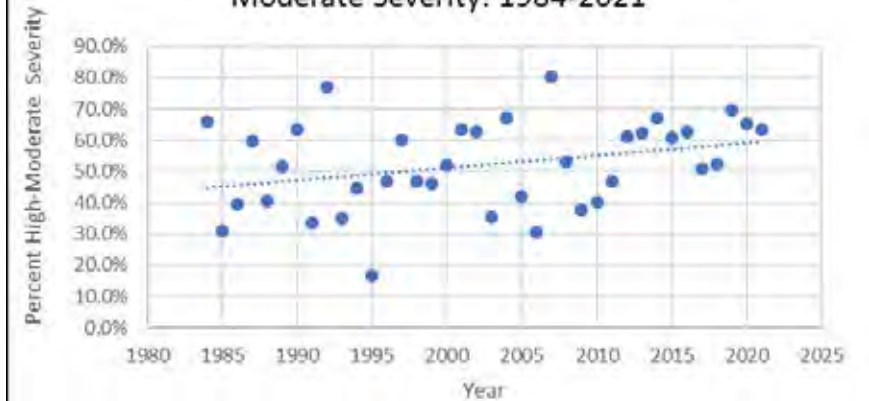
Dixie 2021



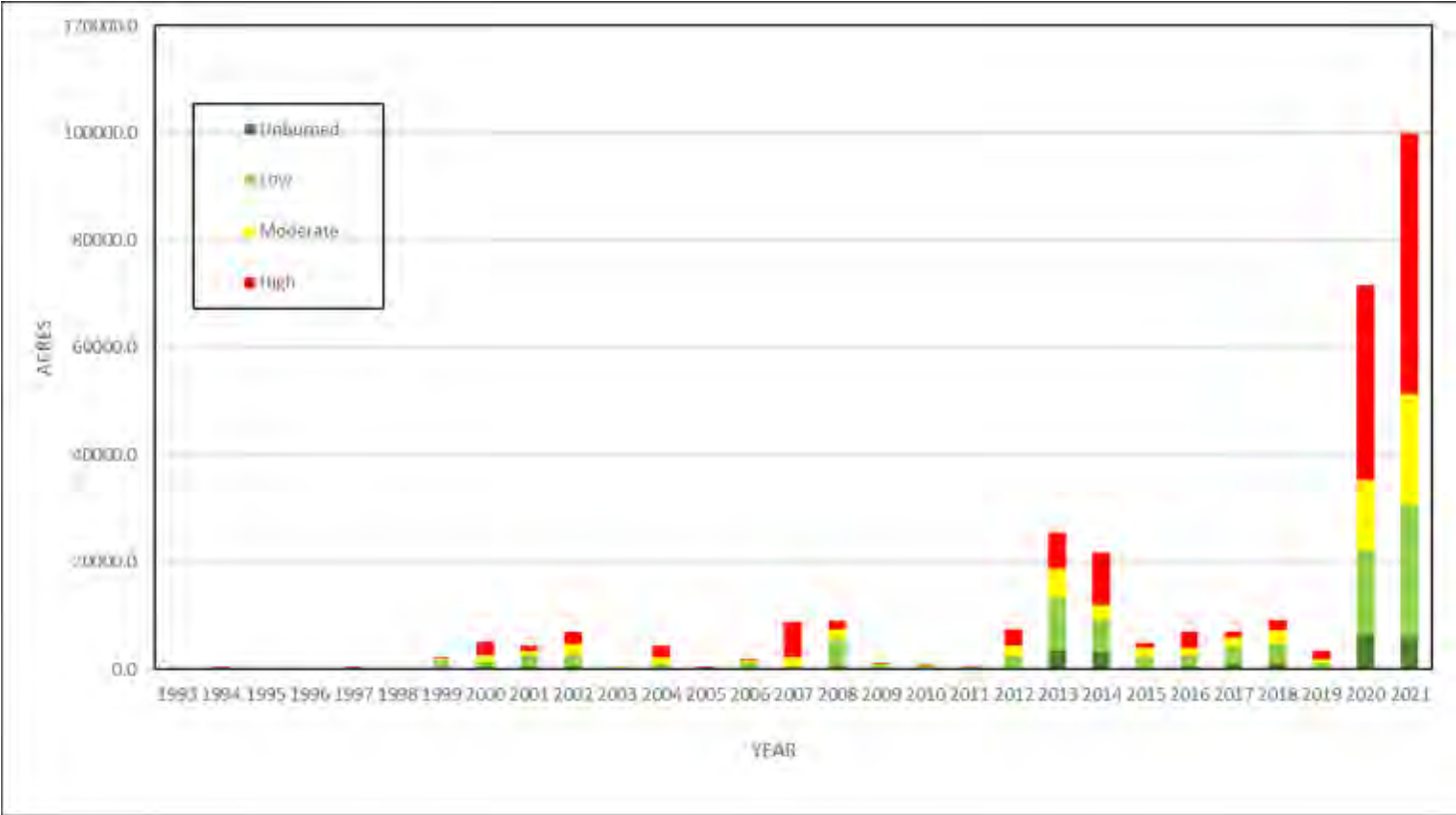
Caldor 2021



Percent of Annual Fire Acres that Burned at High-Moderate Severity: 1984-2021



Annual PAC Acres Burned by Severity Class within CSO Range in the Sierra Nevada: 1993-2021

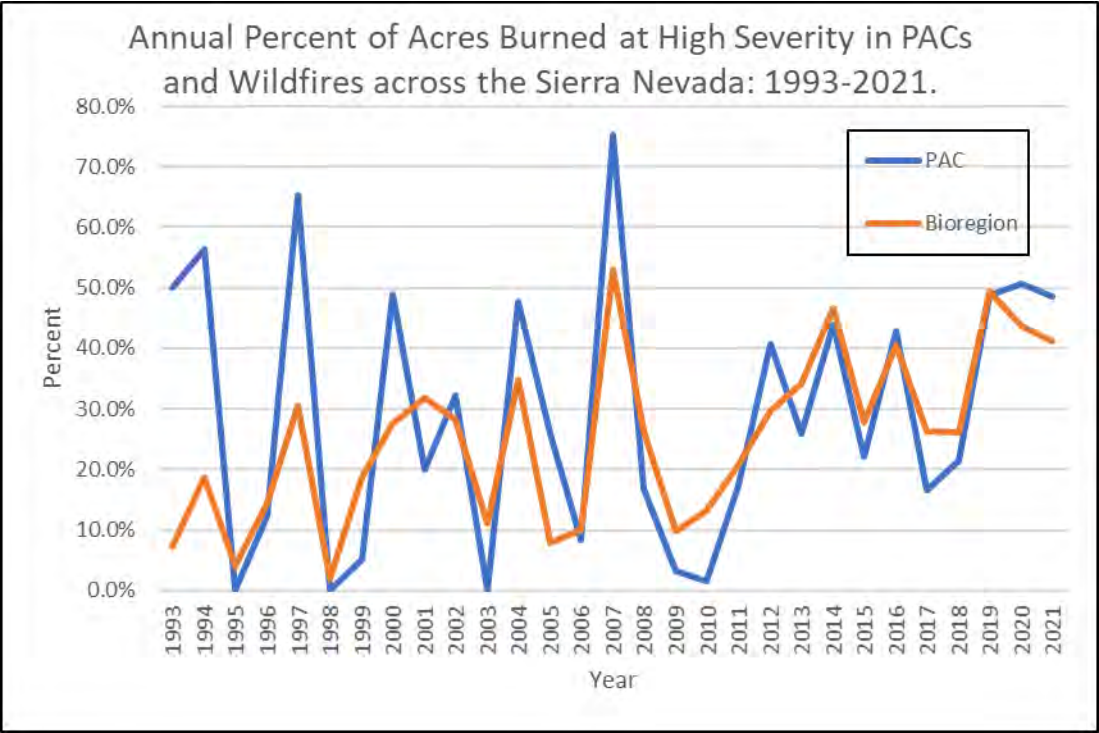


PAC Wildfire Summary: 1993-2021			
Acres	% Burned	% High Severity	% High-Moderate Severity
618,570	49.4%	21.1%	31.1%

Time Period	Acres Burned	Percent Total Acres Burned	Acres High Severity	Percent of High Severity
1993-2019	133,880	44.0%	45,540	34.8%
2020-2021	172,372	56.0%	84,600	65.2%
Total	306,252		130,140	42.5%

Total PAC Acres: Burn Amounts and Severity by National Forest: 1993-2021.				
National Forest	Total PAC Acres	Percent Burned	Percent High Severity	Percent High & Moderate Severity
Eldorado National Forest	107,327	57.4%	25.0%	35.7%
Lake Tahoe Basin MU	8,281	15.5%	8.2%	11.9%
Lassen National Forest	51,846	57.3%	24.7%	35.2%
Plumas National Forest	127,289	64.7%	33.2%	44.2%
Sequoia National Forest	63,554	75.1%	30.4%	51.1%
Sierra National Forest	99,422	44.7%	19.6%	29.6%
Stanislaus National Forest	77,299	35.9%	8.5%	15.6%
Tahoe National Forest	83,552	12.7%	2.6%	5.8%
Grand Total	618,570	49.4%	21.0%	31.1%

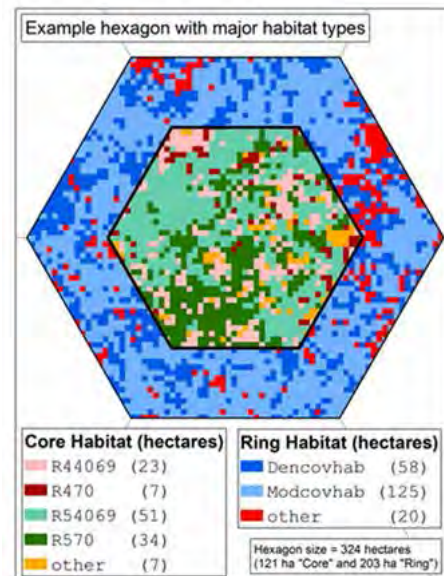
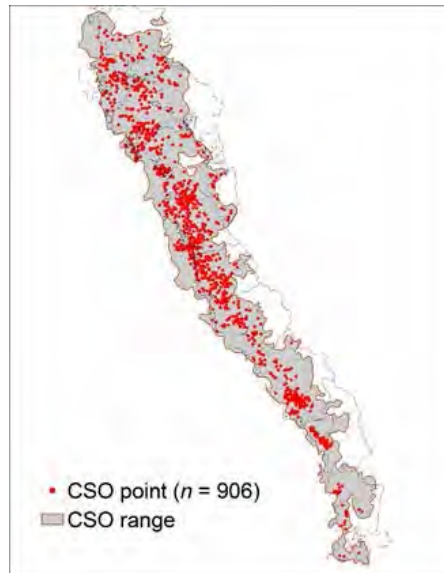
PAC Acres Within Fire Perimeters: Severity Patterns by National Forest: 1993-2021.			
National Forest	PAC Acres Burned	Percent High Severity	Percent High & Moderate Severity
Eldorado National Forest	61,694	43.5%	62.2%
Lake Tahoe Basin MU	1,285	52.8%	76.8%
Lassen National Forest	29,682	43.2%	61.5%
Plumas National Forest	82,403	51.2%	68.3%
Sequoia National Forest	47,700	40.5%	68.0%
Sierra National Forest	45,151	43.2%	65.2%
Stanislaus National Forest	27,765	23.6%	43.4%
Tahoe National Forest	10,572	20.9%	45.8%
Grand Total	306,252	42.5%	62.9%



Effects of Fire on CSO Habitat across the Sierra Nevada: 2012-2021.

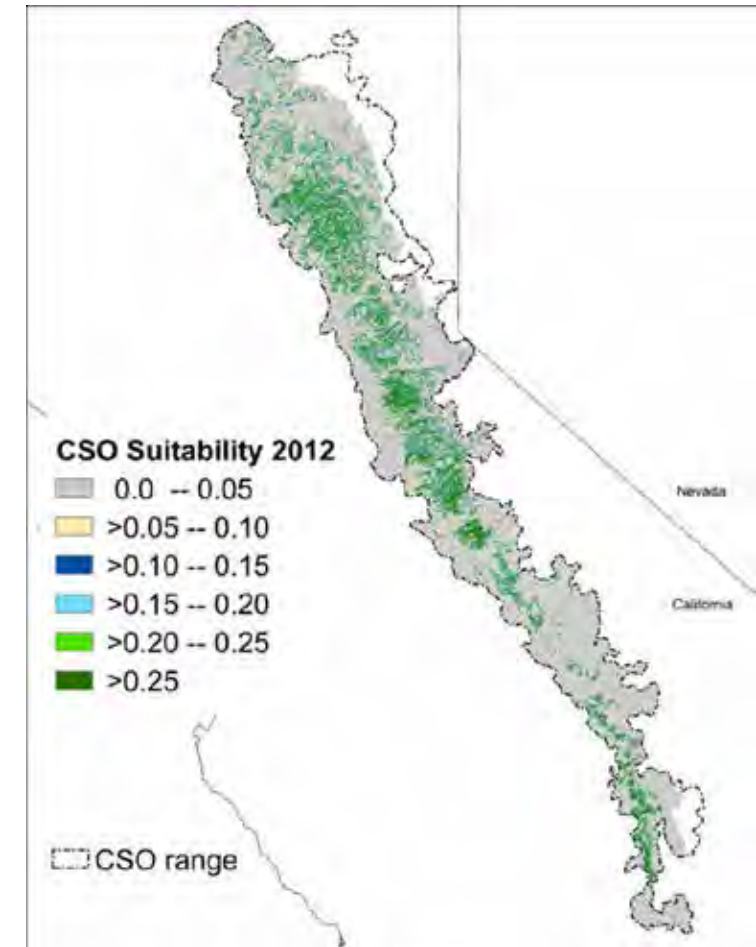
Development of a CSO Habitat Suitability Model

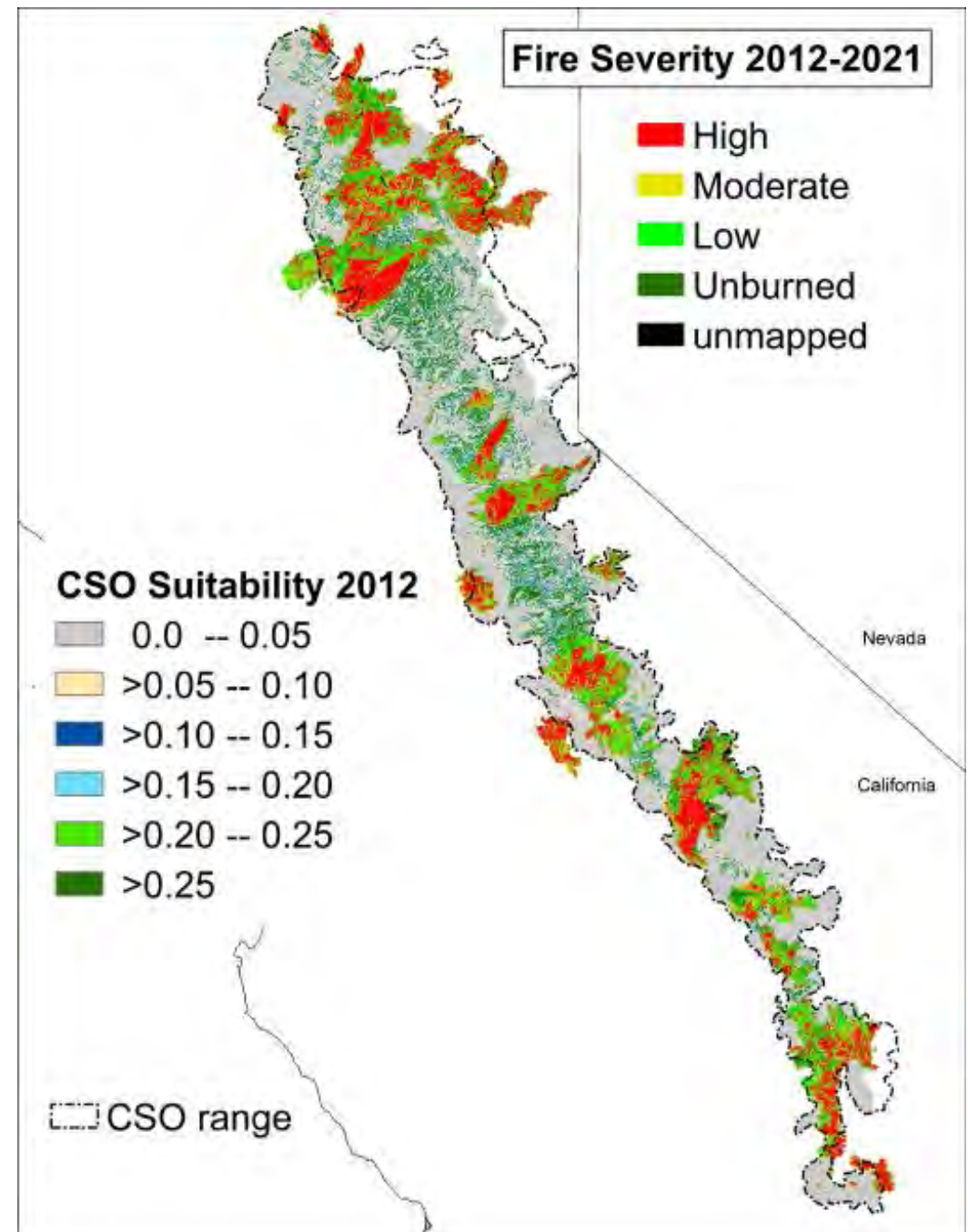
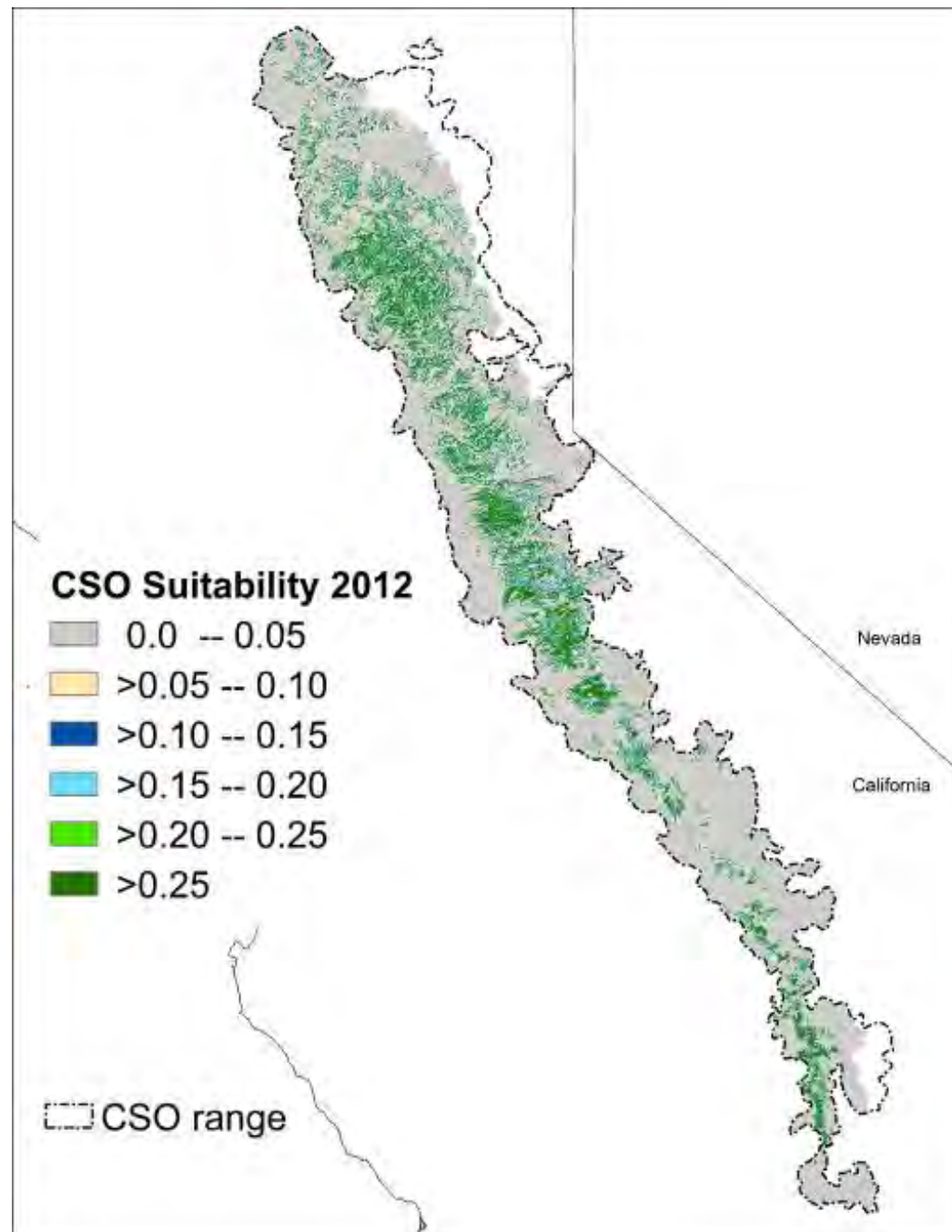
- Logistic Regression & Information Theoretic Approach to evaluate candidate habitat models.
- Total of 906 CSO sites reported as occupied between 2009-2014.
- Used 2012 GNN vegetation map for modeling habitat.
- Core-Ring Model.
- Bioregional and Ecoregion-scales.
- Used moving window to create a continuous map of CSO habitat suitability across Bioregion.

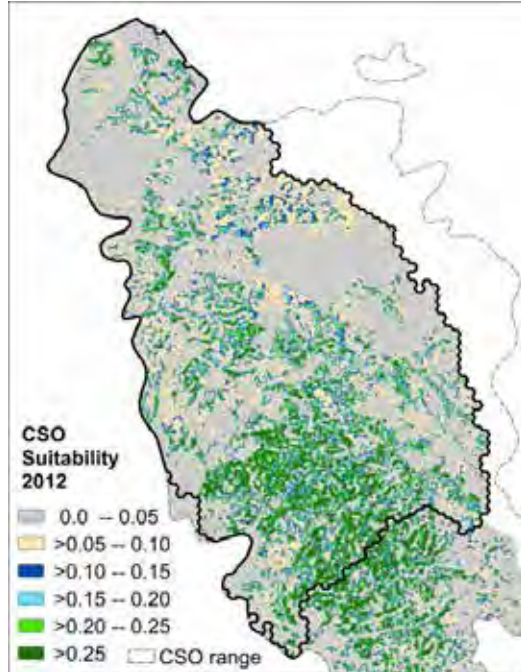


Top Bioregional Model

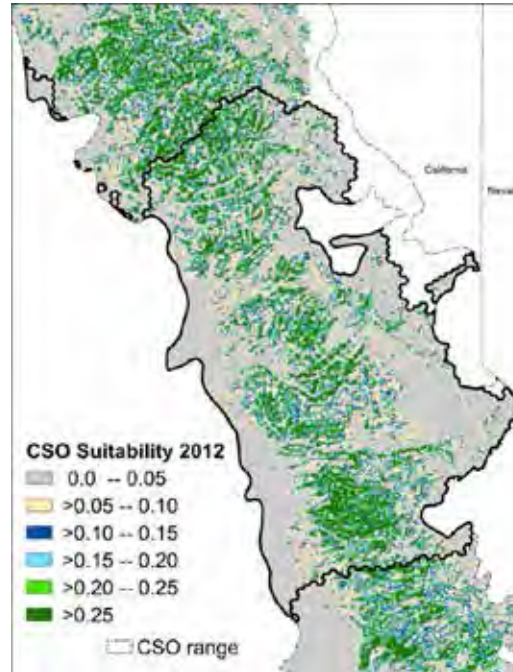
- Elevation, Lat-Long, LMU Class, Ownership, HexSize.
- CORE-scale: Positive Linear - Large and Medium Trees with Dense & Medium Cover.
- RING-scale: Quadratic - Dense Cover and Medium Cover Habitat.



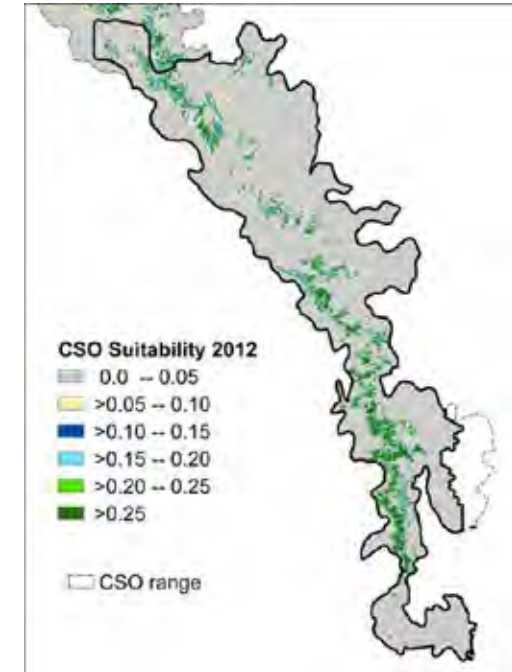




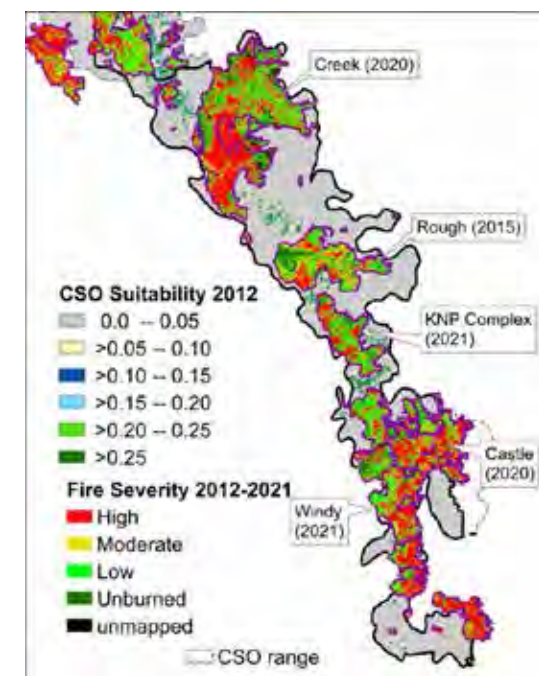
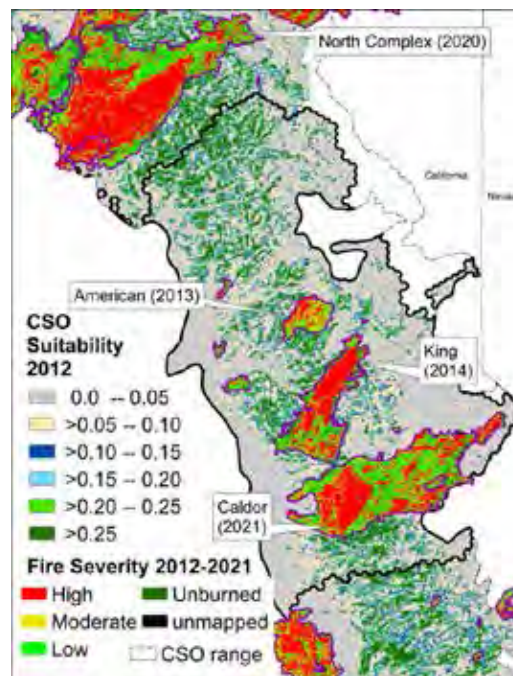
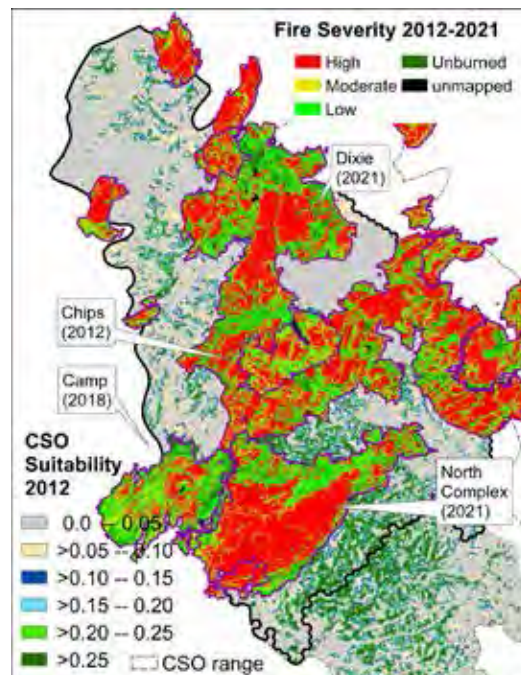
North Zone



Central Zone



South Zone



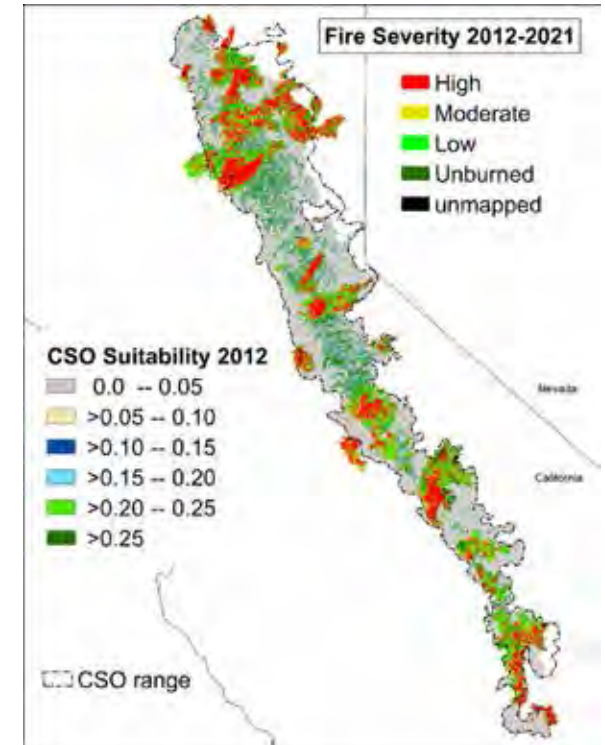
Fire Severity Patterns and CSO Habitat Suitability: 2012-2021.

High Suitability CSO Habitat: Amounts and Fire Severity Patterns by Zone

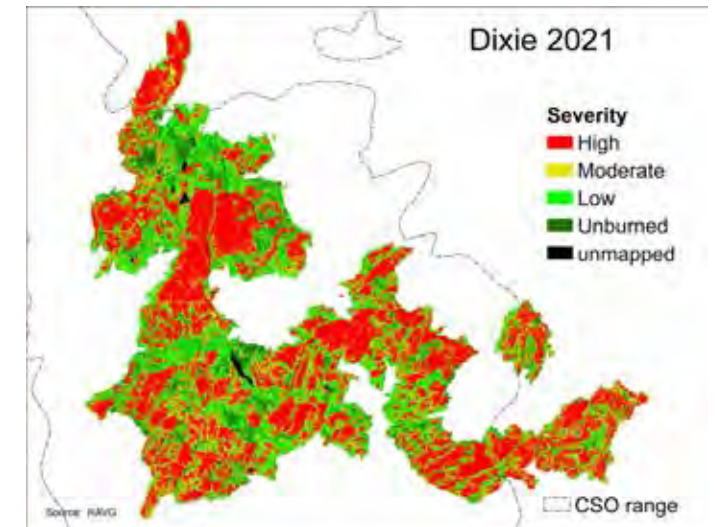
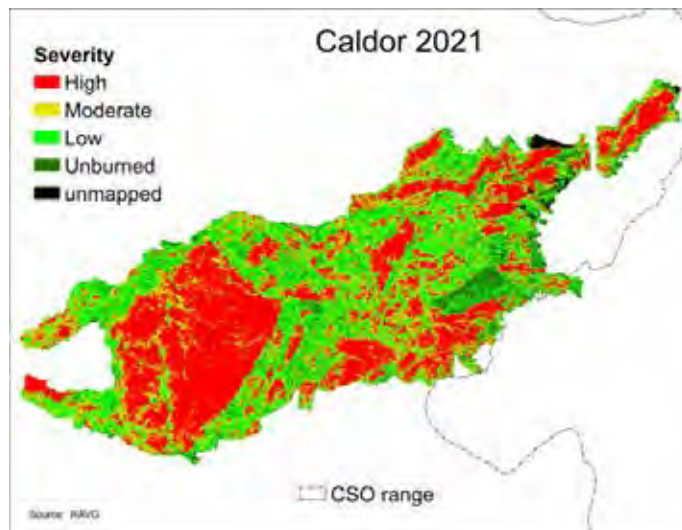
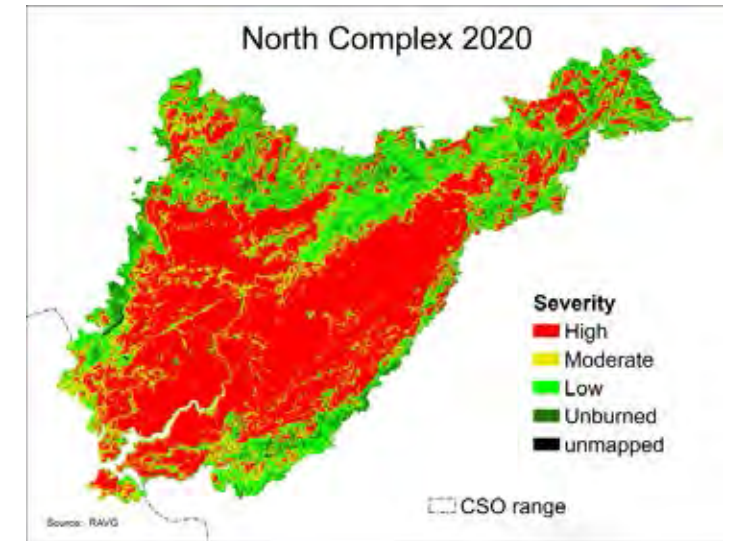
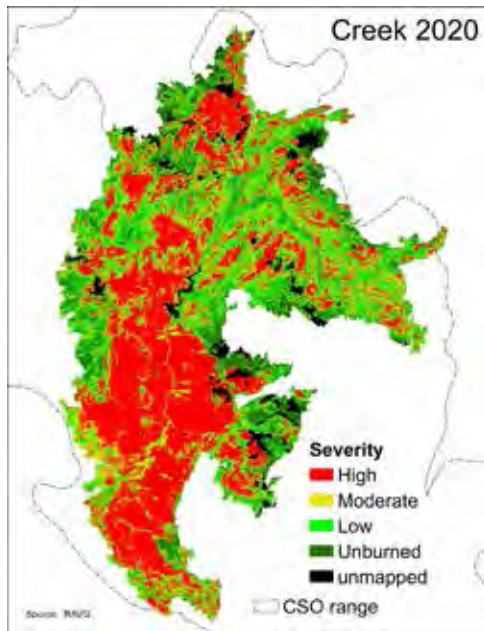
Eco Zone	Acres	% of Total Available	% Burned	% Burned High Severity	% High or Moderate Severity
North	699,330	30.3%	55.8%	25.1%	35.8%
Central	1,197,722	33.4%	28.6%	10.6%	16.9%
South	316,729	13.9%	73.1%	25.9%	42.6%
Bioregion	2,213,780	27.1%	43.5%	17.4%	26.5%

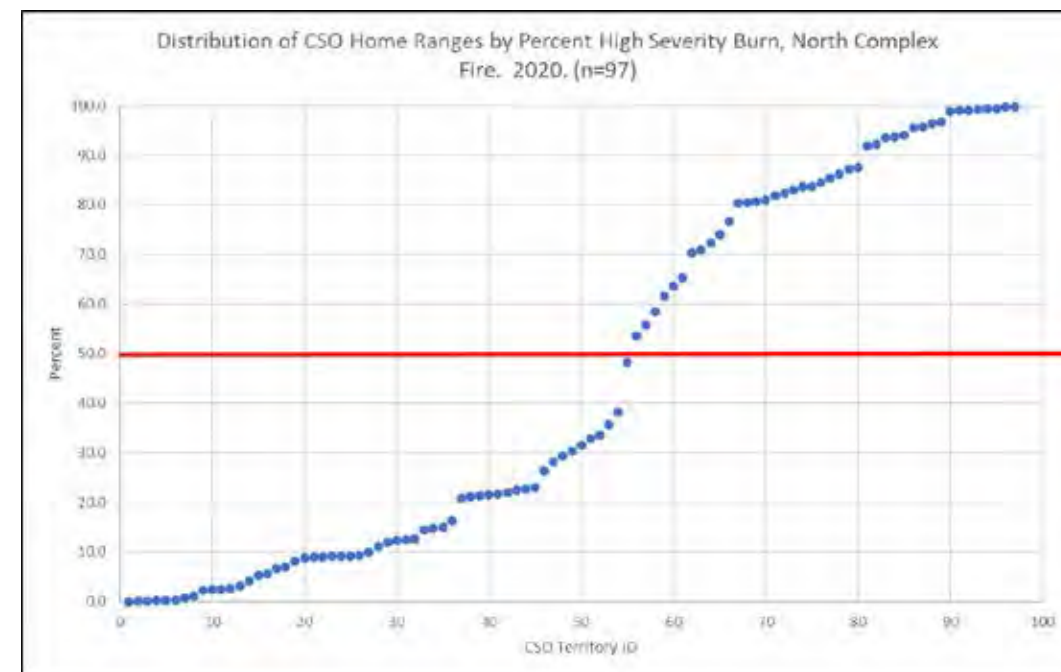
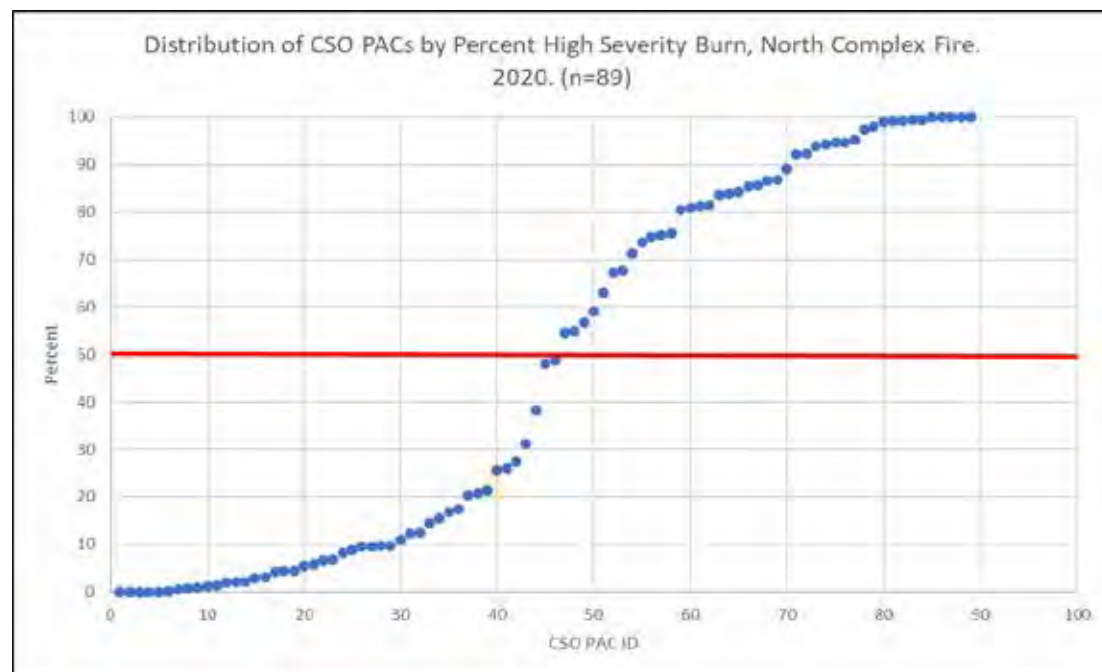
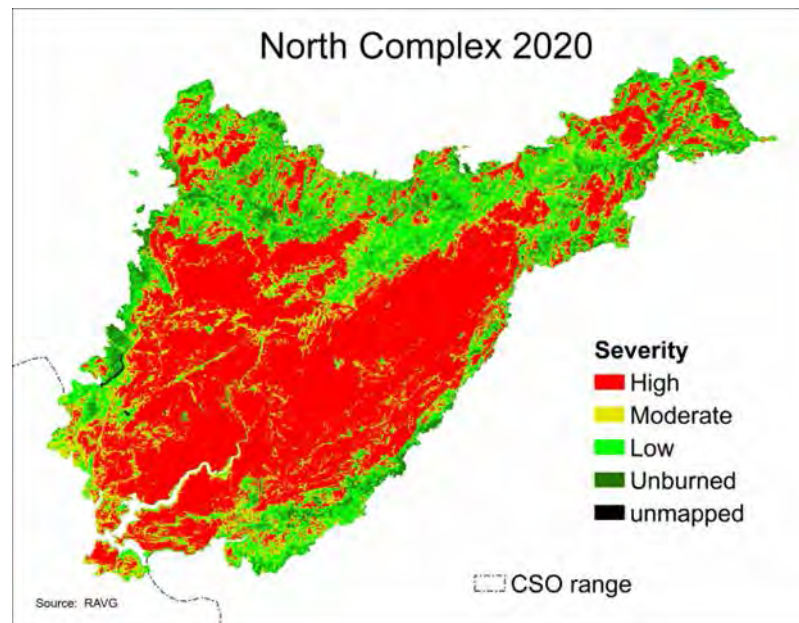
Fire Severity within Burned Acres across all CSO Habitat Suitability Classes by Zone

Eco Zone	Burned Acres	% Burned High Severity	% Burned High or Moderate Severity
North	1,143,800	45.6%	66.8%
Central	789,153	38.8%	63.4%
South	1,075,251	34.0%	60.1%
Bioregion	3,008,204	39.7%	63.5%



Case Study: Effects of Creek, North Complex, Caldor and Dixie Fires on CSO PACs and Territories: 2020-2021.





Summary of Effects of Creek, North Complex, Caldor and Dixie Fires on CSO PACs and Territories: 2020-2021.



Fire	Year	Size (acres)	Percent High Severity	No. PACS	Percent PACs >50% High Severity	No. Territories	Percent Territories >50% High Severity
North Complex	2020	288,787	52.2%	89	48.3%	97	43.3%
Creek	2020	366,400	39.6%	102	42.2%	106	34.9%
Caldor	2021	224,576	40.7%	89	43.8%	93	43.0%
Dixie	2021	848,828	42.6%	168	38.1%	181	31.5%
Total		1,728,590	43.3%	448	42.2%	477	36.9%

Conclusions

- In 2020-2021 witnessed unprecedented increases in total acres burned, fire size, and overall proportion and patch sizes of high-severity fire.
- Current wildfire burning at approximately 40-50% high-severity and 60-70% high or moderate severity within PACs and across the Bioregion.
- Approximately 50% of PAC acres have been affected by wildfire, with 56% of that total occurring in 2020-2021.
- 65% of Pac acres burned at high severity occurred during 2020-2021.
- Between 2012-2021, 17% of high suitability habitat has experienced high severity fire (>25% within North and South Zones)
- Recent large fires affect large number of CSO PACs and territories.



Rachel Bauer

Conclusions

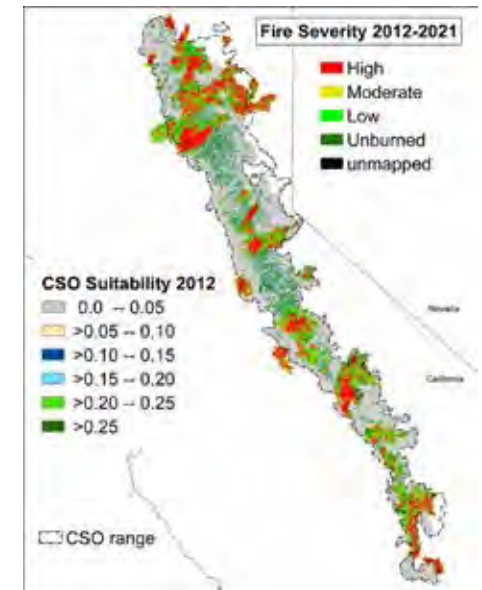
Ecological Context and Drivers:

- Historic forest management and 150+ years of fire suppression have shaped current forest conditions.
- Ongoing 22-year megadrought.
- Effects of megadrought amplified by interaction with climate change.
- Projected continued megadrought and warming climate
- 2020-2021 may be harbinger of future wildfire dynamics.
- Interactions with additional stressors: drought-insects-tree mortality.



Conservation and Management Challenges:

- Requires Immediate Management Action and New Perspectives to reduce risk to fire and other stressors (insects – tree mortality) in unburned landscapes.
- Post-fire and Unburned Landscapes – lessons from post-fire conditions can provide guidance on sustainable habitat.
- Need to Consider Landscape Trajectories – initial treatments, follow-up treatments, need for longer-term perspective, restoration of disturbance regimes.
- Management of Large Tree/Dense Canopy Patches – specific need to conserve and perpetuate these important habitat elements and conditions distributed across landscapes in topographical/geographical areas with higher probabilities of sustaining these conditions under future climate scenarios.



PROJECT DOCUMENTATION FORM
Tiers to Forest Service California Spotted Owl
Sierra Nevada Distinct Population Segment
Programmatic Biological Assessment

Version: March 25, 2024

PROJECT OVERVIEW

Project Name: Caldor Fire Restoration Project

Current Date: June 27, 2024

Service Project File Number: 2024-0045080

Contact Information

Point of Contact: Martha Kawasaki

Phone Number: 530-903-6209

Email: martha.kawasaki@usda.gov

Project Location

Forest: Eldorado National Forest

Ranger District: Placerville, Pacific, and Amador Ranger Districts

County: El Dorado and Amador Counties

Project Timeline

Anticipated start date: Approximately summer/fall 2024

Anticipated end date: Approximately fall 2029

Determination for California Spotted Owl

☒ May affect, not likely to adversely affect (NLAA)

☐ May affect, likely to adversely affect (LAA)

PROJECT ACTIVITIES AND DESCRIPTION

Activity Type (can check more than one box)

- ☒ Vegetation Management ☐ Special Use Permits ☒ Invasive Species Management
☒ Road, Trail, and Recreation/Administration Site Maintenance

Brief Project Description

The Eldorado National Forest (ENF) is proposing management actions to respond to conditions created by the 2021 Caldor Fire. The Caldor Fire burned in El Dorado and Amador counties, on the Placerville, Pacific, and Amador Ranger Districts of the ENF. The Caldor Fire burned 221,835 acres across Forest Service and private lands, with approximately 170,057 of those acres on the public lands managed by the ENF. The Caldor Fire, the largest recorded fire to have occurred on the ENF, was characterized by periods of intense fire growth that created large high-severity openings (composed of mostly dead trees) with patches greater than 30,000 acres in size. The fire also burned at low to moderate intensity in some areas, which may have enhanced or maintained existing forest conditions.

Purpose and Need

The overall purpose of the Caldor Fire Restoration Project (Caldor FRP) is to reduce risk to public health while restoring a healthy, resilient, and diverse ecosystem to lands affected by the 2021 Caldor Fire and surrounding areas, as well as managing ecosystem functions at a landscape scale. Additionally, the project purpose includes reestablishing recreational opportunities diminished by the 2021 Caldor Fire.

The purpose and need for the project are described in detail in the full Environmental Assessment for the project. In summary, the objectives of this proposal are to:

1. Reduce risk to public health and safety, as well as improve conditions for fire fighter and other forest worker safety;
2. Reduce the threat of uncharacteristic wildfires, increase ecosystem resilience to climate change and large-scale disturbances, restore fire return intervals in areas where fuel profiles allow; reduce hazardous fuel buildup, and eradicate nonnative invasive plant species;
3. Develop and maintain desired ecological processes and habitat conditions; restore and improve watershed health; and
4. Restore existing recreation sites and features impacted by the Caldor Fire.

Proposed Action

The proposed action includes the following activities, which are described in **Appendix A** (Proposed Activities), within the project area:

1. Hazardous fuels reduction, fuel break development and maintenance, temporary road construction, road repair and road decommissioning, and hazard tree abatement to

reduce risk to public health and safety, as well as fire fighter and forest worker health and safety. (Treatment Focus: Public Health and Safety)

2. Hazardous fuels reduction, green tree thinning and fuels reduction, prescribed fire, reforestation, sawlog and woody biomass removal, nonnative invasive plant species treatments and herbicide applications to increase resilience of the ecosystem, restore fire return intervals, reduce fuel buildup, and eradicate nonnative invasive species. (Treatment Focus: Forest Resilience)
3. Reforestation, road and trail repair, watershed, stream and meadow restoration, hazardous fuels reduction, hazard tree abatement, aquatic wildlife habitat improvement, aquatic organism passage, and nonnative invasive plant species removal will support the development and maintenance of desired ecological processes and habitat conditions; restore and improve watershed health. (Treatment Focus: Ecological Restoration)
4. Recreation feature restoration and recreation use management, road and trail repair/road decommissioning, hazard tree abatement, and hazardous fuels reduction will support restoration of recreation facilities and features adversely affected by the Caldor Fire. (Treatment Focus: Public Use)

The Caldor Fire is the largest wildfire recorded on the ENF; therefore, our post-fire recovery planning proposes to address restoration needs within the larger post-fire landscape for both immediate and long-term recovery. Planning at this large scale allows for a holistic approach to post-fire recovery, but some flexibility must be maintained to address changing conditions on the ground; post-fire landscapes present dynamic and unpredictable conditions over time with changing vegetation conditions and continued threats from wildfire, climate change, insect infestation, and drought. The full project, as described in the Project Environmental Assessment, proposes restoration activities under a broad spatial and temporal scale over the course of the next 15 to 20 years. However, the Forest Service has prioritized treatments to occur in the near-term (**next 5 years; Phase 1**) based on the post fire assessments described above. This Biological Assessment discloses our estimated implementation schedule for Phase 1 of the Caldor FRP.

Phase 1 Implementation

Table 1 summarizes the estimated implementation plan for proposed activities within the first five years across the project boundary. Acres and miles identified for these activities have been spatially identified. The activities described under the Proposed Activity column are described in detail in **Appendix A** and displayed in Figure 1 (**Appendix B**).

Table 1. Estimated Implementation Plan for Phase 1 (2024 – 2029)		
Proposed Activity (Appendix A)	Acres/Miles	Brief Description of Extent of Activity
Hazardous Fuels Reduction	27,660 acres	Ground Based: 12,886 acres Skyline: 533 acres

Table 1. Estimated Implementation Plan for Phase 1 (2024 – 2029)		
Proposed Activity (Appendix A)	Acres/Miles	Brief Description of Extent of Activity
		Additional Planned Units: 14,241 acres
Sawlog or Woody Biomass Removal	27,660 acres	Most likely to occur within hazardous fuels reduction units, but may be applied to treatment units for fuel break development and maintenance or green tree thinning and fuels reduction.
Hazard Tree Abatement	Where identified across the project area	Within all treatments units or areas leading to treatment units where workers could be injured during operations.
Green Tree Thinning and Fuels Reduction	Currently identified: 2,167 acres Maximum Annual: 5,000 acres	Currently identified units under the Independent Badger, subproject.
Fuel Break Development and Maintenance	Development: 123 miles Existing/Maintain: 70 miles Total: 193 miles	See Appendix A for description of fuel break ¹
Reforestation (Site Preparation, Planting, and Conifer Release)	27,234 acres	Generally following hazardous fuels reduction units, areas with low probability of natural conifer regeneration, and following sawlog and biomass removal units.
Recreation Feature Restoration & Use Management	Elkins Flat OHV Trail System: 14,057 acres Fleming Meadow Trail System: 1,231 acres	Work will focus on prioritizing restoration of existing motorized and non-motorized system trails to mitigate hazards and meet trail management objectives. Work may include trail reroutes, delineation of trails and/or blocking or obliterating user created trails.
Nonnative Invasive Plant Treatments	Currently identified: 275 acres	Additional treatment may be prioritized as target species are identified within the project area.
Watershed Restoration	Currently identified: Soil Restoration including non-system roads: 160 miles; Level 1 & 2 roads impacting water quality and aquatic habitat: 60 miles; dispersed recreation: 322 acres. Stream improvement: as identified in 2024 field season. Aspen Restoration: TBD	Preliminary work would focus on watershed improvements identified for Phase 1. Out-year projects will continue to be identified throughout the life of the project (15 – 20 years). Restoration goals would include improving and restoring degraded watershed conditions by reducing erosion, restoring hydrologic function, and restoring wildlife habitat. Work would focus primarily on impacts from system and non-system roads, logging and grazing, fires, and dispersed camping.

Table 1. Estimated Implementation Plan for Phase 1 (2024 – 2029)		
Proposed Activity (Appendix A)	Acres/Miles	Brief Description of Extent of Activity
Road Repair and Road Decommissioning	Road Repair: up to 648 miles Maintenance Level 1 System Roads: 57 miles	Priority on roads leading to treatment units within Phase 1, roads identified as public safety hazard, and roads that access critical infrastructure.
Prescribed Burning	Within identified units as a follow-up treatment Applied broadly to prioritized potential operational delineations (PODs) east of Grizzly Flat community	Post-treatment fuels reduction and maintenance activity; site preparation tool for reforestation; fuel break maintenance. Prescribed fire units may extend past primary activity units boundaries to utilize natural and existing holding features, such as roads, ridges, water features.
Activities Associated with Treatments Listed Above		
Temporary Road Construction	2 miles	Associated with existing Hazardous Fuels Reduction units.
Aquatic Organism Passage	Where identified across the project boundary	Roads and trails identified as needing new or improved stream crossings.

Conservation Measures

Which class of conservation measures is the project following?

- ☒ Class 2 (Vegetation Management) ☒ Class 2 (Other Activity Type)
☐ Class 3 (Vegetation Management)

Is the project proposing any modifications to the PBO conservation measures or will the project follow measures from multiple classes? ☐ Yes ☒ No

If yes, please describe any modifications to the PBO conservation measures.

No modifications to the Programmatic Biological Opinion (PBO) conservation measures are proposed.

In addition to fully adopting all applicable PBO Class 2 conservation measures, the proposed action includes several design features developed by ENF that would avoid or reduce potential impacts on California spotted owl (CSO) and suitable habitat. During the development of the proposed action, design features were identified to reduce or avoid potential adverse effects and ensure consistency with the Forest Plan and applicable laws, regulations, and policies. Some design features are specifically for the protection of CSO and other federally listed or Forest Service sensitive species (i.e. aquatic and terrestrial), while other design features (e.g., for soils and other biophysical resources) will help to reduce the potential for indirect effects to listed species and their habitats. All design features relevant to this analysis are provided in **Appendix C**, including those for species not being consulted on. Design features are referenced in the analysis below.

Is the project following a limited operating period (LOP)? ☒ Yes ☐ No

If yes, what is the duration of the LOP and where is it being implemented (e.g. within 0.25 mile from an active nest/roost site, within a PAC, or in and within 0.25 mile of nesting/roosting habitat)?

Pursuant to the Class 2 conservation measures and project design feature 3.2 (**Appendix C**), an LOP prohibiting vegetation treatments and other project activities that may affect spotted owl nesting behavior and nest success will be implemented during the CSO breeding season (March 1 through August 31). Specifically, the LOP will be implemented within: 1) approximately 0.25 mile of a PAC, and 2) in any suitable nesting habitat outside of a PAC located within approximately 0.25 mile of treatment activities. The LOP will not be required if protocol-level surveys confirm that CSO is not currently nesting in these areas.

Action Area

Total size of treatment units/construction footprint (acres): 72,531.2 (not including linear features such as road and trail treatments located outside of vegetation treatment units).

Size of the action area (acres): 290,609.4

Please describe how the action area was delineated:

The action includes all areas assumed to be potentially affected directly or indirectly by the federal action and not merely the immediate area involved in the action. The action area for the Caldor FRP, for the purposes of analyzing effects on CSO, is defined as ENF and other lands that include the project area boundary and a 0.25-mile buffer surrounding this area. Vegetation treatments and associated disturbances to habitat would be limited to these project locations, and this analysis assumes that project-related disturbances or indirect effects on CSO would not extend beyond a 0.25-mile disturbance buffer with implementation of applicable conservation measures. Figure 2 (**Appendix B**) displays the project area and action area identified for the Caldor FRP.

PROJECT-SPECIFIC CALIFORNIA SPOTTED OWL ANALYSIS

Owl Presence and Nesting Status

Table 2 summarizes the recent CSO survey history for all CSO protected activity centers (PACs) fully or partially contained within the action area. Because of the large number of PACs in the action area (68) and length of this table, Table 2 is provided in **Appendix D**.

Please provide any additional information or context regarding owl surveys and owl presence within the action area.

ENF conducted surveys for CSO presence following the Caldor Fire in 2022 and 2023, using a passive acoustic monitoring in conjunction with the Regional California Spotted Owl Acoustic Monitoring Program. Following this program, autonomous recording units (ARUs) were deployed within and near CSO PACs and territories, and areas of suitable habitat outside of these areas. Although survey coverage was well-distributed across the project area, not all areas of

suitable habitat were surveyed in 2022 and 2023. ARU surveys for CSO conducted post-fire in 2022 and 2023 documented presence of CSO at multiple locations (Table 2 [**Appendix D**]). The current nesting status associated with these detections has not yet been determined. Pacific Southwest Regional surveys (USDA 2006) for CSO presence following the Caldor Fire are underway for the 2024 field season within the action area. The surveys will continue where proposed vegetation treatments are likely to influence habitat quality in suitable CSO habitats with unknown occupancy, in the project area for compliance with the SNFPA.

Are barred owls known or suspected to occur within or near the action area? ☒ Yes ☐ No

If yes, please provide details:

Barred owls have been documented by ENF but were removed in 2019 and 2020. These removals occurred outside of the action area. The current occupancy status of barred owl in the action area is unknown; but the species is not expected to be abundant if present.

Existing Owl Habitat

General notes for Tables 2-5: **“Action area”** includes treatment units plus an appropriate buffer to account for additional effects such as noise disturbance. Refer to action area definition above. **“Suitable habitat/suitable”** refers to nesting/roosting and foraging habitat. **“Other”** includes dispersal habitat and non-habitat. **“NA”** means not applicable. Territories include PAC acres.

Table 3 summarizes the amount of CWHR-modeled nesting/roosting, foraging, and total suitable habitat estimated within treatment units by treatment type, and in the full action area. Key assumptions and details for interpreting the values presented in Table 3 are provided in the footnotes.

Table 3. Summary of CSO Habitat within the Treatment Units and Action Area ¹						
	Treatment Type ²	Total Nesting/ Roosting (ac or mi)	Total Foraging (ac or mi)	Total Suitable Habitat (ac or mi)	Suitable Habitat in PACs (ac or mi)	Suitable Habitat in Territories (ac or mi)
Treatment units	All treatments - Area Features	13,410.0 ac	11,922.0 ac	25,332.0 ac	3,579.0 ac	8,119.3 ac
	All treatments - Linear Features	122.9 mi	191.3 mi	314.3 mi	43.2 mi	102.5 mi
	<i>Hazardous Fuels Reduction</i>	3,369.0 ac	3,273.3 ac	6,642.3 ac	241.8 ac	746.0 ac
	<i>Green Tree Thinning and</i>	1,428.8 ac	556.1 ac	1,985.0 ac	461.7 ac	1,179.55 ac

Table 3. Summary of CSO Habitat within the Treatment Units and Action Area ¹						
	Treatment Type ²	Total Nesting/ Roosting (ac or mi)	Total Foraging (ac or mi)	Total Suitable Habitat (ac or mi)	Suitable Habitat in PACs (ac or mi)	Suitable Habitat in Territories (ac or mi)
	<i>Fuels Reduction</i>					
	<i>Fuel Break Development and Maintenance</i>	2,646.4 ac	3,599.0 ac	6,245.5 ac	1,057.8 ac	2,448.8 ac
	<i>Reforestation (Site Preparation, Planting, and Conifer Release) Phase 1</i>	4,128.1 ac	4,082.5 ac	8,210.6 ac	175.6 ac	655.9 ac
	<i>Recreation Feature Restoration & Use Management</i>	2,524.6 ac	2,075.7 ac	4,600.3	707.9	1,720.4
	<i>Non-native Invasive Plant Treatments</i>	140.0 ac	570.9 ac	710.9 ac	75.4 ac	281.6 ac
	<i>Meadow Restoration Phase 1</i>	36.4 ac	9.5 ac	45.8 ac	0 ac	4.7 ac
	<i>Watershed Restoration</i>	44.3 ac	110.1 ac	154.4 ac	9.3 ac	68.9 ac
	<i>Prescribed Burning</i>	9,410.5 ac	5,346.2 ac	14,756.7 ac	1,980.8 ac	4,453.5 ac
	<i>Sawlog or Woody Biomass Removal</i>	Included in other treatment types and acreages	Included in other treatment types and acreages	Included in other treatment types and acreages	Included in other treatment types and acreages	Included in other treatment types and acreages
	<i>Hazard Tree Abatement</i>	Included in other treatment types and acreages	Included in other treatment types and acreages	Included in other treatment types and acreages	Included in other treatment types and acreages	Included in other treatment types and acreages
	<i>Recreation Feature</i>	1.9 miles	10.5 miles	12.4 miles	2.1 miles	5.6 miles

Table 3. Summary of CSO Habitat within the Treatment Units and Action Area ¹						
	Treatment Type ²	Total Nesting/ Roosting (ac or mi)	Total Foraging (ac or mi)	Total Suitable Habitat (ac or mi)	Suitable Habitat in PACs (ac or mi)	Suitable Habitat in Territories (ac or mi)
	<i>Restoration & Use Management (Linear)</i>					
	<i>Road Repair (linear)</i>	97.4 mi	148.2 mi	245.6 mi	31.2 mi	79.3 mi
	<i>Road Obliteration (linear)</i>	23.2 mi	32.7 mi	55.9 mi	9.9 mi	17.6 mi
	<i>Road Closure (linear)</i>	11.4 mi	12.3 mi	23.7 mi	3.4 mi	8.8 mi
Action area		47,786.3 ac	71,205.5 ac	118,991.8 ac	15,628.1 ac	35,125.7 ac

¹For most treatment types, values are reported in acres (ac) of CWHR-modeled nesting/roosting, foraging, and total suitable habitat within treatment units. However, for proposed linear treatment types such as roads or trails, values are reported in miles (mi) that intersect habitat.

²For several treatment units, multiple treatment types would be implemented at the same location over the project duration to accomplish post-fire restoration objectives that require multiple techniques. Therefore, the acreages displayed for several individual treatment types in Table 3 overlap with those for other treatment types. For example, in some treatment units at the same location, hazardous fuels reduction activities and prescribed burning, followed by reforestation actions, would be implemented; and Table 3 reports acreages for each treatment type separately. However, for the “all treatments” summaries in the first rows of Table 3, overlap of acreages were removed to provide a total amount nesting/roosting, foraging, and total suitable habitat subject to any treatment type.

Table 4 summarizes current habitat in CSO PACs and territories within the action area. Because of the large number of territories in the action area and length of this table, Table 4 is provided in **Appendix D**. Definitions of nesting/roosting habitat and foraging habitat, which follow those established in the PBO, are provided below.

Describe the duration of project activities in owl suitable habitat, if known: Phase 1 of implementation, which includes all actions presented here, assumes a 5-year implementation time frame. It is likely that full implementation could take longer based on capacity, funding, and prioritization. Additionally, actions such as prescribed fire will have re-entries to maintain desired conditions over the long term. The project proposed action assumes a 15-20 year potential implementation timeframe including the Maximum Extent scenario.

Please describe the owl suitable habitat in the action area:

To characterize and quantify existing habitat conditions for CSO, vegetation/habitat types in the project area and analysis area were classified and mapped according to the California Wildlife

Habitat Relationships (CWHR) system (CDFW 2014) using the best available vegetation data for the action area. Habitat analysis for CSO was conducted using GIS vegetation layers to discern only those suitable cover and structure types as described in the CWHR system that reasonably estimate potentially suitable habitat, using criteria for nesting/roosting and foraging habitat provided in the PBO. Potentially suitable habitat for CSO was modeled using the following parameters:

- ▶ Habitat Potentially Suitable for Nesting and Roosting. Conifer forest (ponderosa pine, Jeffrey pine, Sierran mixed conifer, red fir, white fir, lodgepole pine, subalpine conifer, montane hardwood-conifer), aspen, and montane riparian stands of tree size class greater than 24 inches diameter at breast height (DBH) (CWHR Tree Size classes 5 and 6) and with canopy cover 40 percent or greater (CWHR Canopy Cover class M [40–59 percent] and D [60–100 percent]).
- ▶ Habitat Potentially Suitable for Foraging. In addition to potentially suitable nesting/roosting habitat defined above, which also provides foraging habitat, conifer forest, aspen, and montane riparian stands of tree size class 11 inches or greater DBH (CWHR Tree Size class 4) and with canopy cover 40 percent or greater (CWHR Canopy Cover class M [40–59 percent] and D [60–100 percent]).

While the CWHR definitions of suitable habitat described for CSO provide a rough and simplified metric for establishing the suitability of habitat as nesting/roosting or foraging habitat, they can be both over inclusive and under inclusive in characterizing suitable habitat (USDA Forest Service 2019, p. 23). CWHR characterizes stand sizes based on average stand diameter and the large tree size class does not differentiate categories beyond more than 24 inches DBH. So, when a stand has a mix of tree sizes, it can be difficult to distinguish between younger and older stands. The CWHR categories are also very broad and the classification system does not reflect habitat elements that are important aspects of nesting habitat, such as very large/tall trees and snags, slope position, or elevation (USDA Forest Service 2019, p. 23).

Prior to the 2021 Caldor Fire, CSO occurrences and nesting throughout the action area were well-distributed across suitable habitat historically. The Caldor Fire burned 221,784 acres across a range of land ownership and vegetation types. A total of 86 CSO PACs, established to protect key nesting and roosting habitats for CSO, were located within the fire perimeter on the ENF. Over 40 percent of the area burned in the Caldor Fire burned at a high severity, resulting in loss of greater than 95 percent of the forest basal area. CSO habitat experienced a range of fire severities, with nearly half experiencing no to low-severity fire, and nearly half experiencing high severity fire. Only a relatively small amount of CSO habitat experienced a loss in basal area in intermediate fire severity classes. (USDA Forest Service 2022). Accordingly, the abundance, quality, and distribution of CSO habitat in the fire perimeter shifted significantly as a result of the Caldor Fire; and, the number, locations, and configuration of PACs were revised by ENF as a result of post-fire conditions and distribution of remaining suitable habitat.

Presently, the action area contains all or portions of 68 CSO PACs and territories with variable amounts of suitable nesting/roosting and foraging habitats, and approximately 33,400 and 50,466 acres of potentially suitable nesting/roosting and foraging habitat, respectively, outside

of designated PACs and territories. Table 4 in **Appendix D** provides a detailed summary of habitat acreages within each PAC and territory in the action area.

Species Effects Analysis

Tables 5 and 6 summarize potential effects of project implementation on CSO PACs and territories, respectively, in the action area. Because of the large number of PACs and territories in the action area and length of these tables, Tables 5 and 6 are provided in **Appendix D**.

Table 7 summarizes overall effects of treatments on CSO suitable habitat in PACs, territories, and the full action area, including potential change in availability of nesting/roosting, foraging, and total suitable CSO habitat as a result of project implementation. The values presented in Table 7 are based on maximum estimates of potential habitat downgrade, which are likely overestimated. Key assumptions and details for deriving and interpreting the values presented in Table 7 are provided in the footnotes.

Table 7. Summary of Total Effects of Treatments on CSO Habitat¹					
	Total Nesting/ Roosting	Total Foraging	Total Suitable Habitat	Suitable Habitat in PACs	Suitable Habitat in Territories
Pre-treatment habitat within action area (ac)	47,786.3	71,205.5	118,991.8	15,628.1	35,125.7
Habitat maintained (ac)	≥ 42,960.0	≥ 66,370.7	109,330.7	15,628.1	35,125.7
Habitat downgraded (ac)	≤ 4,826.3	≤ 4,834.8	≤ 9,661.1	0	0
Habitat removed (ac)	0	0	0	0	0
Post-treatment habitat within action area (ac)	≥ 42,960.0	≥ 66,370.7	109,330.7	15,628.1	35,125.7
Change in habitat availability (ac)	≤ -4,826.3	≤ -4,834.8	≤ -9,661.1	0	0
Change in habitat availability (%)	≤ -10.1	≤ -6.8	≤ -8.1	0	0

¹Values for total and PAC/territory-specific nesting/roosting and foraging habitat were derived by initially assuming that treatment types with potential to modify average canopy cover and other key forest structure variables (including primarily fuels reduction, sawlog or woody biomass removal, green tree thinning and fuels reduction, hazard tree abatement, and fuel break development and maintenance treatments) could potentially downgrade habitat, then applying habitat retention standards in the Class 2 conservation measures and project design features to these areas, which would reduce the acreage potentially downgraded. The main Class 2 measures related to CSO habitat retention or downgrade require: 1) no downgrade/loss of suitable nesting/roosting and foraging habitat in PACs; 2) for territories outside of PACs with ≥ 60% total suitable habitat, retain ≥ 40-59% of the total suitable habitat in the territory; 3) for territories outside of PACs with 40-59% total suitable habitat, retain all existing nesting/roosting habitat and ≥ 40% total suitable habitat; and 4) for territories outside of PACs with less than 40% total suitable habitat, retain all suitable nesting and foraging habitat in the territory. Additionally, project

design feature 3.9 requires retention of $\geq 50\%$ canopy cover (where it currently exists) averaged within the treatment unit, where feasible, within CSO territories and home range core areas (HRCAs) outside wildland urban interface (WUI) defense zones. Because treatments that may result in tree removal within CSO territories would target relatively small size classes, average DBH of treated stands is not expected to be reduced and may increase; and, therefore, through maintaining $\geq 50\%$ canopy cover where present within territories, this analysis assumes no downgrade in PBO-defined nesting/roosting (CWHR 5M, 5D, and 6 types combined, with minimum of 40% canopy cover) or foraging (4M and 4D types combined, with minimum 40% canopy cover) habitat within territories. (Note: for purposes of acreage estimates, this analysis assumed that treatments where CSO territories and the WUI defense zone overlap would also retain $\geq 50\%$ canopy cover where present and/or not result in a downgrade in existing suitable habitat for those portions of territories.) Additionally, because treatment prescriptions have not been developed, and vegetation treatments would be designed to incorporate a range of specific habitat protection and retention standards following the Class 2 conservation measures and project design features, these project activities within many areas containing suitable habitat may be limited to understory treatments that would not substantially alter overstory canopy cover or average DBH of stands. Furthermore, per design feature 3.9, ENF would additionally maintain $\geq 50\%$ canopy cover within HRCAs, which include some areas outside of territories; however, the amount of suitable habitat proposed for treatment and subject to this retention standard outside of territories but within HRCAs has not been quantified or subtracted from potential effects acreages. Therefore, the estimated amount of habitat downgrade outside of PACs and territories shown in Table 7 is considered a maximum and likely an overestimate.

Are all the project's potential effects on the owl consistent with those described in the Programmatic BA?

☒ Yes ☐ No

Please describe the effects to the owl within the context of this specific project:

Direct and Indirect Effects

Potential Effects on Nesting and Reproductive Success

Presently, the action area contains all or portions of 68 CSO PACs and territories, and approximately 33,400 and 50,466 acres of potentially suitable nesting/roosting and foraging habitat outside of designated PACs and territories. ARU surveys for CSO conducted post-fire in 2022 and 2023 documented presence of CSO at multiple locations (Table 2 [Appendix D]). The current nesting status associated with these detections has not yet been determined; however, this analysis assumes that CSO currently nests in some portions the action area where suitable vegetation and other biophysical conditions remain.

The majority of proposed vegetation treatments would target high-severity burn areas, which generally do not support suitable nesting/roosting habitat for CSO currently. However, where mechanical and other intensive treatments would treat stands with structural characteristics considered potentially suitable for CSO nesting/roosting (i.e., CWHR classes 5M, 5D, 6; discussed further below under "Effects on Habitat in PACs, Territories, and Other Areas") during the breeding season, disturbances to nesting behavior and associated foraging activities near nest stands, and potentially loss of active nests, may occur during implementation of treatment activities. Proposed treatment activities that remove large trees or snags (i.e., hazardous fuels reduction, sawlog or woody biomass removal, green tree thinning and fuels reduction, hazard

tree abatement, fuel break development and maintenance) could result in inadvertent loss of nest trees/stands or active nests if present and not identified prior to treatment implementation. Use of heavy machinery or chainsaws during implementation of several proposed treatment activities or road treatments could result in increased visual stimuli (e.g., presence of personnel, vehicles, equipment) or increased noise within the vicinity of an active nest. Increased disturbance in the vicinity of active nests could result in direct impacts including abandonment of the active nest and subsequent loss of eggs or young.

The PBO Class 2 conservation measures and design feature 3.2 included as part of the proposed action, would be implemented to avoid inadvertent loss of active nests, eggs, or individuals. An LOP prohibiting vegetation treatments and other project activities that may affect spotted owl nesting behavior and nest success will be implemented during the CSO breeding season (March 1 through August 31). The LOP will be implemented within: 1) approximately 0.25 mile of a PAC, and 2) in any suitable nesting habitat outside of a PAC located within approximately 0.25 mile of treatment activities. The LOP will not be required if protocol-level surveys confirm that CSO is not currently nesting in these areas. Therefore, potential direct effects on CSO would be reduced to a negligible level; and, project activities would not substantially disturb or result in the loss of active CSO nests or otherwise impair CSO reproductive success in the action area.

Effects on Habitat in Protected Activity Centers, Territories, and Other Areas

Table 3 summarizes the amount of CWHR-modeled nesting/roosting and foraging habitat within proposed treatment units, for each treatment type and the full action area. Table 3 also summarizes the total amount of suitable habitat (nesting/roosting and foraging habitat combined) within treatment units located within CSO PACs and territories. Tables 5 and 6 in **Appendix D** provide detailed acreage estimates and other metrics for suitable habitat subject to treatments in individual PACs and territories, respectively. Table 7 summarizes overall effects of treatments on CSO suitable habitat in PACs, territories, and the full action area, including potential change in availability of nesting/roosting, foraging, and total suitable CSO habitat as a result of project implementation. The following discussion of project-related effects on CSO habitat is based on some of the metrics and values presented in these tables.

Of the 68 PACs located entirely or partially in the action area, treatments would be implemented in 54; the remaining 14 PACs would not be treated under the proposed action (see Table 5). Of the 54 PACs where any type of treatment is proposed, 34 contain proposed treatment types that could reduce overstory canopy cover and affect other stand structure variables important for CSO habitat quality (e.g., average DBH; frequency of tall, large-diameter trees and snags; coarse woody debris; structural complexity). These treatment types primarily include hazardous fuels reduction, sawlog or woody biomass removal, green tree thinning and fuels reduction, hazard tree abatement, and fuel break development and maintenance.

Although specific treatment prescriptions have not been developed, with incorporation of the PBO Class 2 conservation measures and applicable project design features, treatments within PACs will be designed to retain and promote key structural habitat elements required by CSO, protect nest stands, maintain existing nesting/roosting and foraging habitat quality, and avoid a habitat downgrade (e.g., changing nesting/roosting habitat to foraging habitat) within PACs (Table 7). Specific requirements and standards for maintaining or improving CSO habitat

suitability in PACs are described in Class 2 conservation measures 3, 4, and 5, and project design features 3.5, 3.6, 3.7, 3.8, 3.9, 3.10, and 3.11 (**Appendix D**).

Each CSO PAC in the action area is located fully within a larger territory associated with the PAC. As described for PACs, prescriptions for treatment activities implemented within CSO territories will be developed to maintain suitable nesting/roosting and foraging habitat quality in accordance with the PBO Class 2 conservation measures and applicable project design features. For territory areas outside of PACs, the Class 2 conservation measures require the following: 1) for territories outside of PACs with $\geq 60\%$ total suitable habitat, retain $\geq 40\text{--}59\%$ of the total suitable habitat in the territory; 2) for territories outside of PACs with $40\text{--}59\%$ total suitable habitat, retain all existing nesting/roosting habitat and $\geq 40\%$ total suitable habitat; and 3) for territories outside of PACs with less than 40% total suitable habitat, retain all suitable nesting and foraging habitat in the territory. Additionally, project design feature 3.9 requires retention of $\geq 50\%$ canopy cover (where it currently exists) averaged within the treatment unit, where feasible, within CSO territories outside wildland urban interface defense zones.

Because treatments that may result in tree removal within CSO territories would target relatively small size classes, average DBH of treated stands (and, accordingly, CWHR tree size class) within territories is not expected to be reduced. Reduction in smaller diameter trees will immediately increase quadratic mean diameter (QMD) across the treatment unit and project area. Over the long term, increased vigor of the remaining trees on the landscape will increase canopy cover. Reduction in smaller diameter class trees meets the CSO Conservation Strategy (USDA Forest Service 2019) to reduce tree densities in overrepresented size classes, while maintaining large, old trees. Therefore, through maintaining $\geq 50\%$ canopy cover where it currently exists within territories, this analysis assumes that vegetation treatments would not result in a downgrade in PBO-defined nesting/roosting (CWHR 5M, 5D, and 6 types combined, with minimum of 40% canopy cover) or foraging (4M and 4D types combined, with minimum 40% canopy cover) habitat within territories (Table 7).

While PACs and territories within the action area were designed to incorporate high-quality late seral habitat, additional suitable CSO nesting/roosting and foraging habitat is present outside these land allocations. The full action area (including PACs and territories) contains approximately 118,992 acres of CSO habitat, including nesting/roosting (47,786.3 acres) and foraging (71,205.5) habitat (Table 7). As summarized in Table 7, treatments in suitable CSO habitat could result in a habitat downgrade of up to 8.1% of the existing total suitable habitat outside of PACs and territories across the full action area. For reasons discussed previously, this amount of potential habitat downgrade is considered a maximum and likely an overestimate.

Please describe any cumulative effects (i.e., those resulting from future non-federal actions):

Land uses and environmental stressors that have resulted in CSO habitat loss, fragmentation, and degradation are primarily the result of past timber harvest and human development activities. Conditions in the project area largely reflect the recent (2021) Caldor Fire and post-fire changes associated with the loss of canopy cover, standing dead trees, and development of erosional features. Other specific non-federal actions that are reasonably likely to occur in the action area are not currently known; however, it is reasonable to assume that private timber production on Sierra Pacific Industries (SPI) lands, including harvest, fuels reduction, and

reforestation, recreation activities and land use changes (e.g., increased agriculture, urbanization and road development, human development) will continue in some portions of the action area that will be more detrimental than beneficial for CSO, potentially resulting in loss, degradation, or fragmentation of habitat for CSO or direct impacts (e.g., injury, mortality) on individual owls.

Determination Rationale for California Spotted Owl

Please describe your rationale for the determination (NLAA vs. LAA):

Based on this analysis, it is determined that implementation of the Caldor FRP, with incorporation of the applicable PBO Class 2 conservation measures and project design features, **may affect but is not likely to adversely affect** the Sierra Nevada distinct population segment (DPS) of the CSO. This determination is based on the following rationale:

- ▶ Pursuant to the Class 2 conservation measures and project design feature 3.2 (**Appendix C**), an LOP prohibiting vegetation treatments and other project activities that may affect spotted owl nesting behavior and nest success will be implemented during the CSO breeding season (March 1 through August 31). Specifically, the LOP will be implemented: 1) within approximately 0.25 mile of a PAC, and 2) in any suitable nesting habitat outside of a PAC located within approximately 0.25 mile of treatment activities. The LOP will not be required if protocol-level surveys confirm that CSO is not currently nesting in these areas. Therefore, project activities would not directly cause potential disturbance or loss of active CSO nests, or otherwise impair reproductive success, of CSO in the action area.
- ▶ Following the 2021 Caldor Fire, ENF reviewed and reconfigured CSO PACs and territories, as needed, to include the best available CSO nesting/roosting habitat, foraging habitat, and known occurrences and activity centers remaining in the action area post-fire. As required by the Class 2 conservation measures, treatment prescriptions will be designed to maintain the existing amount and quality of nesting/roosting and foraging habitat in PACs (i.e., no downgrade or removal of nesting/roosting habitat in PACs would result); additionally, through implementation of the Class 2 conservation measures and design feature 3.9, the existing amount of nesting/roosting habitat will be maintained in territory areas outside of PACs. Overall, implementation of these retention standards would maintain the highest-quality CSO habitat and the areas considered most important for CSO population viability in the action area (i.e., nesting/roosting and foraging habitat within PACs).
- ▶ Although some downgrade in suitable CSO habitat outside of PACs and territories may occur as a result of proposed vegetation treatments designed to meet post-fire restoration objectives (see Table 7 for maximum estimates), the maximum amounts of nesting/roosting and foraging habitat potentially affected are generally small relative to their overall availability in the action area and are within the allowable limits established for PACs and territories in the PBO Class 2 conservation measures.

For these reasons, implementation of the Caldor FRP is not expected to cause reduced occupancy by CSO in the action area over the short or long term, or loss of viability or extirpation of the local and regional CSO population.

OTHER THREATENED & ENDANGERED SPECIES

Are other federally listed species and/or critical habitat affected by this project? ☒ Yes ☐ No

If yes, what species and/or critical habitat and what were the effects determination(s)?

Species	Status	Effects Determination ¹
North American wolverine (<i>Gulo gulo luscus</i>)	Proposed Threatened	May Affect, Not Likely To Adversely Affect
Sierra Nevada red fox (<i>Vulpes vulpes necator</i>)	Endangered	May Affect, Not Likely To Adversely Affect
Yellow-billed cuckoo (<i>Coccyzus americanus</i>)	Threatened	No Effect
California red-legged frog (<i>Rana draytonii</i>)	Threatened	May Affect, Not Likely To Adversely Affect
California red-legged frog Critical Habitat	Designated	No Effect
Foothill yellow-legged frog (<i>Rana boylei</i>) South Sierra DPS	Endangered	May Affect, Not Likely To Adversely Affect
Sierra Nevada yellow-legged frog (<i>Rana sierrae</i>)	Endangered	May Affect, Not Likely To Adversely Affect
Sierra Nevada yellow-legged frog Critical Habitat	Designated	
Layne's Butterweed (<i>Senecio layneae</i>)	Threatened	No Effect
Whitebark Pine (<i>Pinus albicaulis</i>)	Threatened	No Effect

Has Section 7 consultation for the proposed project's effects on the species and/or critical habitat been previously completed? ☐ Yes ☒ No

If yes, what is the Service File Number of the Concurrence Letter or Biological Opinion issued by the Service?

If no, have you followed the process for consulting on multiple species and/or critical habitats as described in the Programmatic Biological Assessment, including the submittal of a project-specific Biological Assessment as part of this consultation package? ☒ Yes ☐ No

SUBMITTED DOCUMENTS

Please ensure that all relevant documents have been submitted to USFWS. Asterisks denote required documents. List all attachments below.

*GIS Shapefile(s)	☒ Yes ☐ No	File name(s):
*Map(s) of Action Area and Activities	☒ Yes ☐ No	File name(s):
*Map(s) of Owl Habitat and PACs	☒ Yes ☐ No	File name(s):
Map(s) of Known Owl Occurrence History	☐ Yes ☒ No	File name(s):
Photo(s) of Representative Habitat	☐ Yes ☒ No	File name(s):
Other document(s)?	☐ Yes ☒ No	File name(s):

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Species Status Assessment Report

for the

California Spotted Owl

(*Strix occidentalis occidentalis*)



Photo provided by Tim Dermers

Version 2.0
November 2022

Acknowledgements

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Suggested reference:

U.S. Fish and Wildlife Service. 2022. Species Status Assessment for the California Spotted Owl (*Strix occidentalis occidentalis*), Version 2.0. November 2022. Sacramento, California.

EXECUTIVE SUMMARY

We, the U.S. Fish and Wildlife Service (Service), were petitioned to list the California spotted owl (CSO) as endangered or threatened under the Endangered Species Act of 1973, as amended (16 U.S.C. 1531-1543) (Act), in December 2014 by the Wild Nature Institute and John Muir Project of Earth Island Institute and again in August 2015 by Sierra Forest Legacy and Defenders of Wildlife. In September 2015, the Service published a 90-day finding that the petition presented substantial scientific or commercial information indicating that listing CSO may be warranted (80 FR 56423, September 18, 2015). In November 2019, the Service published a 12-month finding in the Federal Register that listing CSO was not warranted (84 FR 60371, November 8, 2019). In August 2020, Sierra Forest Legacy, Defenders of Wildlife, and the Center for Biological Diversity filed a complaint challenging our 12-month finding that listing was not warranted. On November 30, 2021, the Service voluntarily remanded the not warranted finding and committed to a deadline of February 15, 2023, for submitting to the Federal Register a 12-month finding on CSO. Therefore, a review of the status of the subspecies was initiated to determine if listing is warranted. Based on the status review, the Service will issue a 12-month finding for CSO.

This report summarizes the results of the Species Status Assessment (SSA) completed for the California spotted owl. To assess the species' viability, we used the three conservation biology principles of resiliency, redundancy, and representation (together, the 3 Rs). These principles rely on assessing the species at an individual, population, and species level to determine whether the species can maintain its persistence into the future and avoid extinction by having multiple resilient populations distributed widely across its range. California spotted owls are currently found throughout their known historical range, although there is evidence of a decrease in abundance in parts of the range. California spotted owls are distributed across habitat in California and Nevada including the Sierra Nevada, coastal California, and southern California. We identified two CSO populations: one in the Sierra Nevada (likely to be a continuously distributed population), and another in coastal and southern California (likely to be several disjoint subpopulations; hereafter referred to as the coastal-southern California population). Available demography data indicate that the California spotted owl may be more or less resilient in different portions of the species range. For our analysis we further divided each of the two populations into analysis units based on land management boundaries, with 11 analysis units in the Sierra Nevada population and 4 analysis units in the coastal-southern California population. For California spotted owl, resiliency was measured by assessing the individual needs of canopy cover, large trees, and habitat heterogeneity, as well as the population needs of dispersal, survival, fecundity, occupancy, and population growth. At the species level, we assess redundancy and representation throughout the entire CSO range to better understand the viability of the species.

Our analysis of the past, current, and future influences on the California spotted owl revealed that there are several factors that contribute to the current condition and pose a risk to future viability of the species. These risks include large-scale high-severity fire, tree mortality, effects of climate change, fuels reductions and forest management, barred owls, rodenticides, development, and regulatory mechanisms and other management actions. Parasites, disease, and recreation are not currently known to have population level impacts on the California spotted owl, but these risks are discussed in the future condition sections as we expect potential changes in these influences in the future. Under current conditions, the California spotted owl has three analysis units that are stable, seven analysis units that are in declining condition, and five analysis units that are in strongly

declining condition, resulting in the Sierra Nevada population having low resiliency and the coastal-southern California population having very low resiliency.

The influences to viability described above play a large role in the future resiliency, redundancy, and representation of the California spotted owl. If populations lose resiliency, they are more vulnerable to extirpation, with resulting losses in representation and redundancy. The rates at which future stressors may act on specific populations or analysis units and the long-term efficacy of current conservation actions (i.e., conservation strategies) are unknown. Therefore, we forecasted how possible future conditions could impact the resiliency, redundancy, representation, and overall condition of the California spotted owl. To assess future condition, we have developed two future plausible scenarios. The following is a description of the two future scenarios, the status of the California spotted owl when analyzed under each scenario, and a summary of the assumptions we made under each scenario:

Scenario 1: Factors that are currently having an influence on California spotted owl populations and analysis units increase in both trend and magnitude, with implemented management efforts having mixed success in addressing those threats. Under Scenario 1, we project the California spotted owl would have zero analysis units in stable condition, four analysis unit that are in declining condition, six analysis units that are in strongly declining condition, and five analysis units that are extirpated.

1. Large-scale high-severity fires increase on the landscape throughout California spotted owl habitat.
2. Tree mortality numbers increase in the future due to drought, disease, and beetles.
3. Drought conditions increase in the future, resulting in both habitat impacts and physiological impacts to California spotted owls.
4. Effects of climate change increase in the future, resulting in both habitat impacts and physiological impacts to California spotted owls.
5. Fuels reductions and forest management actions increase, with both positive and negative impacts on California spotted owls.
6. Barred owls increase in numbers and displace California spotted owls on the landscape.
7. Rodenticides increase on the landscape, impacting California spotted owl population survival rates.
8. Disease and parasites may increase on the landscape, impacting California spotted owl survival.
9. Development increases on the landscape, reducing California spotted owl habitat.
10. Recreation increases on the landscape, resulting in impacts to California spotted owl fecundity and occupancy.

Scenario 2: Factors that are currently having an influence on California spotted owl populations and analysis units continue at the current trajectory into the future, with implemented management efforts being fully successful. Under Scenario 2, we project the California spotted owl would have zero analysis units in stable condition, eight analysis units in declining condition and seven analysis units that are in strongly declining condition with the potential of extirpation in 40–50 years.

1. Large-scale high-severity fires increase slightly or remain stable due to management actions with the goal of maintaining high quality spotted owl habitat while reducing fuel loads on the landscape.

2. Tree mortality numbers remain stable or decrease slightly due to reduced fuel loads, providing larger trees with more resources to be more resilient to drought, disease, and beetles.
3. Drought conditions increase slightly into the future, resulting in both habitat impacts and physiological impacts to California spotted owls.
4. Effects of climate change increase slightly in the future, resulting in both habitat impacts and physiological impacts to California spotted owls.
5. Fuels reductions and forest management actions increase, with both positive and negative impacts on California spotted owls.
6. Barred owl management is effective in minimizing the risk of invasion.
7. Rodenticides remain stable on the landscape, with minor impacts to California spotted owl population survival rates.
8. Disease and parasites remain stable on the landscape, with minor impacts to the California spotted owl.
9. Development trajectories remain stable in potential California spotted owl habitat.
10. Recreation continues at the current rate within California spotted owl habitat with little to no impacts on California spotted owl occupancy or fecundity.

The outcome of future scenario 1 and future scenario 2 are very similar after 40–50 years. Under future scenario 1, where the intensity of the threats increases over time and management actions are not fully effective at addressing threats, the condition of almost all analysis units would decline. Overall, the resiliency of the Sierra Nevada would be very low under scenario 1 and because the condition of the coastal-southern California population would be extirpated, it would have no resiliency under scenario 1. Under future scenario 2, where the magnitude of the threats continues on the current trajectory and current management actions are fully effective in the future, the condition of analysis units and corresponding population resiliency decreases from current condition, although less than under future scenario 1. Under scenario 2, the Sierra Nevada population has very low resiliency, although closer to our scoring boundary of low resiliency, and the coastal-southern California population has very low resiliency. Scenario 2 would likely lead to reduced redundancy and representation for the species, but to a lesser extent than scenario 1, as the species would have less flexibility to adapt to changing environmental conditions. If the current conservation measures that are in place continue under scenario 2, there will be some protection for the species against certain ongoing threats compared to under scenario 1; however, even with these protections in place the species is still vulnerable to large-scale high-severity fire and climate change impacts.

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CHAPTER 1: INTRODUCTION

1.1 Petition History and Previous Federal Actions

The California spotted owl (*Strix occidentalis occidentalis*) is a subspecies of spotted owl that occurs throughout the Sierra Nevada mountains in California and Nevada (hereafter, referred to as Sierra Nevada), along the central California coast in the Coast and Transverse Ranges from Monterey County south into Ventura County (hereafter, referred to as coastal California), in southern California in the Transverse and Peninsular mountain ranges from Ventura County to San Diego County in the south (hereafter, referred to as southern California), and has been documented in the literature as occurring as far south as the Sierra Juarez and Sierra San Pedro Martir mountain ranges in Baja California Norte, Mexico (hereafter, referred to as Baja California). We, the U.S. Fish and Wildlife Service (Service), were petitioned to list the California spotted owl (CSO) as endangered or threatened under the Endangered Species Act of 1973, as amended (16 U.S.C. 1531-1543) (Act), in December 2014 by the Wild Nature Institute and John Muir Project of Earth Island Institute and again in August 2015 by Sierra Forest Legacy and Defenders of Wildlife. In September 2015, the Service published a 90-day finding that the petition presented substantial scientific or commercial information indicating that listing CSO may be warranted (80 FR 56423, September 18, 2015). In November 2019, the Service published a 12-month finding in the Federal Register that listing CSO was not warranted (84 FR 60371, November 8, 2019). In August 2020, Sierra Forest Legacy, Defenders of Wildlife, and the Center for Biological Diversity filed a complaint challenging our 12-month finding that listing was not warranted. On November 30, 2021, the Service voluntarily remanded the not warranted finding and committed to a deadline of February 15, 2023, for submitting to the Federal Register a 12-month finding on CSO. Therefore, a review of the status of the subspecies was initiated to determine if listing is warranted. Based on the status review, the Service will issue a 12-month finding for CSO.

1.2 Methodology

This assessment draws scientific information from resources such as primary peer-reviewed literature, reports submitted to the Service and other public agencies, species occurrence information in Geographic Information Systems (GIS) databases, habitat information in GIS databases, and expert experience and observations. It is preceded by and draws upon analyses presented in other Service documents, including the 90-day finding (80 FR 56423) and the remanded 12-month finding (84 FR 60371). Finally, we coordinated closely with our partners engaged in ongoing research and conservation efforts in state and federal agencies as well as private and non-governmental organizations. This assures consideration of the best scientific and commercial data available.

Analytical Framework

This Species Status Assessment (SSA) Report, developed using the SSA framework (Service 2016a, entire), provides an in-depth review of the species' biology and influencing factors, an evaluation of its biological status, and an assessment of the resources and conditions needed to maintain long-term viability (see Figure 1). This SSA Report, which provides our assessment of the species status, can subsequently be updated as new information becomes available and to support all functions of the Endangered Species Program from Candidate Assessment to Listing to

Consultations to Recovery. As such, this SSA Report will be a living document upon which other documents, such as listing rules, recovery plans, and 5-year reviews, would be based if the species warrants listing under the Act.

This SSA Report for CSO is intended to provide the biological support for the decision on whether to recommend listing the subspecies as threatened or endangered and, if so, also for determining which areas may meet the definition of critical habitat. Importantly, the SSA Report does not include a recommendation or determination by the Service on whether CSO should be proposed for listing as a threatened or endangered species under the Act. Instead, this SSA Report provides a review of the available information strictly related to the biological status of CSO. The decision whether to list CSO will be made by the Service after reviewing this document and all relevant laws, regulations, and policies.

This SSA Report characterizes the species' ability to sustain populations in the wild over time (viability) based on the best scientific understanding of current and future abundance and distribution within the species' ecological settings. To do so, we use the SSA Framework (Service 2016a) and the conservation biology principles of resiliency, redundancy, and representation as a lens to evaluate the current and future condition of the species. We assessed future condition of the species over a time frame of 40–50 years because this range of time represents our best professional judgment of the projected future conditions related to climate change for California, CSO generation time, and regeneration time of large trees.

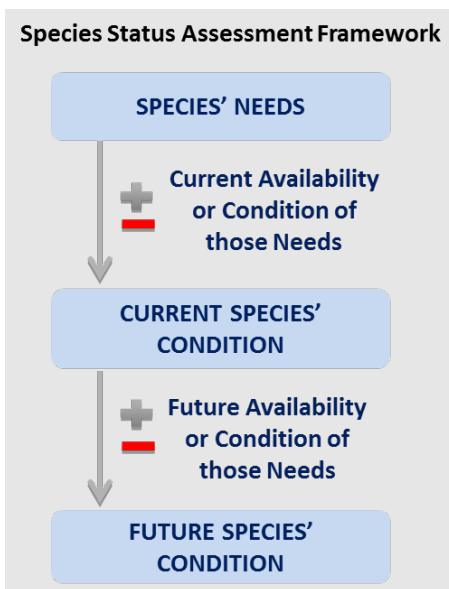


Figure 1: Species Status Assessment Framework.

Resiliency is the ability of a species to withstand stochastic events, the normal year-to-year variations in both environmental conditions (i.e., temperature, rainfall, and periodic disturbances such as fires, floods, and storms), and demographic conditions (i.e., mortality, fecundity) (Redford et al. 2011, p. 40). Determined by the size and growth rate of the populations comprising the species, resiliency can be evaluated to gauge the ability of a species to withstand the natural range of favorable and unfavorable conditions. For CSO, we evaluate resiliency by assessing CSO's

demographic factors of dispersal, survival, fecundity, occupancy, and population growth, and habitat elements of canopy cover and large trees.

Redundancy is the ability of a species to withstand catastrophic events, i.e., natural or anthropogenic stochastic events that would result in the loss of a substantial component of the overall population. Characterization of a species' redundancy takes into consideration both an assessment of the size and distribution of its population(s), and an evaluation of the kinds and likelihood of reasonably plausible catastrophic events to which the species could be exposed. For CSO, we measure redundancy by assessing the number and distribution of populations across the subspecies' range in relation to the scale of catastrophic events that are likely to occur, such as high severity fire, extreme drought, excessive precipitation, or prolonged and persistent competition and displacement due to barred owl expansion.

Representation is the ability of a species to withstand and adapt to long-term changes in environmental conditions (i.e., significant changes outside the range of normal year-to-year variations). The measure of a species' representation may be determined by the breadth of genetic and environmental diversity within and among populations. For CSO, we measure representation by assessing genetic diversity and unique ecological settings across the subspecies' range. For areas where we do not have genetic information, we rely on the extent and variability of habitat and climate characteristics to evaluate representation.

To evaluate the biological status of CSO both currently and into the future, we assessed a range of conditions to allow us to consider the species' resiliency, redundancy, and representation (together, the 3 Rs). This SSA Report provides a thorough assessment of the CSO's biology and natural history and assesses demographic risks and influencing factors (both negative and positive) in the context of determining the species viability and risk of extinction.

The format for this SSA Report includes: a description of CSO, its life history, and habitat (Chapter 2); the habitat and demographic needs of individuals, populations, and the species overall (Chapter 3); a review of the influencing factors that affect the species viability and to what degree (Chapter 4); an analysis of CSO's current condition and a framework for determining population resiliency (Chapter 5); an analysis of the species future condition under three plausible future scenarios (Chapter 6); and a conclusion that describes the viability of CSO in terms of resiliency, representation, and redundancy (Chapter 7). This document is a compilation of the best available scientific and commercial information and a description of the past, present, and likely future risk factors to CSO.

CHAPTER 2: SPECIES BACKGROUND

2.1 Species Description and Taxonomy

California spotted owls are medium-sized brown owls measuring 46.6–48.3 centimeters (cm) (18.3–19.0 inches (in)) with a mottled appearance, round face, large pale brown facial disks, dark brown eyes, and a yellowish green bill (Verner et al. 1992, p. 55; Gutiérrez et al. 2020), “Appearance” section). Females are generally slightly larger than males (Verner et al. 1992, p. 55). The mass of males is approximately 470–685 grams (g) (16.6–24.2 ounces (oz)), whereas the mass of

females is approximately 535–775 g (18.9–27.3 oz) (Gutiérrez et al. 2020, "Appearance" section). The spotted owl was first described by John Xanthus in 1859 as *Syrnium occidentale* based on a specimen collected at Fort Tejon, Kern County, California (Xantus 1859, pp. 189–190). The species was later reassigned to the genus *Strix* (Ridgway 1914, pp. 648–650).

The American Ornithological Society currently recognizes three distinct subspecies of spotted owls: northern spotted owl (*Strix occidentalis caurina*), California spotted owl (*Strix occidentalis occidentalis*), and Mexican spotted owl (*Strix occidentalis lucida*) (AOU 1957). Subspecies of spotted owls have historically been distinguished based on body size, plumage, and range. More recently, there have also been genetic studies including all three subspecies. We have no information to suggest there is scientific disagreement about the California spotted owl's taxonomy.

Given similarities between the subspecies of spotted owls, this SSA Report uses available relevant literature for both the northern spotted owl and the Mexican spotted owl as necessary and appropriate. The term CSO is used when talking only about the California spotted owl subspecies. Spotted owl is used when talking about the species as a whole. We clearly identify when northern spotted owl or Mexican spotted owl is referred to in this SSA Report.

2.2 Genetics

Genetic studies have been useful in reinforcing subspecific identification between spotted owl subspecies, including studies using mitochondrial DNA (Barrowclough et al. 1999, 2005; Haig et al. 2004; Miller et al. 2017), microsatellite loci (Funk et al. 2008; Miller et al. 2017), and whole-genome assemblages (Hanna et al. 2018; Fujito et al. 2021). Phylogenetic analyses of the mitochondrial haplotypes (specific regions of mitochondrial DNA that cluster together to show phylogenetic origins) confirmed significant differences between northern spotted owls and the other spotted owl subspecies (Haig et al. 2004, pp. 688–690). Although Haig et al. (2004) found weaker support distinguishing between CSO and Mexican spotted owls, their study found CSO and Mexican spotted owl did further segregate into separate California and Mexican clades. In another study, most variation of mitochondrial DNA was distributed at the level of three subspecies (i.e., northern spotted owl, CSO, and Mexican spotted owl) (Barrowclough et al. 1999, pp. 922–923). Integrating microsatellite loci with previous mitochondrial DNA studies also supported recognition of the three subspecies (Funk et al. 2008, pp. 165–166). Species-specific principal component analyses using a spotted owl genome assembly showed clear separation between northern spotted owl and CSO samples, but the study did not include Mexican spotted owl samples (Fujito et al. 2021, pp. 3–4).

There is some overlap in range between northern spotted owl and CSO, and interbreeding between the two subspecies occasionally occurs (Haig et al. 2004, p. 690; Barrowclough et al. 2011, pp. 581, 583–586; Miller et al. 2017, pp. 6871, 6875–6877; Hanna et al. 2018, pp. 3947–3948, 3950–3951). Genetic studies support existence of a hybrid zone in north central California (Haig et al. 2004, pp. 688–690; Barrowclough et al. 2005, pp. 1111–1113; Miller et al. 2017). Gene flow between spotted owl subspecies indicates bidirectional introgression between northern spotted owl and CSO; that is, both subspecies are mating with each other when dispersing through their respective ranges (Barrowclough et al. 2005, pp. 1113–1114, 2011; Funk et al. 2008, pp. 165–166). Results from

analysis of microsatellite loci indicate that both hybridization and long-distance migration occur between spotted owl subspecies (Funk et al. 2008, p. 167).

California spotted owls have the lowest genetic diversity among the subspecies compared to northern and Mexican spotted owls, suggesting CSO is of more recent origin than the other spotted owl subspecies or the CSO population is much smaller than the northern and Mexican spotted owl populations (Barrowclough et al. 1999, pp. 919, 927; Haig et al. 2004, p. 683). Within CSO, genetic differences between CSO found in the Sierra Nevada and CSO found in mountain ranges throughout southern California suggest limited interbreeding between these two areas (Barrowclough et al. 2005, pp. 1113–1114; Hanna et al. 2018, pp. 3947–3948, 3950). However, these genetic studies are limited by sample size and sampling locations. We are only aware of one study that includes CSO from coastal California; Barrowclough et al. (2005, p. 1114) shows gene flow between geographically adjacent spotted owl samples, with some evidence of asymmetrical gene flow between CSO in Carmel, California (coastal California), and the Sierra Nevada.

Genetic studies have also looked at hybridization with invasive barred owls (*Strix varia*). Spotted owl and barred owl species cluster separately from each other in genetic analyses, with hybrids scattered between the two species clusters (Fujito et al. 2021, pp. 3–4). See Chapter 4.6 Competition and Hybridization with Barred Owls for more information about CSO hybridization with barred owls.

2.3 Geographic Distribution

California spotted owls are distributed across habitat in California and Nevada including the Sierra Nevada, coastal California, and southern California. The California spotted owl has also been documented in the Sierra San Pedro Martir mountains in Baja California Norte, Mexico, with a few scattered records of the spotted owl in Baja California between 1887 and 1972 (Grinnell 1928, p. 242; Wilbur 1987, p. 170), and early ornithological references described the spotted owl's range as Lower California, which can be interpreted as Baja California (AOU 1886, p. 199; Ridgway 1887, p. 259). However, there is some disagreement in the literature over how to interpret these early accounts. Some view these records as valid documentation of the species occurring in Baja California in the past and that the current lack of records suggests the species is now extirpated from this area (Howell et al. 2001, p. 27; Erickson et al. 2013, p. 605), whereas others consider that they represent uncommon or rare occurrences of the species outside of their range (Wilbur 1987, p. 170). In addition, an early 20th century ornithologist questioned the status of the species in Baja California and noted there were no specimens or records of the species from the area in the U.S. National Museum (Grinnell 1928, p. 242), and many researchers now question whether the species ever actually occurred in Baja California (Erickson in litt. 2022; Unitt in litt. 2022). However, other anecdotal accounts over the last 20 years (approximately 2005 through 2019) report periodically seeing or hearing spotted owls. In some instances, these occurrences were during the fall and winter season after a good year of summer rains in Sierra San Pedro Martir National Park (Bowers pers. comm. 2022; Porras-Peña in litt. 2022; De Leon Giron in litt. 2022). There are only a few accounts of the species with none of those accounts mentioning breeding or evidence of breeding pairs. Therefore, we consider CSO only a rare visitor of Mexico, and do not consider Baja California as its own population. It is possible this population was historically connected with southern California, as

the Sierra San Pedro Martir and Sierra Juarez are southern extensions of the Peninsular Ranges that include CSO in southern California (Gutiérrez et al. 2017, p. 240). Dispersal patterns among the sky islands of forest in Mexico and southern California may be more similar to the Mexican spotted owl that disperses across unsuitable habitat (see 3.2.3.1 Natal Dispersal), but we have no evidence to determine what the level of connectivity is today. Given the uncertainty surrounding CSO observations/occurrences in Baja, and lack of information on its habitat or breeding status, we will not be addressing the status of CSO in Baja in this SSA Report. We acknowledge that an earlier version of the CSO SSA Report included Baja California as its own population (Service 2019), but we have changed our approach based on new information available to us, as described above. Figure 2 represents our understanding of the current range of CSO, with Baja California also identified in this instance (based on Gutiérrez et al. 2017 and other CSO occurrence information). The term “range” used throughout the SSA Report refers to the CSO range only within the limits of California and Nevada.

California spotted owls are continuously distributed throughout the forests of the western side of the Sierra Nevada from Shasta County south to the Tehachapi Pass in Kern County (Gutiérrez et al. 2017, pp. 13–14). They are sparsely distributed on the eastern side of the Sierra Nevada into western Nevada (GBBO 2012, p. Spp-47-4). Outside of the Sierra Nevada, the species range is not contiguous. Along the California coast and into southern California, the species is found in the Coast, Transverse, and Peninsular mountain ranges from Monterey County in the north to San Diego County in the south (Gutiérrez et al. 2020, “Distribution” section). However, there is a large gap in the species range around San Luis Obispo County where the species is not known to occur (see Figure 2). The Tehachapi Pass between the Sierra Nevada to the east and the Transverse Range to the west is a significant gap between CSO in the Sierra Nevada and CSO in coastal and southern California (Verner et al. 1992, p. 4). California spotted owls are absent from the Santa Cruz Mountains (part of the Coast Range) in California, where suitable habitat appears to be present (Gutiérrez et al. 2017, p. 240).

California spotted owls are currently found throughout their known historical range, although there is evidence of a decrease in abundance in parts of the range including both the Sierra Nevada and southern California (Franklin et al. 2004, pp. 23–42; Tempel et al. 2014b, pp. 90–94, 2022, p. 18; Conner et al. 2016, pp. 7–18; Hanna et al. 2018, pp. 3947–3949) (see Chapter 5: Current Condition for more information about abundance). The majority of CSO are found in mid-elevation, mixed-conifer forest on the west slope of the Sierra Nevada (Gutiérrez et al. 2017, p. xviii). California spotted owl nest trees were found from 305 meters (m) (1,000 feet (ft)) to 2,340 m (7,740 ft) in elevation in the Sierra Nevada and between 1,000 m (3,281 ft) and 2,560 m (8,400 ft) in the Los Padres National Forest and San Bernardino Mountains in southern California (Verner et al. 1992, p. 60).

California Spotted Owl Range

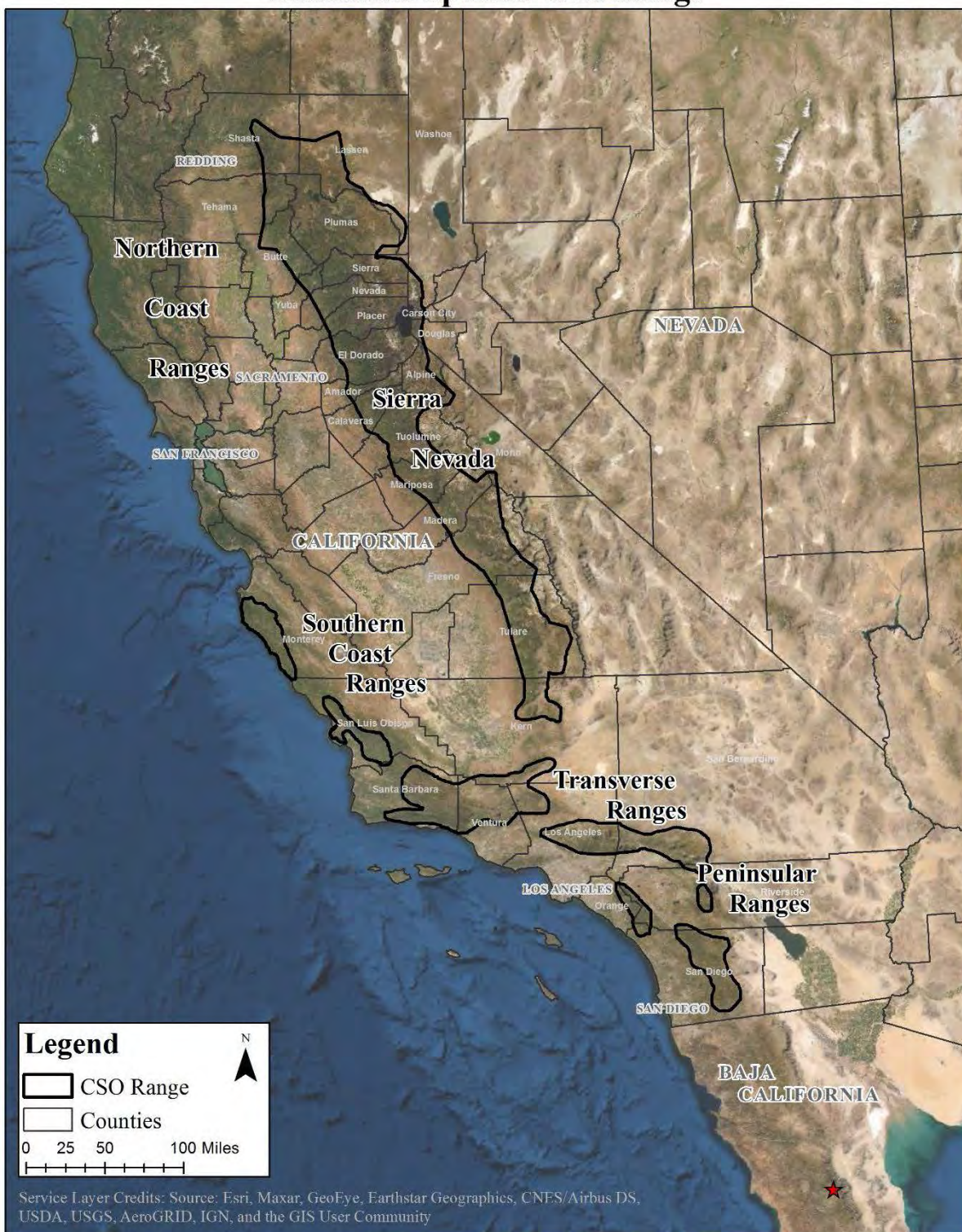


Figure 2: California spotted owl range map. Maps were developed with occurrence data from U.S. Forest Service, California Department of Fish and Wildlife, Nevada Department of Wildlife, and eBird. The red star indicates the approximate location of CSO occurrences in Baja California and was extracted from Gutiérrez et al. 2017 (p. 13). This will be the only map with Baja California, Mexico, identified as part of the CSO range.

2.4 Life History

California spotted owls are long-lived (approximately 16–23 years) with high adult survival and low reproductive output (Seamans and Gutiérrez 2007a, p. 57; Gutiérrez et al. 2020) “Demography and Populations” section). California spotted owls form monogamous pair bonds, although occasionally bonds may break and new bonds may form due to circumstances such as the death of a mate or low reproductive output with a previous mate (Blakesley et al. 2006, p. 74; Gutiérrez et al. 2011, p. 592, 2020) “Behavior” section). Pairs will defend a territory from neighboring pairs and vagrant CSO, and they exhibit high territory fidelity (Gutiérrez et al. 2020, “Sounds and Vocal Behavior” and “Behavior” sections). Passively recorded audio data suggests that CSO use active territorial defense (i.e., through vocalizations) close to sunset and at the edges of territories, where habitat is generally lower-quality than preferred foraging sites, roost sites, and core territory areas (Wood et al. 2019b, pp. 232, 236–239). Territories—the area actively defended by a breeding pair—can overlap with neighboring pairs and are smaller than home ranges (Gutiérrez et al. 2017, pp. xvi, 294). Estimates of territory size have varied from 203 ha (502 ac) to 813 ha (2,009 ac) with higher estimates in the northern Sierra Nevada and lower estimates in southern California (Bingham and Noon 1997, p. 136; Blakesley et al. 2005, p. 1556; Seamans and Gutiérrez 2007b, p. 568; Tempel et al. 2014a, p. 2091). Higher quality territories measured in adult survival, territory colonization, and territory extinction, tend to have a greater proportion of higher canopy cover ($\geq 70\%$) (Tempel et al. 2014a, p. 2089; Gutiérrez et al. 2017, pp. 271–273). Home ranges, or areas used by a pair to meet requirements for survival and reproduction, are about 400–1,200 hectares (ha) (1,000–3,000 acres (ac)) in size (Gutiérrez et al. 2017, p. xviii). Home ranges are typically larger in the northern portion of the range ($>1,000$ ha (2,470 ac)) and smaller in the southern portion of the range ($<1,000$ ha (2,470 ac)) due to differences in selected prey species (Gutiérrez et al. 2017, p. xviii). Male and female home range size for CSO were not statistically different in a study looking at habitat use in a burned landscape (Eyes et al. 2017, p. 381). However, female CSO home ranges were twice the size of male home ranges in unburned forest, with nonbreeding females having the largest home range sizes (Blakey et al. 2019, pp. 917, 919).

Breeding season begins in mid-February and the juvenile dependency period can last through mid-September; nesting generally starts earlier at lower elevations (Gutiérrez et al. 2017, p. 53; Gutiérrez et al. 2020, “Breeding” section). During the breeding season, CSO tend to spend the majority of their time at activity centers of around 121 ha (299 ac) (Verner et al. 1992, p. 87; Berigan et al. 2012, p. 299). Activity centers are the area where CSO spend most of their time in which they nest, roost, and forage (Verner et al. 1992, p. 87; Gutiérrez et al. 2017, pp. 270–271). In the Sierra Nevada, a majority of CSO used more than one nest/roost area over the three-year study period (2015–2017; 86% of 36 GPS-marked CSO, range 2–6) (Berigan et al. 2019, p. 474). Spotted owls typically have only one nest per breeding season and they rarely re-nest if the first nests fails (Gutiérrez et al. 2020, “Breeding” section), although there is some evidence that northern spotted owls may nest more than once per season if their initial nesting attempt fails (Sovern et al. 2011, p. 103). Peak egg laying occurs in mid-April (Verner et al. 1992, p. 62). Females typically lay 1–3 eggs, with survival of offspring into adulthood highest when two young fledge in comparison to singletons and triplets (Peery and Gutierrez 2013, p. 132; Gutiérrez et al. 2020, “Demography and Populations” section). Incubation in northern spotted owls lasts for 30 ± 2 days (Forsman et al. 1984, p. 33) and is likely similar for CSO. Male spotted owls provide food and protection for the

female while the female incubates and broods the nest (Gutiérrez et al. 2020, “Breeding” section). After hatching, owlets are covered in natal down for about 10 days, which then starts to be replaced by juvenile plumage (Gutiérrez et al. 2020, “Breeding” section). Hatchlings rely on both parents for protection and food (Gutiérrez et al. 2020, “Breeding” section). Juvenile northern spotted owls fledged approximately 35 days after hatching (Forsman et al. 1984, p. 33), and time to fledging is presumed to be similar for CSO. Juveniles will leave the nest and climb in nearby trees before they can fly, relying on multi-layered forest structure to move among trees and about the forest floor (Whitmore 2009, pp. 4–5). After fledging, juveniles rely on parents for food and protection, although parental care will progressively decrease over time (Gutiérrez et al. 2020, “Breeding” section). In northern spotted owls, parental care usually ends in late August or September, and is likely similar for CSO (Forsman et al. 1984, p. 5). Although difficult to estimate due to dispersal, juvenile survival in CSO is low: approximately 0.368 for CSO in the San Bernardino Mountains in southern California (LaHaye et al. 2004, p. 1056), and 0.333 for CSO in the northern portion of the Sierra Nevada (Blakesley et al. 2001, p. 667). Juvenile spotted owls are particularly vulnerable during the fledging and early dispersal stages, with a high mortality rate due to predation, starvation, and accidents (e.g., falling from a tree) (Gutiérrez and Carey 1985, pp. 41, 63). No information is available regarding juvenile survival for CSO in other portions of the species’ range.

Spotted owls have obligate juvenile dispersal, meaning they always disperse from their natal areas in the year they hatch. Natal dispersal occurs during the fall, after juveniles have reached adult weight and parental care stops (Gutiérrez et al. 2020, “Breeding” section). Studies of juvenile dispersal of CSO in southern California, based on recaptures of banded birds, found that average juvenile dispersal was 9.7–11.3 kilometers (km) (6–7 miles (mi)), and ranged from 3.2–37.0 km (2–23 mi) (LaHaye et al. 2001, p. 691). In the San Bernardino Mountains, females dispersed slightly farther than males, although this result was not statistically significant (Gutiérrez et al. 2017, p. 250). In northern spotted owls, females generally disperse farther than males (Forsman et al. 2002, p. 15; Miller et al. 2018, p. 830). Larger dispersal distances, up to 177 km (110 mi), have been documented in both northern and Mexican subspecies (Gutiérrez and Carey 1985, p. 60; Ganey et al. 1998, p. 206; Hollenbeck et al. 2018, p. 533). California spotted owl sub-adults are non-territorial and considered “floaters” until they occupy a territory (LaHaye et al. 2001, p. 696; Gutiérrez et al. 2017, p. 16). Sub-adults in southern California typically acquire territories after 1–3 years, with most individuals settling in areas that had been previously occupied by CSO (LaHaye et al. 2001, p. 696). Adult CSO typically do not shift territories or undergo breeding dispersal from an established territory (Blakesley et al. 2006, p. 76; Zimmerman et al. 2007, p. 963; Gutiérrez et al. 2011, p. 592); however, some breeding dispersal occurs in adults or pairs that have been unsuccessful in mating or if habitat is altered (Blakesley et al. 2006, p. 71).

Breeding only occurs once a pair is formed and settled into a territory (Gutiérrez et al. 2017, p. 15). Pairs can breed in consecutive years, but in certain conditions may use a “bet hedging” reproductive strategy in which they postpone reproduction until temporarily poor environmental conditions improve ((Stearns 1976, pp. 4, 15–26; Franklin et al. 2000, p. 539; Gutiérrez et al. 2017, p. xvi). The number of young fledged annually per territorial female CSO in several areas within the Sierra Nevada ranged from 0.478–0.988 (Blakesley et al. 2010, pp. 1, 18). The number of offspring a

female produced annually was higher in adult females than first and second year sub-adult females (LaHaye et al. 2004, p. 1056; Blakesley et al. 2010, p. 1). Figure 3 summarizes the life history of CSO.

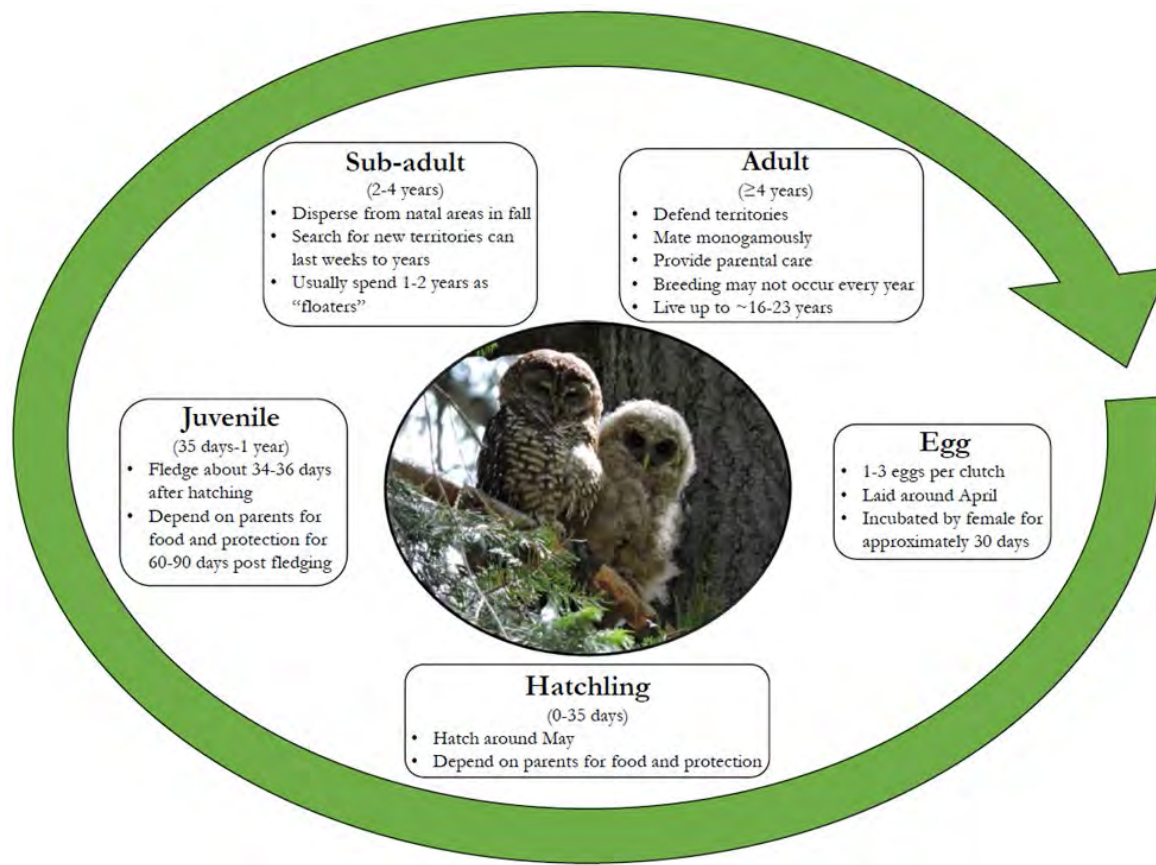


Figure 3: California spotted owl life history diagram. Photo of adult and young California spotted owl, Carson Range, Nevada provided by Mark Enders, Nevada Department of Wildlife.

2.5 Habitat

In general, CSO nest in areas of mature, multistoried forests with complex structure, larger trees, multi-layered high canopy cover, and large amounts of coarse woody debris, while areas with higher heterogeneity of forest types and the edges between them are important for foraging (Gutiérrez et al. 2017, p. xvii). These habitat components provide structure and characteristics required for nesting, roosting, and foraging. Coarse woody debris for the purpose of this SSA Report refers to fallen dead trees and the remains of large branches on the ground. Coarse woody debris in areas of multi-layered high canopy cover is conducive for fungal growth, a food source for many CSO prey species (Verner et al. 1992, pp. 71–72; Pyare and Longland 2002, pp. 1016–1017).

In the Sierra Nevada, a majority of CSO occur within mid-elevation ponderosa pine (*Pinus ponderosa*), mixed-conifer, white fir (*Abies concolor*), and mixed-evergreen forest types, with few occurring in the lower elevation oak woodlands of the western foothills (Gutiérrez et al. 2017, p. 109). It is important to note that most of the available literature on habitat for the Sierra Nevada is focused on the westside of the mountain range and does not include habitat characteristics from the

eastside, where habitat is more open and less dense compared to the westside. In coastal and southern California, CSO are found in riparian/hardwood forests and woodlands, live oak/big cone fir forests, and redwood/California laurel forests (Gutiérrez et al. 2017, p. xxvi). Further information on these habitat types can be found at California Wildlife Habitat Relationship (<https://wildlife.ca.gov/Data/CWHR/Wildlife-Habitats>). In southern California, vegetation types differ relative to the Sierra Nevada and what is considered a large tree in southern California may not be comparable to what is considered a large tree in the Sierra Nevada (see section 2.5.1 Nesting Habitat). However, CSO in southern California still select for territories containing larger trees (LaHaye et al. 1997, pp. 42, 47) and predominantly closed canopy cover (Smith et al. 2002, pp. 137, 142, 144).

2.5.1 Nesting Habitat

California spotted owls can use a variety of habitat types for nesting. At higher elevations, the species primarily uses conifers for nesting, and as elevations decrease, they increasingly use hardwoods (Gutiérrez et al. 2020, “Habitat” section). Important components of nesting habitat include high canopy cover, larger trees, and high habitat heterogeneity. High canopy cover is an important predictor for CSO nest locations (North et al. 2017, pp. 166, 172–175) and multi-layered high canopy cover around the nest tree and in territories is an important factor associated with CSO reproductive success (Hunsaker et al. 2002, pp. 693–699; Blakesley et al. 2005, pp. 1554, 1558–1562). A nest area with canopy cover of greater than 70% is associated with higher site occupancy, and occupancy sharply declines in habitat with less than 40% canopy cover (Blakesley et al. 2005, p. 1559; Seamans 2005, pp. iii, 90, 100; Seamans and Gutiérrez 2007b, pp. 566, 568; Tempel et al. 2014a, pp. 2089, 2091, 2016, pp. 747, 759). After substantial changes in the landscape due to drought and a megafire in Yosemite National Park (i.e., the 2013 Rim Fire), habitat selection analysis found that CSO still selected territories with higher canopy cover relative to what is available. California spotted owls selected areas with at least 40% canopy cover in burned forest and areas with 48% canopy cover in unburned forest (Schofield et al. 2020, pp. 3, 5). In the same study, an equal number of CSO were found nesting in burned and unburned forest (Schofield et al. 2020, pp. 3, 5), although CSO avoided areas with more than 30% high severity fire (Schofield et al. 2020, p. 5). Gaps and small openings of canopy cover are important components of foraging habitat (see Section 2.5.2), but there are generally no gaps around the nest stand (North et al. 2017, p. 166). Even in southern California where the habitat is naturally more fragmented with less canopy cover available, CSO still select for nest areas with higher canopy cover relative to what is available (Smith et al. 2002, pp. 142–143).

California spotted owls use a subset of larger trees or snags as their nest trees, with the average nest tree measuring 124 cm (49 in) diameter at breast height (dbh) and 31 m (103 ft) tall in the Sierra Nevada (Gutiérrez et al. 2017, p. 50). In addition to nest tree size variation according to nest type, nests also vary between hardwood and conifer species, with the typical hardwood nest tree greater than 76.2 cm (30 in) dbh and 16.8 m (55 ft) tall (Verner et al. 1992, p. 92). The nest tree itself is critical for CSO reproductive success because it provides the space and structure needed for nests and fledglings, along with protection from predators and inclement weather. California spotted owls do not build their own nest but rely on larger trees that provide multi-layered high canopy cover with open cavities (created because of fallen branches, woodpeckers, etc.), broken tops, platforms,

and old raptor nests (Gutiérrez et al. 2020, “Habitat” and “Breeding” sections). The nest tree chosen within a territory is typically one of the oldest and largest live or dead trees within the nesting territory with many defects like cracks, disease scars, or decaying wood (Verner et al. 1992, pp. 6, 60, 71; North et al. 2000, p. 797). The average age of nest trees in the southern Sierra Nevada was found to be >227 years (North et al. 2000, p. 802). In southern California, CSO use cavity, broken-top, and platform nests with different characteristics - cavity nest trees are 108.3 cm (42.6 in) dbh, broken-top nest trees 122.3 cm (48.1 in) dbh, and platform nests are typically smaller with overall combined nest trees measuring 90.8 cm (35.7 in) dbh and 24.4 m (80.1 ft) tall when all nest types, including platform nests, were considered (LaHaye et al. 1997, pp. 42, 47; Gutiérrez et al. 2017, p. 50; Tanner 2022, pers. comm.). In southern California CSO use of platform or old raptor nests is more common; thus, owls with these types of nests were observed using trees as small as 33 cm dbh (13 in; Tanner 2022, pers. comm.) with mean values of 75.0 cm (29.5 in) dbh (LaHaye et al. 1997, p. 45). Within their nesting territory, CSO select for nest sites farther away from the forest edge (Phillips et al. 2010, p. 312). California spotted owl nest trees with higher reproductive output, measured by number of young fledged per territory, tend to be used repeatedly, whereas nest trees with low reproductive output are usually only used once (North et al. 2002, pp. 118–119).

California spotted owl occupancy, colonization, adult survival, and reproductive success are all positively associated with an increasing amount of structurally complex (i.e. multistoried) habitat on the landscape (Franklin et al. 2000, p. 578; Blakesley et al. 2005, p. 1562; Tempel et al. 2014a, pp. 2103–2104). The biological and physical components that create habitat heterogeneity and complex structure are areas of multi-layered high canopy cover, large trees, coarse woody debris, understory and mid-story vegetation, patches of burned habitat, riparian habitat, large diameter standing dead trees (snags), and areas with small openings of canopy cover within a home range. As discussed above, CSO select for habitat with multi-layered high canopy cover and large trees especially for nesting; however, there are a variety of other habitats within a heterogeneous landscape that CSO use and which may provide specific resources, such as prey.

2.5.2 Foraging Habitat and Prey

California spotted owls can also use a variety of habitats to forage. California spotted owls primarily prey upon a variety of small to medium sized mammals, including but not limited to flying squirrels, woodrats, and pocket gophers, as well as birds, lizards, and insects (Gutiérrez et al. 2017, p. 28). Diet varies across the species’ range and habitat types and following wildfires. In the Sierra Nevada, above approximately 1,200 m (3,937 ft) in coniferous forests, CSO most commonly consume Humboldt’s flying squirrels (*Glaucomys oregonensis*) (Laymon 1988, pp. 130–154; Verner et al. 1992, pp. 4, 65–69; Munton et al. 2002, pp. 99, 101–104). Northern flying squirrels are primarily found in coniferous and mixed forest but can also be found in deciduous woods and riparian woods (Cassola 2016a, p. 3). Humboldt’s flying squirrels in the range of the CSO were previously classified as northern flying squirrels (*Glaucomys sabrinus*) (Arbogast et al. 2017, p. 1027). Preferred habitat conditions of northern flying squirrels include cool, moist, mature forest with abundant standing and down snags where they can forage on mostly fungi and lichens (Cassola 2016a, p. 3). In lower elevation oak woodlands and riparian-deciduous forests in the Sierra Nevada and southern California, CSO select for woodrats, including both dusky-footed and big-eared (*Neotoma* spp.) (Verner et al. 1992, pp. 4, 65, 68–69; Smith et al. 1999, pp. 22, 24–28; Munton et al. 2002, pp. 99,

101–104). Due to this elevational gradient in prey distribution, CSO select foraging sites characteristic of flying squirrel habitats at higher elevations and woodrat habitats at lower elevations (Kramer et al. 2021b, pp. 12–14). Both the dusky-footed and big-eared woodrats are found in densely wooded areas with heavy undergrowth including chaparral, riparian woodlands, hardwood forests, conifer forests, and mixed forests. The woodrat diet includes seeds, nuts, acorns, fruits, green vegetation, inner bark, and fungi (Cassola 2016b, p. 3; Álvarez-Castañeda and Lacher 2016, p. 3). In the Sierra National Forest, a multi-year diet study found pocket gophers (*Thomomys* spp.) were the second most common prey species of CSO in both lower and upper elevation vegetation types (Munton et al. 2002, p. 99) following northern flying squirrels or woodrats. Pocket gophers are found in a wide variety of habitats from desert scrub to high elevation coniferous forests in open areas with deep soil (Lacher et al. 2016, p. 3). Pocket gophers primarily eat roots, bulbs, tubers, and occasionally above-ground plant parts (Greene 1999, p. 4).

California spotted owls will also eat mice, voles, birds, lizards, and insects (Laymon 1988, pp. 130–154; Verner et al. 1992, pp. 65, 68–69; Smith et al. 1999, p. 24; Munton et al. 2002, pp. 101–104). California spotted owls have low metabolic rates requiring the caloric equivalent of consuming a flying squirrel every 1.8 days or a woodrat every 3.7 days (Weathers et al. 2001, p. 687). Some individuals have smaller home ranges where woodrats are the primary prey source, presumably because woodrats have a higher caloric gain per successful foraging event and are found in higher densities than northern flying squirrels (Zabel et al. 1995, pp. 433, 435–438).

There is some evidence that CSO diet may shift following wildfires. In national parks in the Sierra Nevada that have implemented longstanding fire management efforts (i.e., prescribed fire and managed wildfire), the CSO diet contains a higher proportion of woodrats and pocket gophers relative to flying squirrels (Hobart et al. 2021, pp. 254, 256). However, in areas with frequent and extensive wildfires, CSO consumed proportionally more flying squirrels although woodrats and pocket gophers still contributed more to the overall diet (Hobart et al. 2021, p. 256). Interestingly, these results did not support the authors' hypothesis that wildfires would shift diet away from flying squirrels since flying squirrels are associated with closed-canopy forests and these forests are more likely to be impacted by wildfire (Hobart et al. 2021, p. 254). Other studies have found pocket gophers are an important prey species following wildfires in the Sierra Nevada (Bond et al. 2013, p. 114).

California spotted owls tend to forage in larger trees (see 3.1.2 Large Trees), likely due to the canopy cover provided by larger trees and the important resources such as shelter and food that larger trees provide for prey species (Laymon 1988, pp. 47, 71, 77, 100; Verner et al. 1992, pp. 9–10, 60, 88; Moen and Gutierrez 1997, pp. 1281, 1284). However, CSO have also been documented utilizing medium size trees (defined by the authors as >25 cm dbh (9 in)) for foraging while avoiding areas dominated by small trees (<25 cm dbh (9 in)) (Kramer et al. 2021a, pp. 4, 6). Coarse woody debris is also an important habitat feature for CSO because it provides food, shelter, and protection for prey species, especially woodrats (Waters and Zabel 1995, pp. 861–862; Pyare and Longland 2002, pp. 1016–1017; Innes et al. 2007, pp. 1523, 1526; Kelt et al. 2013, p. 1208). Recent research shows that CSO were more successful at capturing prey in territories with taller multilayered forests, higher vegetation heterogeneity, and near forest edges (Zulla et al. 2022, pp. 7–8); CSO also had higher reproductive success in territories with higher mean canopy cover, taller trees, and more

shrubby vegetation (Wilkinson et al. in prep., p. 2). However, riparian areas within forested landscapes that provide heterogeneity and increased foraging habitat may not always exhibit high canopy cover and large trees (Meyer et al. 2005, p. 275; Irwin et al. 2007, p. 1189; Bond et al. 2016, p. 1290). Heterogeneous forests, such as those found on private lands, may provide more habitat for CSO than was previously understood (Atuo et al. 2019, p. 295), as some privately-owned study areas have higher numbers of CSO occupied sites than adjacent Forest Service study areas (Roberts et al. 2017, p. 113).

2.5.3 Roosting Habitat

California spotted owl roosting habitat is very similar to nesting habitat. The species can roost in a variety of habitat types, including those habitat types described above for nesting habitat. Specific components of roosting habitat include multi-layered high canopy cover and presence of large trees. As they learn to fly, recently fledged CSO are often found roosting close to the nest tree in multi-layered forest with high canopy cover (Whitmore 2009, pp. 31–33). It is believed that such forests provide the young CSO with protection from predators and from high temperatures. California spotted owls have been found to have a low heat tolerance in comparison to other bird species, beginning to show heat stress at 30–34° Celsius (86–93° Fahrenheit). The cooler microclimates that multi-layered high canopy cover provides are important for both juveniles and adults during warm summers (Weathers 1981, pp. 358–359; Barrows 1981, pp. 303–305; Weathers et al. 2001, pp. 678–679). Behavioral studies show that CSO have an adaptive capacity to roost in cooler microclimates (promoted by higher elevations, taller canopy height, and greater canopy cover), especially in forest stands that are on warmer slopes (McGinn et al. in review, p. 2). Presence of large trees is also important for CSO roosting, as individuals tend to roost in large trees, likely due to the canopy cover provided by large trees and the resources they provide for prey species (Laymon 1988, pp. 47, 71, 77, 100; Verner et al. 1992, pp. 9–10, 60, 88; Moen and Gutierrez 1997, pp. 1281–1284).

CHAPTER 3: SPECIES ECOLOGICAL NEEDS

In this chapter, we discuss the habitat components that support CSO individuals and populations, CSO population needs, and overall species needs.

3.1 Habitat Components

In this section, we assess the best available information to identify the specific habitat components needed to support individual fitness at all life stages for CSO. For CSO, an individual must have adequate nesting, foraging, and roosting habitat to be successful, and for the purpose of this SSA Report, the components of nesting, foraging, and roosting habitat that we considered most significant include canopy cover, larger trees, and habitat heterogeneity. Forest heterogeneity is important to CSO as it provides protection from predators and extreme weather conditions, variable microclimates, and habitat for different prey species. Table 1 summarizes these habitat components by life stage and season. We acknowledge that these habitat components are not all-inclusive and there may be other components of nesting, foraging, and roosting habitat that are not being considered (such as prey). We also acknowledge that a history of fire suppression in the western United States, including throughout the CSO range, has caused many ecological changes that are not

fully understood (Mallek et al. 2013, p. 2) and are a significant departure from the natural range of variation in these forests (Safford and Stevens 2017, p. i). This includes, but is not limited to, model estimates that canopy cover was historically lower (less than 50%) than is currently observed today (Safford and Stevens 2017, p. 90). However, we chose to focus on habitat components for which there are available spatial data across the range of the species. Furthermore, prey is indirectly considered in our analysis since the primary CSO prey species also select for high canopy cover and coarse woody debris (Waters and Zabel 1995, p. 858), which are considered here as components of habitat heterogeneity. Populations of CSO require the same habitat components as individuals but at larger scales.

Table 1: Habitat components needed for all life history stages of the California spotted owl.

Life History Stage				
Habitat Components	Winter	Spring	Summer	Fall
Canopy cover	Juveniles, Sub-adults, Adults	Hatchlings, Sub-adults, Adults	Hatchlings, Juveniles, Sub-adults, Adults	Juveniles, Sub-adults, Adults
Large Trees	Sub-adults, Adults	Eggs, Hatchlings, Sub-adults, Adults	Eggs, Hatchlings, Sub-adults, Adults	Sub-adults, Adults
Habitat Heterogeneity	Juveniles, Sub-adults, Adults	Hatchlings, Sub-adults, Adults	Hatchlings, Juveniles, Sub-adults, Adults	Juveniles, Sub-adults, Adults

3.1.1 Canopy Cover

Multi-layered, or complex, high canopy cover is considered an important resource for spotted owls because it provides cool shaded microclimates, camouflage/cover for protection from predators and extreme weather conditions, and habitat for prey species (Forsman 1975, pp. 4, 90, 105; Barrows 1981, p. 302; Forsman et al. 1984, p. 5). High canopy cover from tall trees is associated with higher probability of successful prey capture by CSO, while heterogeneity of forest types also facilitates prey capture (Zulla et al. 2022, p. 8). Furthermore, high canopy cover from tall trees is an important predictor for CSO nesting habitat (North et al. 2017, pp. 166, 172–175), and multi-layered high canopy cover around the nest tree and in territories is an important factor associated with CSO reproductive success (Hunsaker et al. 2002, pp. 693–699; Blakesley et al. 2005, pp. 1554, 1558–1562). Areas with canopy cover greater than 70% is considered optimal for CSO nest sites and occupancy sharply declines when canopy cover is less than 40% (Blakesley et al. 2005, p. 1559; Seamans 2005, pp. iii, 90, 100; Seamans and Gutiérrez 2007b, pp. 566, 568; Tempel et al. 2014a, pp. 2089, 2091, 2101, 2016, pp. 747, 759). Further, CSO in Yosemite National Park had territory centers with average values of 40% canopy cover in burned forests (Schofield et al. 2020, pp. 4–5).

3.1.2 Large Trees

Presence of large trees, defined as trees that are greater than 61 cm (24 in) dbh (Seamans and Gutiérrez 2007b, pp. 566, 571–574; Tempel et al. 2014a, p. 2094; Jones et al. 2018, p. 344), is important for CSO foraging, roosting, and nesting. California spotted owls tend to forage and roost in large trees, likely due to the canopy cover provided by large trees and the important resources

such as shelter and food that large trees provide for prey species (Laymon 1988, pp. 47, 71, 77, 100; Verner et al. 1992, pp. 9–10, 60, 88; Moen and Gutierrez 1997, pp. 1281, 1284). The presence of tall (>48 m (157 ft)) trees, and the canopy cover they provide, is the best predictor for CSO occupancy and areas with a high density of large trees is considered high quality habitat (Blakesley et al. 2005, pp. 1554, 1558–1562; North et al. 2017, pp. 166, 171–176). California spotted owls use a subset of large trees or snags as their nest trees (LaHaye et al. 1997, pp. 42, 47; Blakesley et al. 2005, pp. 1554, 1558–1562; Gutiérrez et al. 2017, p. 50) and the nest tree itself is critical for CSO reproductive success because it provides the space and structure needed for nests, along with protection from predators and inclement weather. California spotted owls do not build their own nest but rely on larger trees that provide multi-layered high canopy cover with open cavities (created as a result of fallen branches, woodpeckers, etc.), broken tops, platforms, and old raptor nests (Gutiérrez et al. 2020, “Habitat” and “Breeding” sections). The nest tree chosen within a territory is typically one of the oldest and largest live or dead trees within the nesting territory with many defects like cracks, disease scars, or decaying wood (Verner et al. 1992, pp. 6, 60, 71; North et al. 2000, p. 797).

3.1.3 Habitat Heterogeneity

The preferential use of mature forests with high canopy cover and large trees, as described above, is well-known for CSO (Gutiérrez et al. 2017, p. iii). However, there have been several recent studies showing the importance of other habitat types, habitat edges, and/or habitat heterogeneity (Atuo et al. 2019; Hobart et al. 2019; Kramer et al. 2021b; Zulla et al. 2022; Wilkinson et al. in prep.). These results may California spotted owl occupancy, colonization, adult survival, and reproductive success are all positively associated with the proportion of structurally complex forests (Franklin et al. 2000, p. 539; Blakesley et al. 2005, p. 1562; Tempel et al. 2014a, p. 2089, 2016, p. 747). The biological and physical components that create habitat heterogeneity and complex structure are areas of multi-layered high canopy cover, large trees, coarse woody debris, understory and mid-story vegetation, patches of burned habitat, riparian habitat, large diameter standing dead trees (snags), and some open areas within a home range.

Coarse woody debris (i.e. fallen dead trees and the remains of large branches on the ground) is an important habitat feature for CSO because it provides food, shelter, and protection for CSO prey species, especially woodrats (Waters and Zabel 1995, pp. 861–862; Pyare and Longland 2002, pp. 1016–1017; Innes et al. 2007, pp. 1523, 1526; Kelt et al. 2013, p. 1208). Coarse woody debris in areas of multi-layered high canopy cover is conducive for fungal growth, a food source for many CSO prey species (Verner et al. 1992, pp. 71–72; Pyare and Longland 2002, pp. 1016–1017). Rates of prey capture by CSO are observed to be higher in taller multilayered forests, in areas with higher vegetation heterogeneity, and near forest-chapparral edges (Wilkinson et al. in prep., p. 2). Similarly, CSO captured more prey in areas with more large trees and in areas with greater forest heterogeneity, i.e. a greater mixture of forest types (Zulla et al. 2022, pp. 7–8). There are a variety of habitats within a heterogeneous landscape that CSO use and which may provide specific resources. Studies have found that the size of a CSO home range increases as the heterogeneity, or number of different vegetation patches, increase (Williams et al. 2011, p. 333); the hypothesis is that there may be an optimal point of habitat heterogeneity for CSO beyond which territory quality declines (Williams et al. 2011, p. 333). Open areas (defined as forest with less than 40% canopy cover) can be important for foraging, although the probability of CSO site occupancy is lower in areas with more open areas and younger forest (Hobart et al. 2019, p. 197). Differences in habitat use by CSO at different scales are highlighted by analyses showing that GPS-tagged CSO select areas with relatively

high heterogeneity of seral stages except for the core of their home range (i.e. the nest location), where CSO selected for relatively homogeneous forest with large trees and closed canopies (Atuo et al. 2019, p. 302).

Low severity or patchy mixed severity wildfire is a historical natural occurrence throughout the range of the CSO, creating elements of a heterogeneous landscape under which CSO are adapted. There is evidence to suggest that more pyrodiverse landscapes support greater landscape heterogeneity (Steel et al. 2021, pp. 7–8; Stephens et al. 2021, p. 5). For example, in areas where woodrat is the primary prey species, a juxtaposition of mature forests and open canopy patches may promote higher prey diversity and abundance and northern spotted owls preferentially select for these areas (Zabel et al. 1995, p. 433, 2003, p. 1027; Ward and Noon 1998, p. 79; Franklin et al. 2000, p. 539). Burned areas can reduce the amount of high canopy cover available for owls, but studies have found that CSO forage on the edge of and within areas that have been burned at a range of severities (Bond et al. 2009, p. 1116, 2016, p. 1290; Eyes et al. 2017, p. 375) although typically avoiding larger areas of high-severity fire (Jones et al. 2016a, p. 304; Eyes et al. 2017, p. 383; Kramer et al. 2021a, p. 7). The negative impacts of current regime large-scale high-severity fires are further discussed in section 4.1 of the SSA Report. Riparian areas are also considered important, particularly for foraging habitat, even though they may not always exhibit high canopy cover and large trees (Meyer et al. 2005, p. 275; Irwin et al. 2007, p. 1189; Bond et al. 2016, p. 1290).

3.2 Population Needs

In this section, we define what a CSO population is and how we further divide populations into separate analysis units based on land management boundaries. The reason we further divide populations into analysis units is to conduct a more focused analysis of how different areas within each population contribute to that population's overall resiliency. We also define resiliency and identify the demographic factors that can be used to assess CSO analysis unit condition and population resiliency. As mentioned previously, populations of CSO have the same habitat needs as individuals but at larger scales and in the appropriate configuration.

3.2.1 Definition of a Population and an Analysis Unit

Within this SSA Report, we define a population as a group of interbreeding CSO that are more likely to breed among that group than outside of that group. We use information from genetic studies and habitat features to identify two CSO populations: one in the Sierra Nevada, and another in coastal and southern California (hereafter referred to as the coastal-southern California population).

In the western Sierra Nevada, habitat is relatively continuous, without significant gaps in distribution (Gutiérrez et al. 2017, p. xviii); however, in the eastern Sierra Nevada, habitat is more discontinuous with disjunct patches (Dilts 2022, pp. 5–9). Though CSO still have substantial gene flow within the Sierra Nevada (see section 2.2 Genetics). Further, there is limited gene flow to coastal or southern California, and large-scale fragmentation of suitable habitat divides the Sierra Nevada from this other population (Barrowclough et al. 2005, pp. 1114–1116). Barrowclough et al. (2005, p. 1114) found limited asymmetrical gene flow from Carmel, California (i.e., central California coast) to the Sierra Nevada, indicating that there has been some historical low-level interbreeding between these populations. This level of gene flow is not at a similar level to the gene flow

documented in areas within the Sierra Nevada. We are not aware of specific information about individual CSO moving between these two population areas.

In coastal and southern California, the CSO population consists of subpopulations distributed among discrete mountain ranges, resulting in habitat “islands” surrounded by unsuitable habitat (Verner et al. 1992, p. 187). Areas between these habitat “islands” that constitute the subpopulations are typically lowland desert scrub and chaparral that is unsuitable for CSO, or substantially modified by human-induced development and fragmentation (Verner et al. 1992, p. 187). Some of the subpopulations are separated by relatively narrow gaps, such as the gap between the San Gabriel and San Bernardino Mountains, while other gaps are more significant, such as the gap between the Northern and Southern Santa Lucia Mountains. Verner et al. (1992, p. 188) reported CSO nearest-neighbor distances in southern California that are as great as 45 miles. The Barrowclough et al. (2005) study described above did not calculate gene flow between the Carmel sample and any samples from southern California because gene flow was only calculated between geographically adjacent samples, and there were no southern California samples that fit those criteria. California spotted owls in coastal and southern California are less well-studied than those in the Sierra Nevada, but there is a notable lack of documented CSO movement between the coastal and southern subpopulations and we are not aware of any dispersal between them. This population is also described in the literature as being a presumed metapopulation (Verner et al. 1992, pp. 187–206; LaHaye et al. 1994, p. entire; Gutiérrez et al. 2017, p. 241) despite the documented lack of connectivity, even though dispersal among populations is a defining characteristic of a metapopulation (see Hanski and Gilpin 1991 for more on metapopulation theory). However, spatial structure of a metapopulation within and among subpopulations is critical for metapopulation functioning, and available evidence does not document successful dispersal between the San Bernardino, San Gabriel, and San Jacinto Mountains, which are adjacent mountain ranges, indicating that if mixing does occur it is very rare (LaHaye et al. 2001, p. entire, 2004, p. entire; Gutiérrez et al. 2017, pp. 242, 250). Further, Gutiérrez et al. (2017, pp. 241–242, 250) discusses that not all subpopulations within the metapopulation have equal likelihood of “blinking out” or being rescued/recolonized by other subpopulations, which are important components of metapopulation theory. Within the coastal-southern California population, the subpopulation inhabiting the San Bernardino and San Gabriel mountains is the largest subpopulation and is the subject of most ecological studies. The persistence of this subpopulation has been identified as important for persistence of the coastal-southern California population (Verner et al. 1992, pp. 197–206), which is discussed more in Chapter 5: Current Condition.

To conduct a more focused analysis of how different portions of each population’s ranges contribute to that population’s overall resiliency, we further divided the Sierra Nevada and coastal-southern California populations into analysis units (see Figure 4). Table 2 provides the size of each analysis unit and the proportion of land ownership between federal, state, local, and private entities. We chose analysis units roughly based on public land management boundaries because of varying demographic data and management strategies across the range. Dividing the population up into analysis units based on land management boundaries allows a better assessment of the varying conditions across the range. We identified a total of 15 analysis units.

California Spotted Owl Analysis Units and Populations

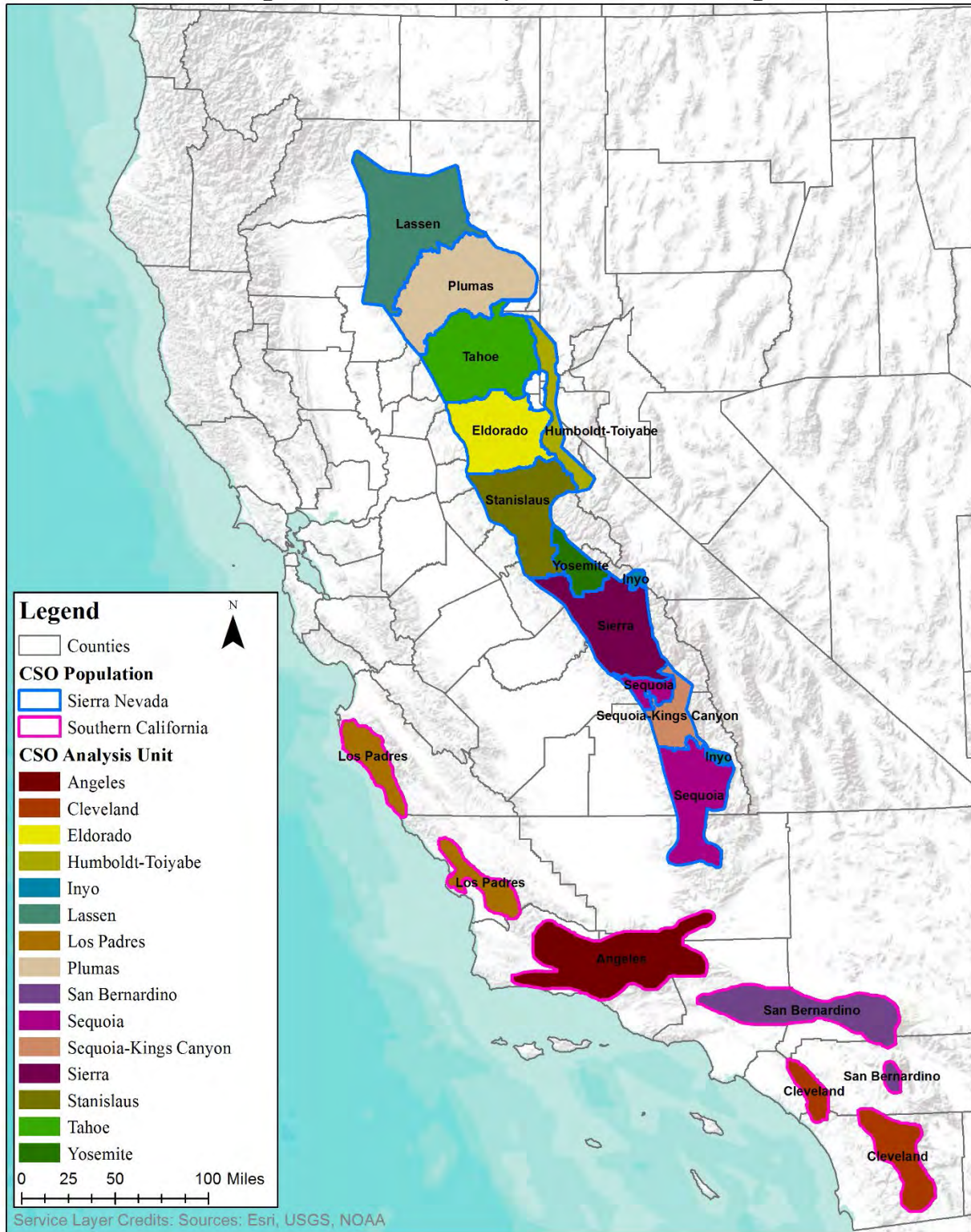


Figure 4: California spotted owl analysis units for the Species Status Assessment. Analysis units were defined broadly using public land boundaries, incorporating surrounding private lands.

Table 2: California Spotted Owl Analysis Unit Size and Land Ownership Percentage using the digital file, BLM CA Land Status – Surface Management areas dated September 23, 2019, to calculate proportions of federal, state, local government, and private lands within the species’ range.

Analysis Unit	Size of Analysis Unit (hectares)	Proportion Federal Land	Proportion State Land	Proportion Local Land	Proportion Private Land
<i>Sierra Nevada</i>					
Lassen	774,456	51%	<1%	<1%	48%
Plumas	693,786	70%	1%	0%	28%
Tahoe	625,183	59%	<1%	0%	40%
Eldorado	467,257	63%	<1%	<1%	37%
Humboldt-Toiyabe	116,901	85%	2%	0%	13%
Stanislaus	499,536	67%	<1%	<1%	32%
Yosemite	138,873	99%	0%	<1%	<1%
Sierra	534,163	86%	<1%	0%	14%
Sequoia-Kings Canyon	180,702	91%	<1%	0%	9%
Sequoia	498,606	84%	<1%	0%	15%
Inyo	41,771	98%	0%	0%	2%
<i>Coastal-Southern California</i>					
Los Padres	342,617	44%	3%	<1%	53%
Los Padres-Angeles	732,520	72%	<1%	<1%	28%
San Bernardino	505,937	79%	<1%	<1%	20%
Cleveland	360,320	48%	5%	<1%	46%

3.2.2 Resiliency

Resiliency is the ability of a species to withstand stochastic events, the normal year-to-year variations in both environmental conditions (i.e., temperature, rainfall, and periodic disturbances such as fires, floods, and storms) and demographic conditions (i.e., mortality, fecundity) (Redford et al. 2011, p. 40). Determined by the size and growth rate of the populations comprising the species, resiliency can be evaluated to gauge the ability of a species to weather the natural range of favorable and unfavorable conditions.

Populations of CSO must have adequate amounts of nesting, foraging, and roosting habitat containing the habitat components described above in sufficient amounts and the appropriate configuration on the landscape to support a stable or increasing growth rate. They also need connectivity between territories and home ranges. Populations meeting these requirements are better able to withstand stochastic events. In many instances, however, data are insufficient or completely lacking regarding a population’s size and growth rate. In the absence of such data, it can be reasonable to examine other characteristics that may serve as surrogate indicators of general population health and, subsequently, resiliency. Essentially, an assessment of the availability of a species’ identified needs (e.g., suitable habitat, food, breeding sites) may allow us to make

assumptions about the potential resiliency of any given population. However, unless there is a documented positive correlation between species needs availability and a population’s known demographic condition, the uncertainty regarding such assumptions must be made clear.

3.2.3 Demographic Factors Influencing Analysis Unit Condition and Population Resiliency

In this section we describe the demographic factors that are being considered in this SSA Report as important for CSO, including natal dispersal, survival, fecundity, occupancy, and population growth. We describe the importance of each demographic factor to CSO persistence and how the habitat needs discussed in the previous section influence these factors. Figure 5 is a conceptual model that shows the relationship between habitat needs and demographic factors, which affect analysis unit condition and, ultimately, a way to measure population resiliency.

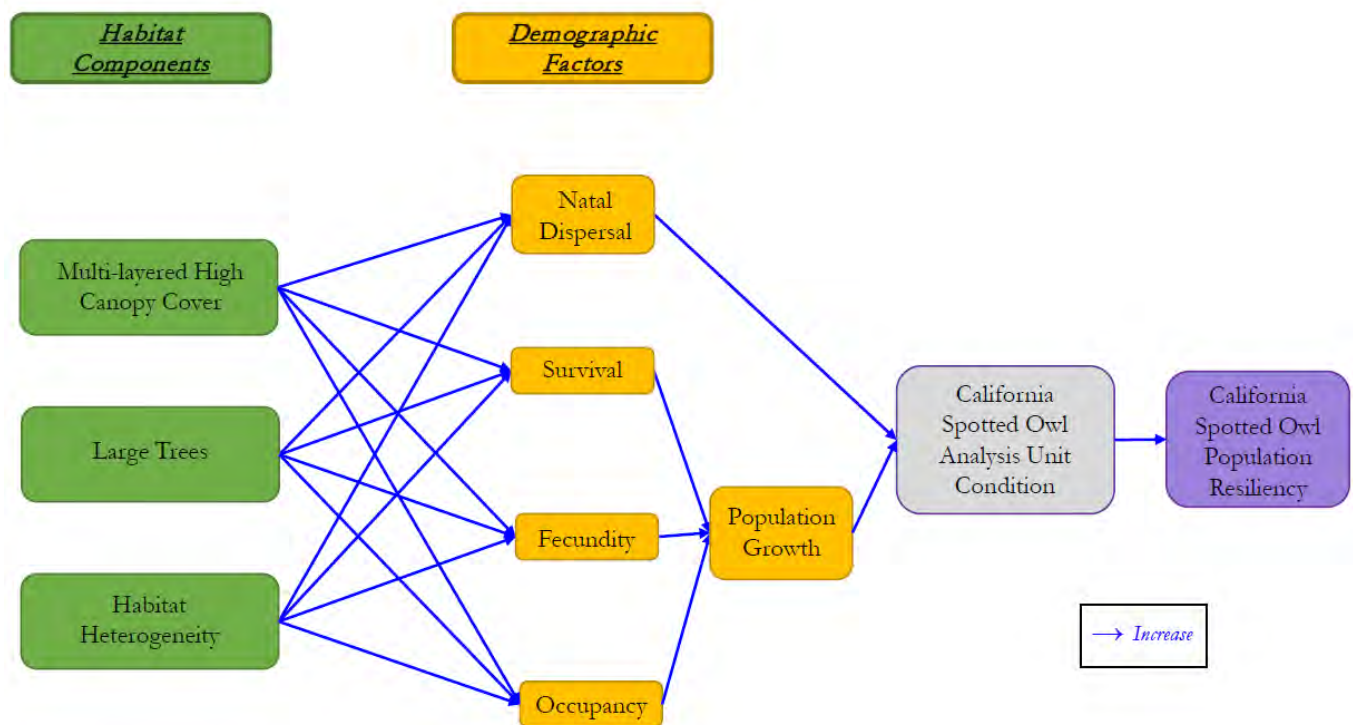


Figure 5: Conceptual model showing the relationship between habitat needs and demographic factors, and how they influence analysis unit condition and resiliency of California spotted owl populations. The blue arrows represent influences showing relationships between varying needs.

3.2.3.1 Natal Dispersal

As discussed in the “Life History” section of the SSA Report, natal dispersal is the primary mechanism for juvenile and sub-adult birds to find their own territory, and throughout this document when we refer to dispersal it means natal dispersal. Dispersal decreases the likelihood of incestuous mating, which is rarely observed in spotted owls (Carlson et al. 1998, pp. 562–563; Forsman et al. 2002, p. 2). For dispersal to be successful, many of the habitat components must be present within the areas CSO disperse to. Canopy cover, large trees, and coarse woody debris, all

must be available in sufficient amounts and the appropriate configuration on the landscape (i.e., provides heterogeneity) for juveniles or sub-adults to successfully settle into a territory to begin breeding.

There is little available information about dispersal and dispersal habitat between the areas we define as CSO populations and analysis units within this SSA report. Dispersal habitat is described for northern spotted owl as 50% of the forest matrix outside of activity centers in stands with an average of 28 cm (11 in) dbh and 40% canopy closure (Thomas et al. 1990, p. 15). This contrasts with dispersal for Mexican spotted owls, which may move across large areas of unforested habitat to access suitable habitat on different mountain ranges (Gutiérrez et al. 1995, p. 5, 2017, p. 242). It is unknown how far CSO will disperse across unsuitable habitat to find a new territory, but adult northern spotted owls have been found to occasionally move long distances if forced out of a territory (Forsman in litt. 2018, p. 22).

3.2.3.2 Survival

Survival is defined as individuals in a population persisting across years. As discussed in the “Life History” section of the SSA Report, the CSO is a long-lived species with low reproductive rates. Survival, particularly adult survival, is closely linked to population growth in spotted owls and is important for maintaining population resiliency (Seamans and Gutiérrez 2007a, p. 57; Blakesley et al. 2010, p. 27). Adult CSO have high annual survival rates ranging from 0.796-0.814 in different study areas within analysis units in southern California (LaHaye et al. 2004, p. 1056; Franklin et al. 2004, p. 22), and 0.811-0.891 in study areas within analysis units in the Sierra Nevada (Blakesley et al. 2001, p. 671, 2010, p. 10; Franklin et al. 2004, p. 22; Tempel et al. 2014b, p. 92). In comparison, juvenile survival is difficult to estimate due to dispersal, and has been found to be low, ranging from 0.087-0.333 in study areas within analysis units in the Sierra Nevada (Blakesley et al. 2001, p. 671; Tempel et al. 2014b, p. 92), and 0.368 for southern California (LaHaye et al. 2004, p. 1056). For northern spotted owl, juveniles tend to have high mortality during the dispersal phase (Miller 1989, pp. 41–44; Forsman et al. 2002, p. 18).

All the habitat needs discussed above influence survival. For example, survival is related to the amount of forest dominated by medium to large trees, high canopy cover, and habitat complexity (Blakesley et al. 2005, p. 1554; Tempel et al. 2014a, pp. 2089, 2098; McGinn et al. 2022, p. 9). In northern spotted owls, forest heterogeneity is correlated with higher survival rates (Franklin et al. 2000, p. 539). Weather patterns can also affect survival in both CSO (Seamans and Gutiérrez 2007a, p. entire) and northern spotted owl (Glenn et al. 2011, entire). Further impacts to survival will be discussed in Chapter 4 Influences to Viability of the SSA Report.

3.2.3.3 Fecundity

Fecundity is defined as the ability to produce offspring and is measured by the number of viable female offspring that an individual can produce over a specific time period. Although CSO are considered to have low reproductive output, or number of young fledged per year, reproduction is essential for population persistence and species viability. As discussed in the “Life History” section of the SSA Report, CSO do not always reproduce every year (although they can) and only lay 1–3 eggs when breeding does occur. Annual reproductive output, measured by presence or absence

of offspring in a nest, for female CSO in a demographic study in the Sierra Nevada was found to range from 0.478–0.988 (Blakesley et al. 2010, p. 1). Reproduction throughout all the demographic studies (see 5.1 Current Condition Summary of Methods for more information on the demographic studies) has ranged from no reproduction within a study area to nearly all birds reproducing in a study area in a particular year (Franklin et al. 2004, pp. 32–33; Seamans and Gutiérrez 2007a, p. 65; Blakesley et al. 2010, p. 17; MacKenzie et al. 2012, p. 597; Tempel et al. 2014b, p. 91; Stoelting et al. 2015, p. 46). Fecundity, measured as female young produced per female annually, has been found to range from 0.284–0.409 in the Sierra Nevada and to be 0.362 in southern California (Franklin et al. 2004, pp. 11, 23).

Many of the habitat components discussed in the previous section of this SSA Report influence fecundity. Reproductive output decreases as non-forest habitat increases within the area around the nest, and nest success increases as the presence of large remnant trees within the nest stand increases (Blakesley et al. 2005, p. 1554). Reproduction is positively correlated to the foliage volume above the nest tree (North et al. 2000, p. 797), although forest heterogeneity is also important for reproduction (Franklin et al. 2000, p. 539; Tempel et al. 2014a, p. 2089; McGinn et al. 2022, p. 9) and foraging (Zulla et al. 2022, pp. 7–8). Annual variation in weather also plays a role in reproductive success (North et al. 2000, p. 797; Seamans and Gutiérrez 2007a, p. 57; MacKenzie et al. 2012, p. 597; Stoelting et al. 2015, p. 46). For example, CSO experienced increased fecundity when a dry breeding season followed a previously wet year (LaHaye et al. 2004, pp. 1056, 1062). Although survival of breeding CSO is an important factor that is closely connected to population growth, reproductive output may be more influential to population growth because it varies more than adult survival (Blakesley et al. 2001, p. 667; Seamans and Gutiérrez 2007a, p. 57).

3.2.3.4 Occupancy

California spotted owl occupancy in this SSA Report is defined as the stable (not transient) presence of at least one adult within a territory. California spotted owls select and defend territories in which they spend most of their life. California spotted owl pairs will only reproduce once they have established an occupied territory. The measure of occupancy has been found to be strongly correlated with regional abundance of CSO and can provide reliable inferences on population trends (Tempel and Gutiérrez 2013, pp. 1093–1093). Since the Verner et al. 1992 CSO Assessment of Current Status report, occupancy has been well studied in study areas corresponding to four analysis units within the Sierra Nevada and at one analysis unit in southern California providing long-term demographic information (Gutiérrez et al. 2017, pp. 79–85). The occupancy data that have been collected have been used to assess trends in population change, which will be discussed further in the “Current Condition” section of the SSA Report (Franklin et al. 2004; Tempel et al. 2014b, p. entire; Conner et al. 2016).

Many of the habitat needs discussed in the previous chapter of this SSA Report need to be present in order for CSO to occupy a territory. Occupancy is generally higher and more consistent with an increasing proportion of the territory containing large trees and high canopy cover (Blakesley et al. 2005, p. 1554; Seamans and Gutiérrez 2007b, p. 572; Roberts et al. 2011, p. 610; Tempel et al. 2014a, p. 2089; Gutiérrez et al. 2017, p. vxii). Habitat alteration can negatively impact occupancy for CSO because it removes the habitat needs of large trees and multi-layered high canopy cover (Seamans and Gutiérrez 2007b, p. 566); however, the degree of alteration can have

varying effects on occupancy (see Chapter 6 Influences to Viability). As the proportion of forest types that are not used for nesting (smaller, similar-aged young trees) increases, occupancy tends to decrease (Blakesley et al. 2005, pp. 1554, 1560).

3.2.3.5 Population Growth

California spotted owl population growth in this SSA Report is defined as the change in the number of individuals within a particular study area, which correspond to our analysis units. Population growth is determined by the demographic factors of survival, fecundity, and occupancy, with fecundity likely the most influential because it is more variable (Blakesley et al. 2001, p. 667, 2010, p. 27; Seamans and Gutiérrez 2007a, p. 57, b, p. 566; Tempel and Gutiérrez 2013, pp. 1093–1094; Gutiérrez et al. 2017, p. 99). Population growth is variable throughout study areas in the Sierra Nevada where we have available information, with documented declines ranging from -50% to -31% in some study areas and a population increase of 25% in another (Tempel et al. 2014b, pp. 86, 90–92; Conner et al. 2016, p. 15)(see 5.3.1 Sierra Nevada Population for more information on known population trends). The only available demographic data for southern California is from the San Bernardino National Forest. A population decline of -9% was observed from 1987–1998, with more recent occupancy analyses showing further declines in population size (LaHaye et al. 2004, pp. 1056, 1064; Tempel et al. 2022, pp. 20, Table 5). All habitat components described in the previous chapter need to be present for positive CSO population growth, as described in further detail in the survival, fecundity, and occupancy sections above.

The difference in population rates between occupancy and mark-recapture models could be due to several reasons. For example, occupancy models may not be as sensitive to real changes in population growth, as they measure if a territory is occupied without taking into account to the number of owls inhabiting that territory (an occupied territory was counted as one that included a single owl, a pair of owls, or more than a pair of owls) (Conner et al. 2016, pp. 13–15). Differences in population trends measured in the two Eldorado studies were likely due to the inclusion of additional years in the 2014 study, as well as increased number of territories occupied only by single owls rather than pairs in that analysis (that is, the loss of half of a pair would result in lower fecundity and thus lower population growth) (Tempel et al. 2014b, p. 93). There is some evidence that population declines in these study areas have not been continuous; one study measured stationary population growth rates from 1998–2005, with the greatest increase in survival from 2000–2005 (Blakesley et al. 2010, pp. 17–18). However, the best available evidence does indicate that owls in the study areas have experienced an overall decline in population. None of the models have forecasted whether these trends will continue into the future, and these existing models cannot be used to forecast future trends (Franklin et al. 2004, p. 34).

3.3 Species Needs

At the species level, we assess the redundancy and representation of the entire CSO range to better understand the viability of the species. Viability is defined as the ability of CSO to sustain populations in the wild over time. Redundancy is the ability of a species to withstand catastrophic events and representation is the ability of a species to adapt to changing environmental conditions. Using the SSA framework, we describe the species' viability by characterizing the status of the species in terms of its resiliency, redundancy, and representation (the 3Rs).

3.3.1 Redundancy

Redundancy is the ability of a species to withstand catastrophic events, i.e., natural or anthropogenic stochastic events that would result in the loss of a substantial component of the overall species population. Such a loss could be of one or more populations of a species which is comprised of multiple populations, or the catastrophic loss of a substantial number of individuals from a species with only a single population. However, redundancy is not simply a measure of the total number of individuals or populations of a species, but instead must also be evaluated in the context of an assessment of reasonably plausible catastrophic events. For example, a species with numerous small populations does not necessarily translate to a greater ability to withstand catastrophic events if those populations are very close together, and the only reasonably plausible potential catastrophe is one that would affect them all equally. Conversely, a species with only one population, but one which is very large and widely distributed, could well have a high ability to withstand a catastrophic event that would only affect a small percentage of the overall population. Therefore, our characterization of a species' redundancy takes into consideration both an assessment of the size and distribution of its population(s), and an evaluation of the kinds and likelihood of reasonably plausible catastrophic events to which the species could be exposed.

For CSO, we evaluate redundancy by considering the number of resilient populations distributed across the species' range. Having resilient populations distributed across the range increases the species ability to withstand catastrophic events. Threats, including those that could be catastrophic, are discussed more in Chapter 4.

3.3.2 Representation

Representation is the ability of a species to withstand and adapt to long-term changes in environmental conditions (i.e., significant changes outside the range of normal year-to-year variations). The measure of a species' representation may be determined by the breadth of genetic diversity within and among populations; however, in the absence of information on a species' genetic diversity, we may also evaluate a species' known environmental diversity (i.e., the diversity of environmental conditions over which it is known to occur) as an alternative measure of its ability to withstand and adapt to long-term changes.

For CSO, we evaluate representation by considering the distribution of s populations across their various ecological settings and whether those populations are able to maintain adequate amounts of genetic diversity. Having a variety of ecological settings that the species can occupy and a breadth of genetic diversity increases the species ability to withstand and adapt to long-term environmental changes.

CHAPTER 4: INFLUENCES TO VIABILITY

In this chapter, we evaluate the significant past, current, and future influences that are impacting CSO resiliency, redundancy, and representation. These influences impact the species ecological needs, ultimately affecting the viability of the species.

4.1 Wildfire

Fire is a natural part of CSO habitat (Verner et al. 1992, pp. 247–248) and is necessary for maintaining heterogenous forests. Overall, wildfire accounts for a greater proportion of live tree mortality than any other activity (e.g., timber harvest, development) in California (Sleeter et al. 2011, pp. 262, 264). Wildfire and associated tree mortality can be beneficial or detrimental for CSO depending on scale and severity. Fire severity is often categorized as low, moderate, or high, with low severity fire defined as areas of surface fire with little change in canopy cover and little mortality of the structurally dominant vegetation, moderate severity as a mixture of effects on the structurally dominant vegetation, and high severity as areas where the dominant vegetation has high to complete mortality. Areas that experience fires with predominantly low to moderate severity burn patterns with small patches of high-severity fire scattered throughout the fire perimeter can increase forest heterogeneity, ultimately result in higher prey densities, increase amounts of forest edge for foraging, which benefits CSO, and provide for unburned refugia within the fire perimeter that have higher tree survival and more vegetative cover during the immediate postfire years (Roberts et al. 2011, p. 610; Lee et al. 2012, p. 792; Bond et al. 2013, pp. 114, 122; Eyes et al. 2017, p. 384; Blomdahl et al. 2019, pp. 1046, 1048, 1049). There is also evidence to suggest that more pyrodiverse (i.e., spatial or temporal variability in fire effects; (Jones and Tingley 2021, p. 1) landscapes support greater landscape heterogeneity which may promote greater biodiversity (Steel et al. 2021, pp. 7–8; Stephens et al. 2021, p. 5). For example, in areas where woodrats are the primary prey species, a juxtaposition of mature forests and open canopy patches promotes higher prey diversity and abundance, and northern spotted owls preferentially select for these areas (Zabel et al. 1995, p. 433, 2003, p. 1027; Ward and Noon 1998, p. 79; Franklin et al. 2000, p. 539).

(Kramer et al. 2021a, pp. 8–9) studied CSO in a fire managed landscape (i.e., National Park) and concluded that CSO selected areas of low-severity fire and older burned areas (e.g., fires 16–40 years old), demonstrating owls are likely adapted to frequent low-severity fire. Although burned areas can reduce the amount of high canopy cover available, studies have found that CSO forage on the edge of and within areas that have been burned at a range of severities (Bond et al. 2009, p. 1116, 2016, p. 1290; Eyes et al. 2017, p. 375) although typically avoiding larger areas of high-severity fire (Jones et al. 2016a, p. 304; Eyes et al. 2017, p. 383). Further, Lesmeister et al. (2019, p. 12) concluded there was little effect to nest or roost habitat from low-severity fire in northern spotted owl range. Thus, many researchers advocate for the use of ecologically beneficial fire to help sustain CSO habitat and report that low to moderate severity fire minimizes the effects of future high-severity wildfire (Stephens et al. 2019, pp. 395–396, 2020, p. entire, 2021, p. 5; Taylor et al. 2022, p. 4); also see 4.5. Fuels Reductions and Forest Management).

However, large-scale high-severity fires have a detrimental effect on both CSO and its habitat. Large-scale high-severity fire (i.e., a megafire) is generally defined as over 10,000 ha (24,711 ac) of area burned with 75–100% canopy mortality (Jones et al. 2016a, p. 300; Linley et al. 2022, pp. 6, 8). These megafires can degrade or destroy CSO habitat, completely incinerating large trees and canopy cover (Eyes 2014, p. ii; Roberts et al. 2015, pp. 112–115; Jones et al. 2016a, pp. 300–305). Wan et al. (2020, p. 7) determined habitat suitability for northern spotted owls decreased postfire and depended on fire severity (i.e., higher fire severity resulted in greater declines of habitat suitability); thus, megafires have a greater potential to alter the availability of suitable habitat.

The loss of habitat from large-scale high-severity fires also results in direct impacts to CSO individuals and populations. As megafires alter the number of large trees (including nest trees), multi-layered high canopy cover, forest heterogeneity, and patch size, CSO dispersal, fecundity, and occupancy are subsequently reduced. It has been observed that large patches of high-severity fire significantly reduce colonization (dispersal), occupancy, and habitat use across the CSO range (Eyes 2014, p. 42; Tempel et al. 2014a, p. 2089; Jones et al. 2016a, pp. 300, 303–305; Eyes et al. 2017, pp. 381, 384)(Jones et al. 2019, p. 26, 2020b, p. entire, 2021b, p. 5; Schofield et al. 2020, pp. 5–6; Tempel et al. 2022, p. 13) and for other subspecies (Rockweit et al. 2017, p. entire; Lesmeister et al. 2019, p. 13; Duchac et al. 2021, p. 12). Fires may cause direct mortality to eggs and juveniles during the nesting season and fast-moving fires also have the potential to cause direct mortality to adult individuals (Jones et al. 2016a, p. 305). No data are available on how many CSO are killed annually by direct impacts of large-scale high-severity fire. Thick smoke can debilitate birds and low, thick smoke may also prevent birds from flying away to escape the fire area (Epanchin et al. 2002, p. 141). Although most birds are able to move to escape direct mortality from fires, smoke from fires can impact birds by damaging their lungs (Verstappen and Dorrestein 2005, p. 139). While many species have existed with frequent fire over evolutionary time, there are novel stressors from megafires and extreme smoke events that may act as an additional selective pressure on certain species (Nimmo et al. 2021, p. 5689). It is well-known that birds are more sensitive to air pollution than other taxa (Brown et al. 1997, entire). There is limited research on the effects of wildfire smoke on wildlife in general, but there is clear evidence that smoke can have both acute and chronic health impacts on a variety of taxa, which may ultimately affect demographic rates (Sanderfoot et al. 2021, p. 13). For example, some birds may be more sensitive to the effects of fire when they are caring for young, which can influence nest success and subsequent recruitment (Cahill and Walker 2000, pp. 111–112).

There are several publications that conclude there are no negative effects of high-severity fire for CSO (Lee and Bond 2015, p. entire; Hanson et al. 2018, p. entire, 2021, p. entire; Lee 2018, pp. 12, 16, 2020, p. entire). However, many researchers such as (Jones et al. 2019, p. entire), (Jones et al. 2020b, p. entire), and (Jones and Peery 2019, p. entire) identified several errors, data misrepresentations, and inaccurate conclusions drawn from these owl studies (see previous sentence for citations, and for a larger discussion on misinformation about wildfire). We also recognize that (Jones and Tingley 2021, p. 10) suggest that rather than a binary discussion of high-severity fire and owl use patterns (i.e., owls either use high-severity fire or they do not), focusing instead on forest heterogeneity, pyrodiversity, and severe fire patch size interaction may better explain spotted owl use patterns rather than simply the presence of high-severity fire. There are a number of other publications detailed in (Hagmann et al. 2021, pp. 17–21, Tables 3-6) that also claim there is uncertainty about historical forest conditions, fire regimes, fire frequency, and fire severity, and purport that tree densities and amount of high-severity fire are not outside the natural range of variation expected for western forests. Hagmann et al. (2021, entire) discuss the inaccuracies with these publications (pp. 17-21, Tables 3–6) and conclude they do not represent the "best available science" because the authors do not account for ecological differences in site conditions, they make inappropriate comparisons, and overall use less accurate data sources, methods, or other errors (pp. 16-21). We acknowledge this disagreement in the literature. While we have analyzed all of the above sources, we observe that the vast majority of science discussed in this SSA Report that investigated the effects of fire on CSO (Jones et al. 2020a, p. entire) concludes that, overall, spotted owls avoid

large patches of high-severity fire and that high-severity fire is increasing throughout California and the western United States. Current conditions in the CSO range may contribute to ongoing fire risk, and depending on the portion of the range and the land manager, fire management activities may vary (see 4.5 Fuels Reductions and Forest Management). Decades of fire suppression have led to overall higher canopy cover from small and medium trees, higher dead biomass density, and more surface fuels in forests of the western United States (Verner et al. 1992, pp. 247–248; Agee and Skinner 2005, p. 83). The historical fire return interval for the Sierra Nevada was around 11–16 years, but fire suppression over the last 100 years has led to a change in fire behavior of larger, more severe fires in recent years (Safford and Stevens 2017, pp. v–vi). The multi-layered high canopy cover and biomass provide important habitat for the CSO but also tend to increase the vulnerability of forests to high-severity fire (Verner et al. 1992, pp. 251–258; Agee and Skinner 2005, p. 83) in present day fire-suppressed forests. The higher fuel loads, particularly large dead wood like snags and logs tend to burn at higher severity as densities increase (Lydersen et al. 2019, p. 7). In a recent megafire, dead biomass directly contributed to the fire effects observed with areas burned at high severity associated with areas with high amounts of dead biomass pre-fire (Stephens et al. 2022, p. 8). On top of the higher fuel loads, extended droughts and longer wildfire seasons have led to larger and more severe fires in the CSO range and throughout western North America (Miller and Safford 2012, p. 41; Mallek et al. 2013, p. 1; Nigro and Molinari 2019, p. 20; Parks and Abatzoglou 2020, p. 4; Safford et al. 2022, p. 12). In addition, in 2020 and 2021 over 1 million ha (2.4 million ac) burned in California, resulting in more area burned over these two years than in the past seven years of all California fires combined (Safford et al. 2022, p. 5). This amount is on par with the 1.8 million ha (4.4 million ac) that burned in an average in year in California prior to fire suppression practices brought with Euroamerican settlement in (Safford et al. 2022, p. 5). The acreage burned at high severity in 2020 is nearly three to six times higher when compared to historical conditions prior to Euroamerican settlement (Safford et al. 2022, p. 17). Thus, wildfire itself is not a novel disturbance for CSO, but rather the amount burned at high severity. Further, an increase in high severity fire changes how fire interacts with important habitat features for CSO. For example, fire often killed trees that would subsequently serve as CSO nests. However, large patches of high severity burn hotter and can end up entirely consuming the features important to CSO. Between the years of 2000–2014, 7% of CSO suitable nesting habitat (a total of 85,046 ha (210,153 ac) out of 1,166,560 ha (2,882,633 ac)) was burned either partially at moderate severity (typically 25-50% tree basal area mortality) or entirely at high severity (typically >75% tree basal area mortality), causing ≥50% tree basal area mortality and reducing canopy cover to <25% (Stephens et al. 2016, pp. 1, 9).

The size and severity of a fire determines how much it will impact CSO at the population level. If a high-severity fire occurs in a large enough area, it can eliminate entire territories or home ranges of CSO, displacing individuals that may or may not establish a new territory (Jones et al. 2016a, pp. 300–305). Overall, CSO avoided severely burned (>75% overstory mortality) forest after the 2014 King Fire, one of the first megafires in the Sierra Nevada, and severe fire patch size use varied depending on the quantity of severe fire in their home range (Jones et al. 2020b, p. 1206). Little information yet exists from the megafires of 2020 and 2021 that occurred in the western United States, but a few recent observations of northern spotted owls have documented nests at the edges of high-severity fire patches surrounded by post-fire foraging habitat; the nests themselves were in locations with low- to moderate-severity with nest trees containing dead needles (Hunter in

litt. 2022; Chow in litt. 2022; Siedel in litt. 2022). Some of these nest locations are adjacent to riparian zones that burned at low- and moderate-severity. Often riparian zones burn at lower fire severities; thus, they may serve as refugia for wildlife, but very thick riparian zones may diminish the protective effects of increased moisture making them vulnerable to burn at high severity (Dwire and Kauffman 2003, p. entire; North 2012, p. entire). Although some of these areas that have experienced moderate- to high-severity fire around the nest may provide the canopy cover that northern spotted owls need for one to two years postfire (through dead leaves or needles still present on trees), it is uncertain if northern spotted owls will persist in these locations as trees drop their leaves or snags fall to the ground. Site occupancy by CSO after wildfire appears to be a function of the amount of suitable habitat remaining after the fire (Gutiérrez et al. 2017, p. xxiii). If habitat becomes unsuitable, it takes decades for large trees to reestablish on the landscape. Based on fire activity and anticipated trends over the next 75 years, the cumulative amount of nesting habitat burned at $\geq 50\%$ tree basal area mortality will exceed the total existing habitat in the Sierra Nevada (Stephens et al. 2016, pp. 1, 12). In other words, the loss of suitable CSO habitat would exceed the rate of new forest growing post-fire (Stephens et al. 2016, pp. 11–13). Thus, future habitat persistence for CSO is concerning given that high-severity fire appears to be increasing in the CSO range across all lands (both public and private) occupied by CSO and throughout the western United States (Parks and Abatzoglou 2020, pp. 4–5). When private lands are considered separately, the odds of high severity fire occurring on industrially managed forests and adjacent lands were 1.8 and 1.4 times higher, raising some concern over CSO persistence on private lands (Levine et al. 2022, p. 4).

In the Sierra Nevada, the proportion of high severity fire throughout the CSO range has dramatically increased in recent years. The proportion of high-severity fire in California montane forests in 2020 was on average 43–76% higher than the combined average between 1984 and 2008, and was three to six times higher than the estimates of pre-Euroamerican settlement (Safford et al. 2022, p. 17). In a 2022 analysis by the U.S. Forest Service Pacific Southwest Research Station, between 1984–2019, 2,679,044 acres burned throughout CSO range in the Sierra Nevada with 784,820 acres burned at high severity (Keane in litt. 2022, p. 3). In contrast, between 2020 and 2021 2,131,593 acres burned throughout the CSO range with almost 899,000 of those acres at high severity (Keane in litt. 2022, p. 3). This illustrates how megafires that burned in 2020 and 2021 burned more habitat at high severity in two years than fires over the past three and a half decades. In addition, between 1984 and 2021 a total of 50 percent of California spotted owl PAC acres have been impacted by wildfire, with 56% of that total burned in 2020 and 2021. Further, 65% of the 56% that burned between 2020 and 2021 burned at high severity (Keane in litt. 2022, p. 5). Because individual CSO are displaced from areas where the entire PAC or majority of the PAC has burned at high severity, it is unlikely the species will continue to persist in these areas until the habitat can recover, which can take decades. Protected Activity Centers are designations made by the Forest Service to protect the best available 121 ha (300 ac) of habitat in as compact of a unit as possible around a nest tree (see 4.9 Regulatory Mechanisms and Management Actions for a further description of PACs).

The Service conducted a fire severity analysis within the entire CSO range as defined in this SSA Report. We used the Monitoring Trends in Burn Severity (MTBS) data for 1984–2020 for our fire severity analysis. This data is managed by the U.S. Forest Service Geospatial Technology and

Applications Center and the U.S. Geological Survey Center for Earth Resources Observation and Science, and assessments are done approximately one year after the fire. We used Rapid Assessment of Vegetation Condition after Wildfire data (GTAC 2022) for 2021 fires which tends to overestimate fire severity since the assessment is done within the first few months after the fire stops burning, which may not account for trees that survived the fire after winter precipitation and a spring growing season (Hanson and North 2009, p. 861). This program is also managed by the U.S. Forest Service Geospatial Technology and Applications Center. As described in 4.1 Wildfire earlier in this section, low severity fire is defined as areas of surface fire with little change in canopy cover and little mortality of the structurally dominant vegetation, moderate severity as a mixture of effects on the structurally dominant vegetation, and high severity as areas where the dominant vegetation has high to complete mortality. We considered high severity fire >75% mortality. We calculated the proportion of low, moderate, and high severity fires within CSO range and determined fire has been steadily increasing with a large increase in recent years, leading up to the current condition. We used zonal statistics and tabulate area functions in ArcMap 10.8.1 and R for burn severity calculations. Figure 6 shows the amounts of habitat that have burned at low, moderate, and high severity within the CSO range from 1984 to 2021. This figure and Table 3 provide values of the amount of habitat that has been impacted by wildfire, including high-severity fire, the general trend of fire amount and severity, and a running total of area burned. Additional tables showing fire severity calculations by analysis unit are presented in Appendix I. It represents the variation over years, the proportion of wildfires that burn at high severity vs. moderate or low severity, and the amount of habitat that can be lost within a year to high severity fire. The fire values in Figure 6 represent total area burned and include areas that have burned more than once. Of the CSO range, approximately 47% burned between 1984 and 2021, with 15% at high severity. Most of the area burned at high severity occurred in 2020 and 2021, with 2% and 4%, respectively (see Table 3). Figure 7 shows wildfire locations and severity within the CSO range from 1984 to 2021. It provides a visual of the location and scale of fires within the CSO range. We expect that the pattern of both area burned and wildfire severity will continue or increase into the future. An existing dataset from the California Department of Forestry and Fire Protection examined the potential threat of future wildfire in California and is displayed in Figure 8. Megafires may be more likely to occur, and the likelihood is higher in areas shown in the map as higher threat categories (Safford et al. 2022, p. 17; Taylor et al. 2022, p. 1). To develop the California Wildfire Threat data, the California Department of Forestry and Fire Protection combined fire frequency, or the likelihood of a given area burning, with potential fire behavior to create four threat classes ranging from moderate to extreme. This dataset covers through 2014, so does not consider how the recent fires from 2014 to 2021 affect future fire threat. The majority of the CSO range occurs within the very high wildfire threat category (see Figure 8). Much of the southern California range of CSO falls within the extreme fire risk.

Some regulatory mechanisms and conservation measures can reduce the potential severity or scale of wildfires. Wildfire fuel reduction treatments, for example, prescribed fire and mechanical thinning, can reduce the amount or degree of spotted owl habitat alteration from a high-severity fire, and a balanced approach to fuel reduction treatments may ensure suitable CSO habitat is maintained (see Section 4.5) (Jones et al. 2016a, p. 305; Service 2017, pp. 24–25; Chiono et al. 2017, p. 1; Jones et al. 2021a, p. entire). The 2004 Forest Service Sierra Nevada Forest Plan Amendment has a goal of actively restoring fire-adapted ecosystems by reducing unnaturally dense conditions, but there are

also measures in place in the framework to avoid management actions within CSO activity centers to the greatest extent possible (Forest Service 2004, pp. 34–35) (see 4.9 for more information on Forest Plans). Fuel reduction treatments are actively taking place on Forest Service land, but special considerations including the timing of treatments with the breeding season and the methods that are used are evaluated to avoid impacts to owls within PACs. In 2017 and again in 2020, a memorandum of understanding (MOU) was signed by Sierra Pacific Industries, California Department of Forestry and Fire Protection, National Fish and Wildlife Foundation, and the Forest Service to coordinate on certain actions that may contribute to forest fuel reductions and CSO conservation (see section 4.9). The purpose of the MOU is to try to minimize the threat of large-scale high-severity fire while still providing quality habitat for CSO. However, large-scale high-severity fire cannot be completely addressed by regulatory mechanisms. Fuel reduction treatments may not prevent catastrophic damage in an extreme fire event; however, some studies show that when fire is a part of the fuel reduction treatment, future fire severity can be reduced and more fire treatments should be included to achieve fuels reduction goals, including areas surrounding spotted owl nests and riparian corridors (North et al. 2021, pp. 527, 529; Taylor et al. 2022, p. 4). For more information on measures that address the threat of wildfire, see 4.9 Regulatory Mechanisms and Management Actions.

High severity fire is likely to continue to be a threat into the future for CSO. Though some individuals could be harmed or killed by large fires, the primary impact of this threat is habitat-based. These habitat changes also affect demographic parameters: following high severity fires, colonization declines and territory extinction increases, leading to overall declines in occupancy (Tempel et al. 2022, pp. 13–16). Overall, large-scale high-severity fire is currently and will likely continue to be a threat throughout the range of CSO (Figure 8).

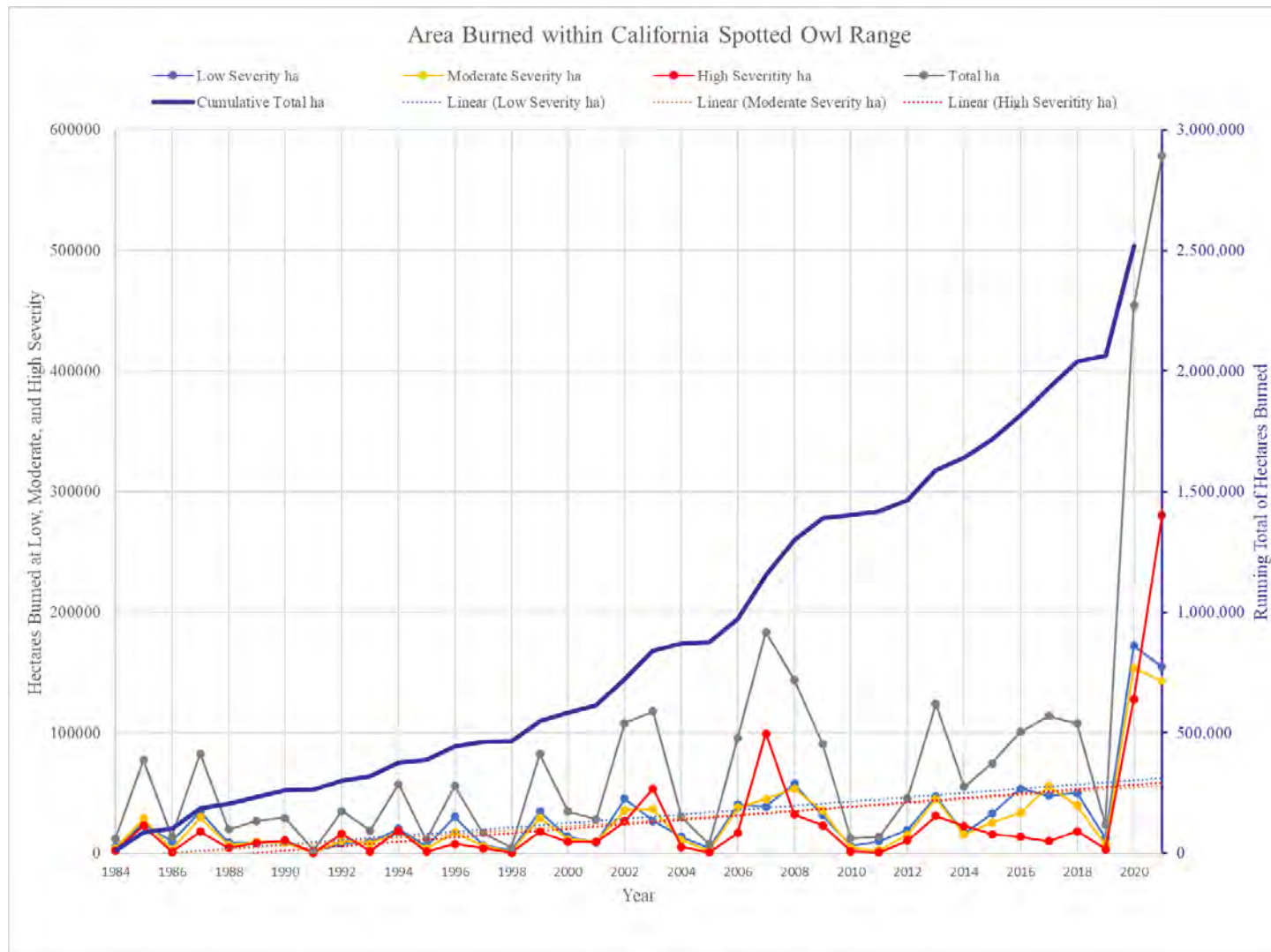


Figure 6: Wildfire area and severity throughout the California spotted owl (CSO) range from 1984–2021. The wildfire severity data from 1984–2020 are from the Monitoring Trends in Burn Severity program (<https://mtbs.gov>) managed by the U.S. Forest Service Geospatial Technology and Applications Center and the U.S. Geological Survey Center for Earth Resources Observation and Science. We used extended survey assessments (i.e., not immediately postfire) for the fire severity calculations. The data for 2021 fires are from Rapid Assessment of Vegetation Condition after Wildfire (<https://burnseverity.cr.usgs.gov/rang/>) managed by the U.S. Forest Service Geospatial Technology and Applications Center to provide a rapid assessment of fire severity based on remotely sensed data. Linear trendlines are displayed for low, moderate, and high severity through time. A running total (with axis on right) displays the running total of area burned within the CSO range.

Wildfire Severity within California Spotted Owl Range

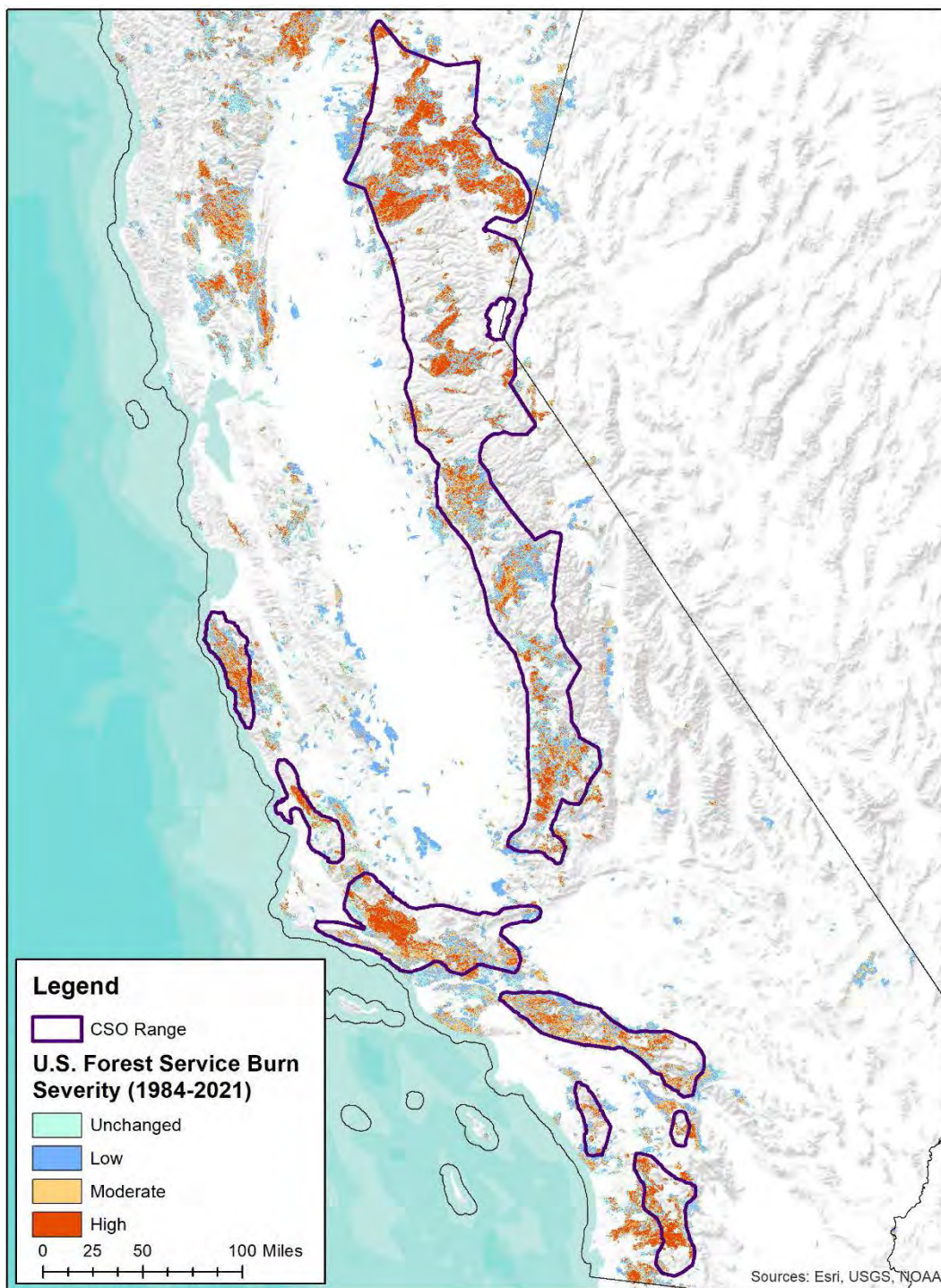


Figure 7: Wildfire location and severity from 1984–2021 within California spotted owl range. The wildfire severity data from 1984–2020 are from the Monitoring Trends in Burn Severity program (<https://mtbs.gov>) managed by the U.S. Forest Service Geospatial Technology and Applications Center and the U.S. Geological Survey Center for Earth Resources Observation and Science. We used extended survey assessments (i.e., not immediately postfire) to present fire severity. The data for 2021 fires are from Rapid Assessment of Vegetation Condition after Wildfire (<https://burnseverity.cr.usgs.gov/ravg/>) managed by the U.S. Forest Service Geospatial Technology and Applications Center to provide a rapid assessment of fire severity based on remotely sensed data.

Table 3: Percentage of CSO range burned at low, moderate, and high severity from 1984 to 2021.

Year	Low Severity (ha)	Moderate Severity (ha)	High Severity (ha)	Total (ha)
1984	0%	0%	0%	0%
1985	0%	0%	0%	1%
1986	0%	0%	0%	0%
1987	1%	0%	0%	1%
1988	0%	0%	0%	0%
1989	0%	0%	0%	0%
1990	0%	0%	0%	0%
1991	0%	0%	0%	0%
1992	0%	0%	0%	1%
1993	0%	0%	0%	0%
1994	0%	0%	0%	1%
1995	0%	0%	0%	0%
1996	0%	0%	0%	1%
1997	0%	0%	0%	0%
1998	0%	0%	0%	0%
1999	1%	0%	0%	1%
2000	0%	0%	0%	1%
2001	0%	0%	0%	0%
2002	1%	1%	0%	2%
2003	0%	1%	1%	2%
2004	0%	0%	0%	0%
2005	0%	0%	0%	0%
2006	1%	1%	0%	1%
2007	1%	1%	2%	3%
2008	1%	1%	0%	2%
2009	0%	1%	0%	1%
2010	0%	0%	0%	0%
2011	0%	0%	0%	0%
2012	0%	0%	0%	1%
2013	1%	1%	0%	2%
2014	0%	0%	0%	1%
2015	1%	0%	0%	1%
2016	1%	1%	0%	2%
2017	1%	1%	0%	2%
2018	1%	1%	0%	2%
2019	0%	0%	0%	0%
2020	3%	2%	2%	7%
2021	2%	2%	4%	9%
TOTAL	17%	15%	15%	47%

California Wildfire Threat

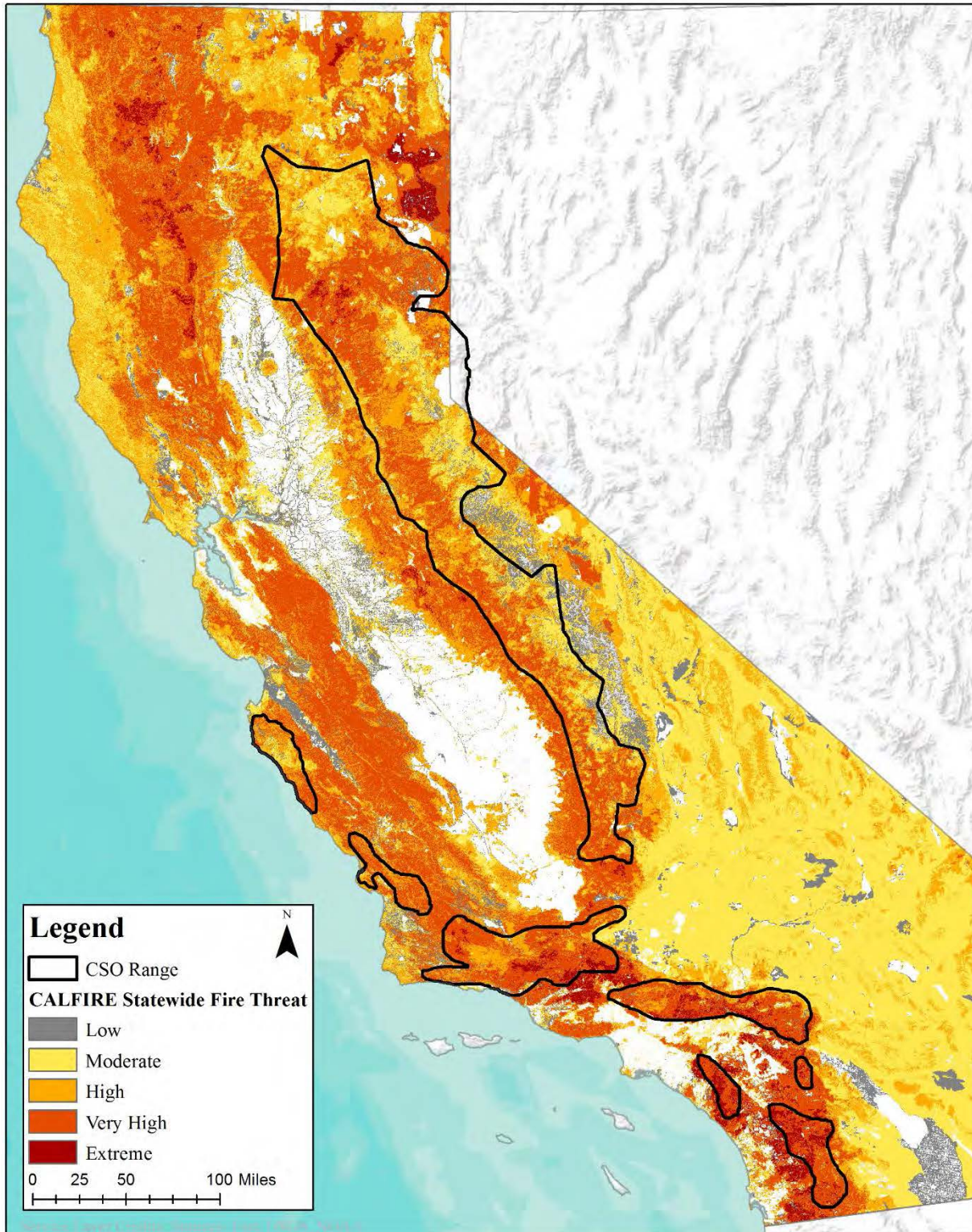


Figure 8: California Department of Forestry and Fire Protection's Fire and Resource Assessment Program statewide wildfire threat map. (<https://frap.fire.ca.gov/mapping/gis-data/>). Wildfire threat shows the potential of a particular area to burn. These data were developed in collaboration with California Department of Forestry and Fire Protection and Pyrologix Inc. using fuel rank data developed in 2005 with fire rotation data updated through 2014.

4.2 Tree Mortality

Widespread increases in tree mortality have been occurring in California due to drought, disease, and bark beetles, above historical levels of mortality (van Mantgem et al. 2009, pp. 521–523; Asner et al. 2015, p. 249; McIntyre et al. 2015, p. 1458; Preisler et al. 2017, p. 166). Drought conditions combined with dense forest conditions have led to severe water stress throughout California (Asner et al. 2015, p. 249; McIntyre et al. 2015, p. 1459; Young et al. 2017, p. 78). Water stress interacts with pathogens, insects, and air pollution to contribute to tree mortality events (Lutz et al. 2009, pp. 2301–2303; McIntyre et al. 2015, p. 1461; Preisler et al. 2017, p. 166). When tree stand densities are too high compared to available resources (water, light, nutrients), trees become stressed due to competition for resources and thus are more vulnerable to mortality (Forest Service 2017, p. 9). Large trees are often more prone to drought, disease, and beetle-related mortality (Smith et al. 2005, p. 266; Mueller et al. 2005, p. 1085; Allen et al. 2010, p. 668; McIntyre et al. 2015, p. 1458). However, it is difficult to quantify how severe the ongoing effects of tree mortality are on CSO and their ability to find habitat with large trees and multi-layered high canopy cover. To further complicate the quantification of impacts from this stressor, tree mortality events can have some positive effects on CSO habitat as they contribute to habitat heterogeneity and the availability of coarse woody debris for prey species. Increased tree mortality may be contributing to a decrease in CSO habitat (Gutiérrez et al. 2017, p. 137), but the magnitude of the impacts on CSO is uncertain. Large-scale tree mortality reduces the availability of the individual CSO need of multi-layered high canopy cover habitat and large trees, potentially then resulting in population declines because of reduced habitat available for dispersal and occupancy.

Between 2010 and 2016, an estimated 102 million trees died across about 3,106,367 ha (7,676,000 ac) throughout California (TMTF 2017, p. 2). By February 2019, total tree mortality in California increased to an estimated 147 million dead trees (CAL FIRE and Forest Service 2019, p. 1). The latest estimate shows that between 2010 and 2021, the drought combined with subsequent beetle attacks resulted in approximately 173 million dead trees in California (Forest Service 2021, p. 5). The tree mortality events are particularly severe in the southern Sierra Nevada area. Most of the tree mortality observed is due to effects from the 2012–2016 drought with less mortality occurring from 2018–2021; however, another drought period started in 2020 (Forest Service 2021, p. 5). Figure 9 presents the Forest Service’s 2017 tree mortality survey and shows dead trees per acre within the CSO range. We are not aware of tree mortality survey information from 2020 or 2022.

In 2015, the California Governor declared a state of emergency due to the unprecedented number of dead and dying trees in the state. In response, the California Tree Mortality Task Force, which is now the Forest Mortality Working Group within the California Wildfire and Forest Resilience Task Force, was created to coordinate emergency protective actions and monitor ongoing conditions. The group collects and manages the tree mortality data, provides recommendations to land managers, presents grants for research funding, and provides public outreach. The task force will likely continue to provide the services listed into the future due to the ongoing and large-scale nature of the tree mortality events in California. The threats that are driving the tree mortality events (drought, disease, and bark beetles) are difficult to manage; therefore, most of the on the ground recommendations involve preventing large-scale high-severity fires, ensuring public health, and

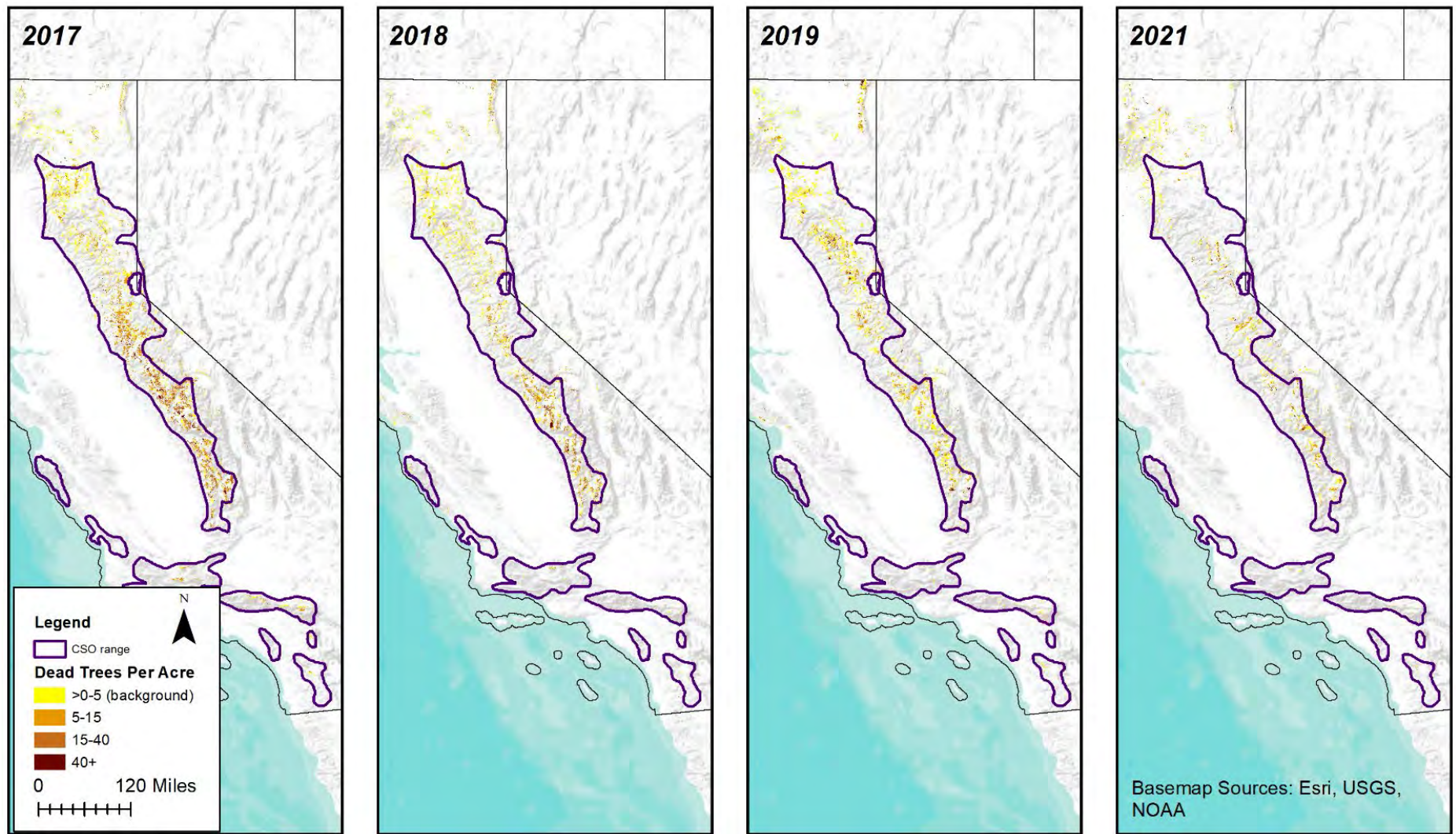


Figure 9: Map portraying tree mortality within California spotted owl range per year. Tree mortality data are from the U.S. Forest Service Tree Mortality Survey 2017-2021 (Forest Service 2021). Data were not available for 2020.

strategizing resilient reforestation. More information about the California Wildfire and Forest Resilience Task Force and their efforts can be found at <https://wildfiretaskforce.org/> (also see Prescribed Fire in section 4.5 Fuels Reductions and Forest Management).

Some regulatory mechanisms and management actions could provide some protection from the effects of tree mortality. Efforts to restore historical forest conditions and reduce stand densities through fuels reduction treatments (mechanical thinning, prescribed fire, etc.) may indirectly contribute to reducing future tree mortality by reducing competition, though these activities cannot completely eliminate future tree mortality. Further, the goal should be to eliminate the excessive levels of tree mortality currently being observed in the landscape and not limit all tree mortality, as tree mortality is a natural part of the forest ecosystem and ultimately creates features important to CSO (snags, tree cavities, etc.). Tree mortality is likely to continue throughout the range of CSO due to predicted increases in drought conditions that will likely continue to weaken trees and make them susceptible to bark beetles and disease (Millar and Stephenson 2015, pp. 823–826; Young et al. 2017, pp. 78, 85). Excessive tree mortality is likely to continue to be a threat into the future for CSO.

4.3 Drought

California has recently experienced extreme drought conditions in 2007–2009, 2012–2016 (Williams et al. 2015, pp. 6823–6824; California Department of Water Resources 2021, p. 4), and as of May 2022 a majority of the CSO’s range is considered in severe to moderate drought (CDWR 2022, <https://cww.water.ca.gov/>). Anthropogenic warming likely contributed to more recent drought anomalies and increases the overall likelihood of extreme droughts in California into the future (Williams et al. 2015, pp. 6819, 6826); CDWR 2022, <https://cww.water.ca.gov/>; see 4.4 Climate Change).

Drought conditions can negatively impact the species ecological needs. As described above, drought conditions contribute to tree mortality, which reduces the CSO habitat component of multi-layered high canopy cover, likely leading to a decline in occupancy. Further, it is likely that drought conditions reduce the availability of prey species (Franklin et al. 2000, p. 589; Glenn et al. 2010, p. 2549, 2011, p. 174). Drought and hot temperatures in the previous summer are linked to lower reproductive success in CSO (LaHaye et al. 2004, p. 1066) and lower survival and recruitment in northern spotted owls in the next breeding season (Glenn et al. 2011, pp. 159, 174). Inversely, increases in precipitation either before or after the nesting season are linked to increased survival and fecundity in all three subspecies of spotted owls (Seamans et al. 2002, p. 321; LaHaye et al. 2004, pp. 1056, 1064; Glenn et al. 2011, pp. 159, 174). Thus, drought likely negatively impacts CSO habitat components, and demographic needs of dispersal, survival, fecundity, and occupancy. There are no regulatory mechanisms or conservation measures in place to ameliorate the direct impacts of drought to CSO. It is likely that drought conditions will continue to be a threat into the future across the CSO range, and will likely worsen, due to the effects of climate change.

4.4 Climate Change

Our analyses include consideration of ongoing and projected changes in climate. The terms “climate” and “climate change” are defined by the Intergovernmental Panel on Climate Change (IPCC). The term “climate” refers to the mean and variability of different types of weather

conditions over time, with 30 years being a typical period for such measurements, although shorter or longer periods also may be used (IPCC 2013a, p. 1450). The term “climate change” thus refers to a change in the mean or variability of one or more measures of climate (for example, temperature or precipitation) that persists for an extended period, typically decades or longer, whether the change is due to natural variability, human activity, or both (IPCC 2013a, p. 1450).

Scientific measurements spanning several decades demonstrate that changes in climate are occurring and that the rate of change has been faster since the 1950s. Examples include warming of the global climate system, substantial increases in precipitation in some regions of the world, and decreases in other regions (for these and other examples, see (Solomon et al. 2007, pp. 35–54, 82–85; IPCC 2013a, pp. 3–29, 2014, pp. 2–8). The IPCC characterizes warming of the global climate system as “unequivocal” (IPCC 2013b, p. 2), and reports that human influence has been detected in warming of the atmosphere and ocean, changes in the global water cycle, reductions in snow and ice, global mean sea level rise, and changes in some climate extremes (IPCC 2013b, pp. 15, 17, Figure SPM.6, Tabel SPM.1). Results of scientific analyses presented by IPCC show that most of the observed increase in global average temperature since the mid-20th century cannot be explained by natural variability in climate, and is “extremely likely” (defined by the IPCC as 95% or higher probability) that this change is due to the observed increase in greenhouse gas concentrations in the atmosphere as a result of human activities (Solomon et al. 2007, pp. 21–35; IPCC 2013b, pp. 2, 15, Figures SPM.4, SPM.5, SPM.6).

Scientists use a variety of climate models, which include consideration of natural processes and variability, as well as various scenarios of potential levels and timing of greenhouse gas emissions, to evaluate the causes of changes already observed and to project future changes in temperature and other climate conditions (Meehl et al. 2007, p. entire; Ganguly et al. 2009, pp. 15555, 15558; Prinn et al. 2011, pp. 527, 529). All combinations of models and emissions scenarios yield very similar projections of increases in the most common measure of climate change, average global surface temperature (commonly known as global warming), until about 2030. Although projections of the magnitude and rate of warming differ after about 2030, the overall trajectory of all the projections is one of increased global warming through the end of this century, even for the projections based on scenarios that assume that greenhouse gas emissions will stabilize or decline. Thus, there is strong scientific support for projections that warming will continue through the 21st century, and that the magnitude and rate of change will be influenced substantially by the extent of greenhouse gas emissions (Meehl et al. 2007, pp. 760–764, 797–811; Ganguly et al. 2009, pp. 15555–15558; Prinn et al. 2011, pp. 527, 529; IPCC 2013b, pp. 19–23). See IPCC 2013b (entire), for a summary of other global projections of climate-related changes, such as frequency of heat waves and changes in precipitation.

Climate projections at the global scale are informative, and, in some cases, the only scientific information available for us to use. However, projected changes in climate and related impacts can vary substantially across and within different regions of the world (IPCC 2013b, pp. 15–16). Therefore, we use “down-scaled” projections when they are available and have been developed through appropriate scientific procedures, because such projections provide higher resolution information that is more relevant to spatial scales used in the analyses of a given species (see (Glick et al. 2011, pp. 58–61) for a discussion of downscaling).

Downscaled climate projections were completed for different regions of California for California's Fourth Climate Change Assessment, including the following four regional assessments that cover the range of CSO: Sierra Nevada (Dettinger et al. 2018, p. entire), Central Coast (Langridge 2018, p. entire), Los Angeles (Hall et al. 2018, p. entire), and San Diego (Kalansky et al. 2018, p. entire). Ten global climate models were used for all four regional assessments and each model considered two different emissions scenarios, one in which greenhouse gas emissions continue to increase into the next century (RCP 8.5) and one in which greenhouse gas emissions stabilize by mid-century and then decline to levels seen in the 1990s by the end of the century (RCP 4.5) (Dettinger et al. 2018, pp. 15, 17; Hall et al. 2018, p. 9; Kalansky et al. 2018, p. 18; Langridge 2018, p. 12).

Under both emissions scenarios, projected annual average temperatures throughout the CSO range are projected to increase. Annual average temperatures in the Sierra Nevada Region, which includes the entire Sierra Nevada Mountain Range, are projected to increase approximately 4–5°F by mid-century (2036–2065) and 5–7°F by the end of the century (2070–2099) under RCP 4.5, and 6°F by mid-century and 9–10°F by the end of the century under RCP 8.5 (Dettinger et al. 2018, pp. 15, 17, Figure 2.1). The largest increases under both emissions scenarios and timeframes are projected for the eastern portions of the Sierra Nevada (Dettinger et al. 2018, pp. 17, Figure 2.3). Projected changes will result in greater temperatures than historically experienced in the Sierra Nevada and this degree of temperature change will likely result in a shift in the rain to snow transition by 1,500–3,000 feet (Dettinger et al. 2018, pp. 17, 20).

Throughout the Central Coast Region, which includes portions of San Benito, Santa Cruz, San Luis Obispo, Monterey, Santa Barbara, and a small portion of northern Ventura counties, projected annual average maximum and minimum temperatures are expected to increase under both emissions scenarios. The annual average maximum temperature under RCP 4.5 is projected to increase 3.5–4.5°F by mid-century (2040–2069) and 4.5–5.5°F by the end of the century (2070–2099), with increases under RCP 8.5 at 4.5–5.5°F by mid-century and 7–8°F by the end of the century, (Langridge 2018, pp. 13, Table 2). Annual average minimum temperatures are expected to increase 3.5–4.5°F by mid-century and 4.5–5°F by the end of the century under RCP 4.5, and 4.5–5°F by mid-century and 7–8°F by the end of the century under RCP 8.5 (Langridge 2018, pp. 14, Table 3). Projected temperature increases are more pronounced in the inland portions of the Central Coast Region with the ocean acting as a buffer for coastal areas (Langridge 2018, pp. 14, Figure 4). In addition, the average number of extremely hot days (defined as days that exceed the 98th percentile of observed, historical (1961-1990) daily maximum temperatures between April 1 and October 31) are expected to increase throughout the Central Coast Region, with counties in the CSO range projected to experience between approximately 2 and 4.5 times as many extremely hot days under RCP 4.5 and between 2.5 and 6.5 times as many extremely hot days under RCP 8.5 by mid-century (historical average number of days is 4.3). By the end of the century, the number increases to 4 to 6 times as many extremely hot days under RCP 4.5 and between 7.5 and 11.5 times as many extremely hot days under RCP 8.5 (Langridge 2018, pp. 14–15, Table 4).

Regional assessments covering southern California include the Los Angeles Region, which includes Ventura, Los Angeles, Orange and portions of San Bernardino and Riverside counties, and the San Diego Region, which covers San Diego County (Hall et al. 2018, p. entire; Kalansky et al.

2018, p. entire). Projected annual average maximum temperatures throughout the Los Angeles Region increase under both emissions scenarios, with increases of 4.2°F by mid-century (2040–2069) and 5.3°F by the end of the century (2070–2100) under RCP 4.5 and increases of 5.7°F and 8.4°F by mid-century and end of the century under RCP 8.5, respectively (Hall et al. 2018, pp. 10, Figure 2).

For the San Diego Region, projected annual average maximum and minimum temperatures increase under both emissions scenarios. By mid-century (2040–2069), annual average maximum and minimum temperatures are projected to increase by approximately 4–5°F and 5–6°F under RCP 4.5 and RCP 8.5, respectively. By the end of the century (2070–2100), the annual average maximum and minimum temperatures under RCP 4.5 are projected to increase 4–6°F, with increases under RCP 8.5 at 7–9°F (Kalansky et al. 2018, pp. 19, Figures 2 and 3). In addition, by the end of the century the average hottest day is projected to increase 4–7°F under RCP 4.5 and 7–10°F under RCP 8.5 for both southern California climate change assessment regions (Hall et al. 2018, pp. 11, Figure 4; Kalansky et al. 2018, pp. 21, Figure 6). Similar to the Central Coast, these changes will be more pronounced in the interior portions of the Los Angeles and San Diego Regions (Hall et al. 2018, pp. 11, Figure 3).

In addition to temperature projections, the regional assessments for California’s Fourth Climate Change Assessment also considered future changes in precipitation, both the amount and the timing. Within the Sierra Nevada Region, changes in precipitation are projected to be relatively small and will vary depending on the area. In general, average annual precipitation in the southern portion of the Sierra Nevada Region is projected to stay similar or decrease by 5%, regardless of emission scenario. In other portions of the Sierra Nevada Region, particularly along the eastern side, the amount of precipitation is projected to increase by up to 10%. In addition to projections showing northern portions of the range will receive more precipitation than southern portions, areas at higher elevations are also more likely to receive an increase in precipitation. One area in eastern Plumas County at approximately 6,000 feet elevation, just south of Honey Lake, has projected increases of 25% under RCP 8.5 (Dettinger et al. 2018, pp. 5, 18, 20, Figure 2.1); however, this larger projected change is in a very small area relative to the rest of the Sierra Nevada Region. Although the average change in precipitation is projected to be small, the models show there will be an increase in extreme conditions with more dry days overall interspersed with higher intensity precipitation events, when they do occur (Dettinger et al. 2018, p. 19). Further, in some areas more precipitation will fall as rain instead of snow as the rain to snow transition is projected to shift by 1,500–3,000 feet (Dettinger et al. 2018, pp. 17, 20).

Similar to the Sierra Nevada Region, interannual variability within the Central Coast Region is expected to increase with more dry days overall, but more precipitation when rain events do occur (Langridge 2018, p. 16). Under RCP 4.5, average annual precipitation is expected to increase 1–2 inches under both time periods (i.e., mid-century and end of century) in Monterey, San Luis Obispo, and Santa Barbara counties, the three counties in which the species occurs (Langridge 2018, pp. 16, Table 6). Under RCP 8.5, average annual precipitation is expected to increase by 1.5–2 inches by mid-century and by 4–5 inches in those same counties by the end of the century (Langridge 2018, pp. 16, Table 6).

In southern California, the amount of precipitation in the Los Angeles and San Diego Regions is highly variable (Hall et al. 2018, pp. 12, Figure 5; Kalansky et al. 2018, p. 24). Projections for the Los Angeles Region do not agree whether changes will be negative or positive, likely because the Los Angeles Region lies between an area that is projected to be wetter (northern mid-latitude) and an area projected to be drier (southern sub-tropics), although there is agreement the overall changes will be small (Hall et al. 2018, p. 13). Similar to other regions, projections for the Los Angeles and San Diego Regions show an increase in extreme conditions such as high intensity precipitation events, known as atmospheric rivers, and severe drought conditions (Hall et al. 2018, pp. 13–14, Figure 6; Kalansky et al. 2018, pp. 24–25, Figures 7 and 9).

Because CSO has such a wide geographic range and the changes in climate vary across the range, the effects those changes will have on the species and its habitat will vary. Future climate projections of Sierra Nevada vegetation distribution indicate that low- and mid-elevation forests are vulnerable to conversion to unsuitable habitat for CSO, such as shrublands and grasslands (Gutiérrez et al. 2017, p. 215). These changes in climate may also include potential shifts in forest communities upslope, which would have impacts on both CSO habitat and prey habitat (Gutiérrez et al. 2017, pp. 132, 215, 288). This potential upslope shift in suitable habitat may mitigate some climate-induced habitat threats over ecological time, although it would require many decades for suitable large nest trees to develop in areas where they do not currently exist (Gutiérrez et al. 2017, p. 215). These differences in net habitat loss versus net habitat gained under future climate scenarios will likely depend upon not only the rate of warming but also how individual plant and prey species respond (Seamans and Gutiérrez 2007a, p. 61).

Changing climatic conditions may have direct impacts on CSO physiology, survival, reproduction, recruitment, or population growth. The thermal neutral zone (i.e., the range of temperatures tolerated by a warm blooded animal) for CSO is 18.2–35.2 degrees Celsius (64.8–95.4 degrees Fahrenheit) (Weathers et al. 2001, p. 682). Above the thermal neutral zone, CSO experience heat stress which negatively affects the physiology of an individual (Weathers et al. 2001, p. 678). The relatively low thermal neutral zone may make CSO more susceptible to increased temperatures or cause behavioral or habitat shifts to cooler microclimates on the landscape. Behaviorally, CSO do show the capacity to select cooler microclimates for roosting, especially within warmer forest stands (McGinn et al. in review, p. 2). Changing climatic conditions may also have indirect impacts including changes in habitat and prey distribution, abundance, and quality. CSO must be able to adjust to the changing climate through behavioral changes, spatial shifts, or adaptation in order to persist. Under projected warming conditions in the future, cooler microclimate refugia are likely to be critically important for the persistence of CSO individuals and populations (McGinn et al. in review, p. 3). It is likely that climate change will reduce the quantity and quality of CSO habitat, which would likely result in population impacts including a decrease in dispersal, fecundity, and occupancy. Both the habitat components and demographic factors of CSO will likely be impacted by climate change, but the full extent of impacts climate change may have on CSO are poorly understood (Wan et al. 2018, p. 690).

Climate modeling specific to the central Sierra Nevada portion of the CSO range has shown that maintaining high canopy cover, especially at higher elevations, will be important for CSO to persist into the future as it helps maintain future refugia for individuals to select for cooler

microclimates (Jones et al. 2016b, entire). (Jones et al. 2016b, p. 901) shows the change in CSO occupancy probability for different climate change scenarios with different forest management strategies for canopy cover. Under both a low climate change prediction scenario (RCP 2.6) and a high climate change scenario (RCP 8.5), CSO occupancy decreases in comparison to baseline climate conditions (Jones et al. 2016b, p. 901). However, it is important to note that this model did not consider projected increases in frequency and size of high-severity fires due to climate change, which would likely result in more significant declines in occupancy than predicted by the model (Jones et al. 2016b, p. 903). Earlier modeling of spotted owl response to projected climate changes show that different subspecies and populations of spotted owls are anticipated to respond differently across the species range (Peery et al. 2011, p. 14).

The climate change projections described above suggest increasing interannual climate variability throughout the range of CSO. Interannual climate variability is defined as when annual weather patterns differ from historical average climate, including prolonged drought conditions, heavy rain conditions, and higher or lower than average temperatures. Interannual climate variability has been shown to have impacts on the survival and reproductive success of CSO. Drought conditions and hot temperatures during the summer have been found to reduce fecundity the next breeding season in CSO (LaHaye et al. 2004, p. 1056). Increases in precipitation either before or after the nesting season are linked to increased survival and fecundity, whereas increased precipitation during the nesting season reduces reproductive success (North et al. 2000, p. 804; LaHaye et al. 2004, pp. 1056, 1064). It is hypothesized that northern spotted owls exhibit a bet-hedging reproduction strategy and an absence of reproduction is linked to environmental conditions (Franklin et al. 2000, pp. 539, 576). California spotted owls likely have a similar bet-hedging reproductive strategy (Stoelting et al. 2015, p. 46; Gutiérrez et al. 2017, pp. 14–15). California spotted owls are sensitive to warm temperatures and therefore may be physiologically sensitive to weather patterns with increased temperatures (Weathers et al. 2001, p. 684). Temperature, either too hot or too cold, may affect spotted owls directly by increasing energy demands (Gutiérrez et al. 2017, p. 20). This may have direct impacts on the physiology of spotted owls or on breeding if mates must bring more food to the nest for the female to survive. Increased interannual climate variability due to climate change will likely impact CSO throughout the range, which would result in lower fecundity.

Regulatory mechanisms and management actions that are or could potentially provide some protection from the effects of climate change include the Clean Air Act and the California Global Warming Solutions Act. Both address climate change by reducing greenhouse gas emissions within the United States and California, respectively. There are no regulatory mechanisms or management actions that fully address the effects of the climate change. For more information on the Clean Air Act and the California Global Warming Solutions Act, see 4.9 Regulatory Mechanisms and Management Actions.

The effects of climate change will continue to impact CSO into the future by exacerbating the negative influencing factors described above, especially extreme weather events such as prolonged drought and severe storms. The loss and/or reduction of suitable habitat throughout the CSO range and will likely reduce reproduction, occupancy, survival, recruitment, and population growth.

4.5 Fuels Reductions and Forest Management

Forest management has long been a controversial topic regarding species that require old growth forest habitat, including the spotted owl (Gutiérrez 2020, p. 337). With the increasing frequency and extent of high-severity fire in California in recent decades, the focus on fire mitigation has become a key issue for spotted owl management and conservation. While spotted owls are adapted to a natural fire regime (Verner et al. 1992, pp. 247–248; Stephens et al. 2019, p. 394), CSO are poorly adapted to the conditions created by large-scale high-severity fires (Jones et al. 2020b, 2021b, p. 5) that have negative effects on both CSO and their habitat (see section 4.1 Wildfire, above). The goal of fuels management is to reduce the buildup of fuels in forests that contribute to these large-scale high-severity fires, which can effectively mitigate subsequent fire behavior and their effects, even under extreme weather (Hessburg et al. 2021, p. 7; Prichard et al. 2021, p. 9). Fuels management may also help bring treated areas closer to the natural range of variation of forest structure and fire severity (Tubbesing et al. 2019, p. 52). Modeling suggests that the long-term benefits of properly managed fuel treatments for reducing the risk of severe wildfire are likely to outweigh the short-term negative impacts to spotted owl habitat (Ager et al. 2007, pp. 54–55; Roloff et al. 2012, p. 7; Jones et al. 2021a, pp. 4–5). These trade-offs are complex and ultimately depend on the extent that treatments alter owl habitat and the magnitude of effects from subsequent wildfires (Jones et al. 2021a, p. 2). Fuels reductions and forest management practices vary throughout the CSO range. In this section we discuss clearcutting, mechanical thinning, salvage logging, and prescribed fire, and the positive and negative influences that these practices can have on the species.

Clearcutting

Clearcutting, sometimes referred to as even-aged management, is defined as an even-age regeneration or harvest method that removes all trees in the stand, producing a fully exposed microclimate for the development of a new age class in one entry (Gutiérrez et al. 2017, p. 292). The natural range of variation for forest gaps in the Sierra Nevada has been found to range from 0.03–1.17 ha (0.07–2.89 ac) (Safford and Stevens 2017, p. 140), and within this SSA Report, clearcutting refers to complete removal greater than the natural range of variation.

Clearcutting is a mostly historical threat to CSO, although it still occurs in some areas of the Sierra Nevada portion of the range. By removing entire stands of trees, clearcutting reduces the amount of large trees, high canopy cover, and coarse woody debris available for CSO. Commercial timber harvest no longer occurs within CSO range in southern California on public lands (Gutiérrez et al. 2017, p. 254). Clearcutting also does not occur on National Forest Service lands on the eastern side of the Sierra Nevada range (Boatner in litt 2018.). Clearcutting prescriptions were incorporated into forest management on Forest Service lands within the CSO range in the 1970s and continued up until the 1990s (Gutiérrez et al. 2017, p. 111). Clearcutting over this time period likely reduced the amount of available CSO habitat. Since the release of the 1992 “California Spotted Owl: Technical Assessment of Its Current State” report (Verner et al. 1992), clearcutting has significantly decreased to a minimal amount on Forest Service land (Gutiérrez et al. 2017, pp. 111–117). Clearcutting still occurs on private timber harvest lands but is limited to 8.1-ha (20-ac) parcels by California state forest practice rules (14 CCR 913). Additionally, there must be at least 91.44 m (300 ft) of forested area between clearcuts, and adjacent lands cannot be cut for at least 5 years (14 CCR 913). Even with the reduction of clearcutting in recent history, it will take decades or centuries for

large trees to grow back from the past removal practices; therefore, there are residual effects that may be impacting CSO populations and the habitat that is available (Jones et al. 2018, p. 1). There is evidence that CSO may use clearcut habitat, likely for foraging activities, but these areas were used significantly less than high canopy cover and large tree areas (Atuo et al. 2019, pp. 295, 301–302). Further, there is evidence of negative impacts from clearcutting to northern spotted owl, including decreased dispersal and decreased use of clearcut areas (Forsman 1980, pp. 4, 52–53, 83–85; Forsman et al. 1984, pp. 25, 54; Carey et al. 1990, p. 11; Bart and Forsman 1992, p. 95; Miller et al. 1997, pp. 140, 145–148).

Mechanical Thinning

Mechanical thinning is a forest management strategy to thin trees either in even or uneven-aged stands by removing trees in rows, strips, or by using fixed spacing intervals, usually implemented to meet forest management objectives. It can be done for commercial harvest of trees or to reduce fuel loads to decrease the likelihood of large-scale high-severity fires (Gutiérrez et al. 2017, p. 292). Within this SSA Report, we use “mechanical thinning” to include both individual tree selection (new age classes are created in uneven-aged stands by removing individual trees of all size classes more or less uniformly throughout the stand to achieve desired stand structure) and group tree selection (treatment involves salvage harvest in a stand where small groups of trees are harvested because of tree mortality due to windstorm, wildfire, insects, disease, or other animals). Mechanical thinning can occur from below, where trees are removed from the lower canopy leaving large trees to occupy the site, or from above (crown thinning), which reduces crowding within the main canopy.

Mechanical thinning is actively used to manage forests occupied by CSO and can have positive or negative impacts on CSO habitat and demographics depending on the specific methods used. The Forest Service’s 2004 Sierra Nevada Forest Plan Amendment promotes reducing unnaturally dense forest conditions on the landscape to reduce the risk of large-scale high-severity fire, which can involve mechanical thinning (Forest Service 2004, pp. 34–35) (see 4.9 Regulatory Mechanisms and Management Actions for more information on Forest Plans). Minimal area is treated mechanically, especially when compared to area burned by wildfire (i.e., 1.4 million acres burned between 2017–2020 versus 152,842 acres previously treated; North et al. 2021, p. 524). Treatments are located to avoid CSO activity centers to the greatest extent possible (Forest Service 2004, pp. 34–35), which often leaves the PACs untreated and potentially vulnerable to stand-replacing fires (Stephens et al. 2019, p. 395). Further, researchers recommend that strategic thinning can promote forest resiliency, but removing some large, fire-intolerant tree species like fir and cedar may be necessary to promote future resilience of forested habitat (Stephens et al. 2020, p. entire; North et al. 2021, p. 530). Resilience of CSO habitat results from low stand densities, which reduces competition and allows trees to grow, so more intensive fuels treatments (mechanical thinning and prescribed fire) may be needed to achieve historically lower levels of tree densities (North et al. 2022, p. 6). When conducted outside CSO activity centers, mechanical thinning will likely reduce the amount of damage their habitat may experience due to high-severity fire while also minimizing short-term habitat impacts (Stephens et al. 2014, p. 904; Tempel et al. 2015, p. 1; Chiono et al. 2017, p. 1). Strategic mechanical thinning to reduce fuel loads and reduce the risk of large-scale high-severity fire, while also maintaining the necessary forest structure components of large trees, multi-layered high canopy cover, forest heterogeneity, and coarse woody debris, will be important for CSO

management into the future (Jones et al. 2016a, p. 305, 2019, p. 22; Tempel et al. 2016, p. 305). Strategically placed landscape fuel treatments can decrease future fire severity while also increasing seedling densities (Tubbesing et al. 2019, p. 54). Many studies emphasize the importance of scaling up fuel reduction treatments (mechanical thinning and prescribed fire) and suggest an increased benefit of treating within CSO territories for long-term persistence, though positive effects would not be observed until mid-century and treatments should still strive to maintain large trees and high canopy cover forest (Jones et al. 2021a, p. 3; Safford et al. 2022, p. 17).

This fuels management technique has little to no impact on occupancy if carried out in a strategic way; for example, maintaining some patches of high canopy cover mixed with patches of moderate canopy cover to provide for the primary habitat of CSO and incorporating limited operating periods that restricts activities from occurring during the critical nesting period (Tempel et al. 2016, p. 747). However, other studies have found that mechanical thinning can decrease CSO occupancy and is negatively correlated with reproduction (Tempel et al. 2014a, p. 2089, 2022, p. 19; Stephens et al. 2014, p. 903). Though Tempel et al. (2022, p. 22) detected some negative effects of fuels reduction treatments on CSO in southern California, they posit that occupancy declines were small compared to the potential negative effects of fire. Similarly, there is evidence of reduced foraging in fuel treatment areas that have a moderate to high proportion of forest gaps with little to no canopy cover (Gallagher et al. 2018, pp. 487, 494–499). Forest thinning has complex effects on both CSO and their mammalian prey species. Thinning may have negative short-term effects on prey species by increasing the risk of predation by removing above-ground cover, reducing canopy connectivity, and by removing suitable nesting substrates; however, there may be positive effects in the long-term (over decades) by promoting growth of the midstory layer of trees that is favorable to certain mammalian prey species (Wilson and Forsman 2013, p. 79).

Salvage Logging

Salvage logging is a practice where damaged or dying trees are removed to recover their economic value and promote forest health (Gutiérrez et al. 2017, p. 293; Jones et al. 2020a, p. 11). Salvage logging often occurs after natural disturbances such as wildfires, disease, and insect infestation (Lindenmayer et al. 2008, p. 4). Post-fire fuels treatment that includes the removal of smaller trees and surface and ladder fuels is not generally considered a threat to CSO relative to the threat posed by megafires (Jones et al. 2021a, p. 7). Negative effects of salvage logging have been documented for wildlife, vegetation, and soils but there is a paucity of literature which may lead to inaccurate comparisons when studies occur across varied geographic regions; nevertheless, the negative effects may be mediated by altering equipment, timing of operations, and harvest prescriptions to leave more large snags (Nemens et al. 2019, p. entire). California spotted owls have been found to inhabit areas of low-medium severity fire, patchy high-severity fire, and areas with dead trees; therefore, salvage logging likely reduces the amount of habitat available for CSO (Gutiérrez et al. 2017, p. 276). Salvage logging can result in short term decreased vegetation regrowth (Wagenbrenner et al. 2015, p. 176), which would likely impact prey species for CSO. However, salvage logging does not appear to make much difference in long term vegetation regrowth, so salvage logged areas have the potential to again become suitable habitat after the centuries it takes to establish large trees in the area (Peterson and Dodson 2016, p. 56). Salvage logging in certain instances may also be necessary to reduce future fire severity as high levels of dead

biomass were associated with high severity fire (Lydersen et al. 2019, p. 7; Stephens et al. 2022, p. 8) and for restoration personnel to safely access an impacted site for re-planting activities (Sawyer in litt. 2022).

California spotted owl response to salvage logging appears to be at least partly dependent on the characteristics of the fire after which it occurs, which can make it difficult to analyze these relationships (detailed in (Jones et al. 2019)). For example, salvage logging that occurs within a large, burned area is less likely to negatively impact spotted owls relative to salvage logging that occurs within a smaller burned area (Jones et al. 2020a, p. 12). There is some evidence that northern spotted owl (Clark et al. 2012, p. 15) and CSO occupancy decreases with salvage logging (Lee et al. 2013, p. 1327; Lee and Bond 2015, p. 228; Hanson and Chi 2021), while other evidence suggests that salvage logging has no effect on CSO persistence or colonization (Jones et al. 2021a, p. 5). Salvage logging can be a threat to CSO when their habitat components of large trees, coarse woody debris, and forest heterogeneity are removed from the landscape, resulting in a decrease in occupancy at the population level. The Forest Service's 2004 Sierra Nevada Forest Plan Amendment prohibits salvage harvest in CSO PACs unless a biological evaluation determines that the areas proposed for harvest have been rendered unsuitable for the purpose they were intended (i.e., CSO habitat) by a catastrophic stand-replacing event (Forest Service 2004, pp. 52–53) (see 4.9 Regulatory Mechanisms and Management Actions for more information on Forest Plans).

Prescribed Fire

Prescribed fire or cultural burning as a tool for ecosystem management had been used for millennia by Native Americans prior to the colonization of North America by Europeans who introduced a culture of fire suppression onto the landscape (Marks-Block et al. 2021, p. 3). Wildfire suppression is still the dominant management practice over prescribed or controlled burning across much of western North America (Stephens et al. 2019, p. 391). Between 2017 and 2020, approximately 120,000 acres per year were treated with prescribed burning across federal, state, and tribal lands in California (Gabbert 2022, p. entire). The state of California recently released a report outlining a plan to increase the use of “beneficial fire” to 400,000 acres annually by 2025 (California Wildfire and Forest Resilience Task Force 2022, p. 3). Spotted owls can persist in low- and moderate-severity fire areas with similar probabilities to unburned landscapes (Roberts et al. 2011, p. 617), demonstrating their adaptation to a natural fire regime (Verner et al. 1992, pp. 247–248; Stephens et al. 2019, p. 394). However, studying the relationship between spotted owls and prescribed fire alone is difficult because there are usually confounding factors of past timber harvest and/or salvage logging (Clark et al. 2012, p. 15). Prescribed “ecologically beneficial” fire is an important tool protecting nesting and roosting habitat from catastrophic fires and for maintaining diverse CSO habitat throughout the landscape (Roberts et al. 2011, p. 617; Stephens et al. 2019, p. 394).

Summary of Fuels Reductions and Forest Management

Fuels reductions and forest management practices within the CSO range include clearcutting, mechanical thinning, salvage logging, and prescribed fire. Depending on the method used and how it is implemented, fuels reductions and forest management practices can have both positive and negative influences on the species. There are no regulatory mechanisms or conservation

measures that completely ameliorate the negative impacts of fuels reductions and forest management practices to CSO; land management direction including the Sierra Nevada Forest Plan Amendment include protective standards and guidelines that must be adhered to while conducting management activities in CSO habitat (see 4.9 Regulatory Mechanisms and Management Actions). Available information suggests that fuels reduction in some form is necessary to ensure CSO habitat persistence because long-term gains in habitat protection outweigh the short-term negative effects, especially when conservation measures are implemented appropriately (Jones et al. 2021b, p. 2, a, p. entire; North et al. 2022, p. entire; Safford et al. 2022, p. entire). Differences in forest management may help explain why CSO populations occurring in some mixed ownership landscapes have higher occupancy, density, and probability of reproduction compared to public land (Roberts et al. 2017, p. 113; Hobart et al. 2019, p. 198; SPI 2022, pp. 9, 17). The need to increase the pace and scale of fuels reduction efforts is recognized across agencies and recently, the Department of the Interior announced funding through the Bipartisan Infrastructure Law to increase fuels treatments across the United States (DOI 2022, entire). The Forest Service also identified preliminary projects to address fuel reduction projects through the “Wildfire Crisis Landscape Investments,” and two projects are expected in the near-term within the CSO range that include mechanical thinning and prescribed fire (Tahoe National Forest and the Stanislaus National Forest; (Forest Service 2022a, p. entire). Fuels reductions and forest management practices will likely continue to have varied effects on CSO throughout the species’ range.

4.6 Competition and Hybridization with Barred Owls

The barred owl (*Strix varia*) is a closely related species to the spotted owl, native to eastern North America (Mazur and James 2000, “Introduction” Section). Since the 1960s, the barred owl has been extending its range westward, first coming in contact with northern spotted owls and more recently moving into the CSO range (Peterson and Robins 2003, p. 1162; Livezey 2009, p. 49; Keane et al. 2018, p. 5). Long and Wolfe (2019, p. 1282) includes a figure with panels demonstrating the range of barred owls from their historical range into western North America, with progression into the ranges of northern, California, and Mexican spotted owls. The barred owl range completely overlaps the northern spotted owl range (Wiens et al. 2020, p. 1), and much of the CSO range (Keane et al. 2018, p. 38). Relevant to CSO, barred owls were first detected in northwestern California in 1982 (Evens and LeValley 1982, p. 890), the Sierra Nevada in 1991 (Dark et al. 1998, p. 53), and along the coast as far south as Marin County in California by 2002 (Jennings et al. 2011, p. 105). Barred owls and spotted owls have similar habitat requirements, with old forests representing high-quality habitat for both, although barred owls use a broad mix of forest types (Wiens et al. 2014, pp. 14, 32). Because barred owls have more habitat flexibility than spotted owls, there is potential for barred owls to expand into spotted owl habitat through corridors of lower-quality habitat. For example, there are recent barred owl sightings from Davis, California (ebird.org, accessed 14 April 2022), suggesting barred owls could expand into CSO habitat from the west in addition to the more likely pathway through forests in the Sierra Nevada. Although the CSO range has a gap between the Sierra Nevada and southern California, barred owls may be able to colonize the southern California CSO range because of their ability to use other forest types. Detections of barred owls in coastal forests in the Santa Cruz Mountains in San Mateo County, California (ebird.org, accessed 14 April 2022), an area notably absent within the CSO range (see 2.2

Geographic Distribution), suggests a pathway towards connectivity to the coastal CSO portion of the range.

Barred owls are aggressively outcompeting and displacing spotted owls on the landscape (Wiens et al. 2014, p. 1; Gutiérrez et al. 2017, p. xvi; Long and Wolfe 2019, entire). Barred owls are larger than spotted owls (Gutiérrez et al. 2007, pp. 185–186) and behaviorally dominant (Van Lanen et al. 2011, pp. 2197–2198). Although diet overlaps between the two species, with both predominantly feeding on nocturnal mammals, barred owls are generalists that consume many more prey species in comparison to spotted owls (Wiens et al. 2014, pp. 24–25; Kryshak et al. 2022, pp. 12–13). Competition between the two species results in negative effects to the survival, productivity, and recruitment of northern spotted owls (Dugger et al. 2016, pp. 69–91) and barred owls have been described as demographically superior to northern spotted owls because they have higher survival estimates and produced on average 4.4 times more young than northern spotted owls over a 3-year study period (Wiens et al. 2014, p. 28). The presence of barred owls has caused lower detection rates and occupancy probabilities in northern spotted owls (Olson et al. 2005, p. 918; Crozier et al. 2006, p. 760; Kroll et al. 2010, p. 1264; Yackulic et al. 2012, p. 1953, 2014, p. 265). Although there is some evidence that lower detection rates may be in part due to northern spotted owls responding less frequently in the presence of barred owls (Crozier et al. 2006, p. 760), the negative effects of barred owls on spotted owls are clear. Although there is no evidence of barred owls wounding or killing northern spotted owls (Wiens et al. 2014, p. 33), competition ultimately has population-level effects because of impacts to occupancy and reproduction. Additionally, barred owls can hybridize with spotted owls (Gutiérrez et al. 2017, p. 211). There are likely broader impacts on the ecosystem of the barred owl range expansion such as an imbalance in predator/prey relationships, causing even greater impacts to spotted owl interspecific competition (Holm et al. 2016, p. 615). Because of the wide and diverse diet of barred owls in comparison to spotted owls, (Kryshak et al. 2022, pp. 15–16) argue that barred owls will not be ecological replacements to the spotted owls that they displace, and this could have widespread ecological impacts.

Barred owl detections within the spotted owl range have continued to increase. From 1989 to 2013, 51 barred owls and 27 barred owl/spotted owl hybrids had been detected in the Sierra Nevada (Gutiérrez et al. 2017, p. xxv). By 2017, the number of barred and barred owl/spotted owl hybrid detections in the Sierra Nevada increased to approximately 145 (Keane et al. 2018, p. 7), with another 2.6-fold increase between 2017 and 2018 (Wood et al. 2020, p. 4). Even these seemingly low numbers of barred owls in the CSO range are of concern, given that in the northern spotted owl range, replacement of northern spotted owls began at a slow rate in the early years of the expansion, followed by a rapid rate of replacement once the barred owl population reached a critical mass (Forsman in litt. 2018, p. 1). Recent observed CSO population declines likely do not yet reflect barred owl impacts (Gutiérrez et al. 2017, p. 99). In the summer of 2017, bioacoustic surveys in Lassen National Forest, the northern end of the CSO range, found that barred owls were approximately five times less abundant than spotted owls (Wood et al. 2019, p. 498). From 2017–2018, a rapid increase in barred owls was observed in Lassen National Forest with site occupancy changing from 0.082 (CI 0.045–0.12) to 0.21 (CI 0.14–0.28) (Wood et al. 2020, p. 4). As shown in Figure 10, barred owl detections in the CSO range have increased over the almost thirty-year period of 1989–2017. Figure 11 represents barred owl individual locations within the CSO range over two

time periods: pre-1990 through 2009 and 2010 through 2022. As shown, over the last 10 years in particular, barred owl detections throughout the CSO range have increased.

Experimental barred owl removal studies were first initiated and are currently ongoing in the northern spotted owl range (Diller et al. 2012, p. entire; Wiens et al. 2020, p. entire). Wiens et al. (2020, p. entire) summarizes efforts to remove barred owls using a before-after-control-impact design in three study areas in Washington and Oregon, which resulted in removals of over 2,000 barred owls from 2015 through 2019. Results indicate that removals successfully decreased site use by barred owls and increased northern spotted owl use within treatment areas. Further, successful barred owl removals can result in competitive release for spotted owls (Wiens et al. 2021, pp. 4–5). In another (smaller) example of barred owl removals within the northern spotted owl range, after nine barred owls were removed from historical northern spotted owl sites, all sites were re-occupied by northern spotted owls within a year of removal: four by the original residents and five by new residents (Diller et al. 2012, p. 405). However, barred owls again replaced the northern spotted owls at 3 sites within 1–4 years of the northern spotted owls reoccupying those territories (Diller et al. 2012, p. 405). Overall, evidence to date indicates some measure of success for northern spotted owls related to barred owl removal efforts in at least some cases. However, species experts caution that forest conditions, densities of barred owls, and numbers of spotted owls would all factor into whether or not similar results could be obtained in other areas (Wiens et al. 2020, p. 1).

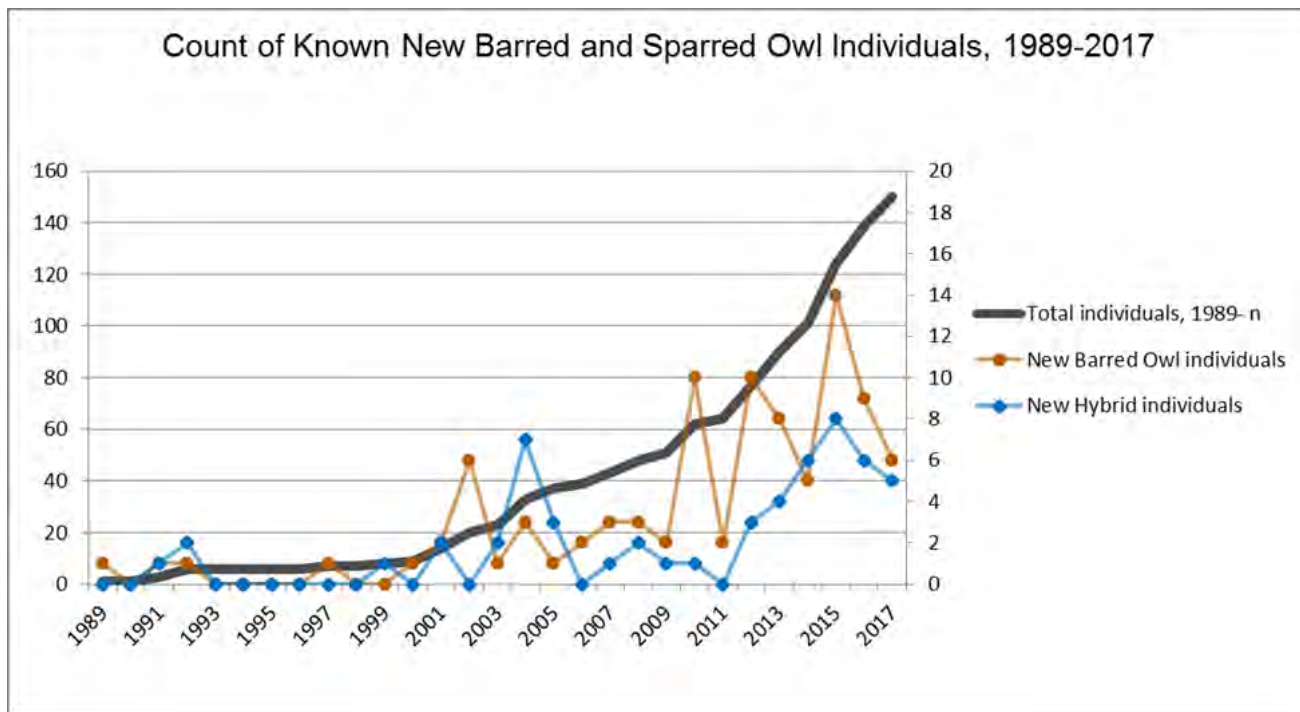


Figure 10: Figure from Keane et al. 2018 shows the barred owl expansion in the CSO range through time. The left y-axis represents the total number of individuals, and the right y-axis represents the number of new barred and hybrid individuals (i.e., sparred owls) each year.

Experimental barred owl removal studies have also recently been initiated in the CSO range, specifically in the Sierra Nevada (Hofstadter et al. 2022, p. entire). In 2017, a CSO conservation

assessment concluded that control measures for barred owls in the CSO range were likely to be more successful and cost efficient while densities of barred owls are still relatively low in the CSO range, and that if control measures were not taken, barred owls would most likely replace CSO on the landscape in the future (though the timescale of this replacement was uncertain) (Gutiérrez et al. 2017, pp. xxxi, xxv); see also (Wood et al. 2020, pp. 5–7). Within the CSO range, barred owl removal experiments were initiated in 2018 and have continued through 2022 (Hofstadter et al. 2022, p. entire). Between 2018 and 2020, researchers removed 76 owls (63 barred owls and 13 hybrids) from the Sierra Nevada, decreasing barred owl occupancy by a factor of 6.3 down to 0.03 (confidence interval: 0.01–0.04). Experimental removals were guided by passive acoustic monitoring, which was also used to measure the efficacy of removals. Partnerships were crucial to the regional-scale removal, with public-private partnerships allowing access to 92% of the CSO range in the Sierra Nevada, including almost all known barred owls in the area and minimizing refugia for barred owls. California spotted owls rapidly colonized territories where barred owls were removed: 15 out of 27 territories were recolonized by CSO within one year of barred owl removals, with successful breeding documented in five of these territories (Hofstadter et al. 2022, pp. 4–5). Early and effective

California Spotted Owl Range and Barred Owl Locations

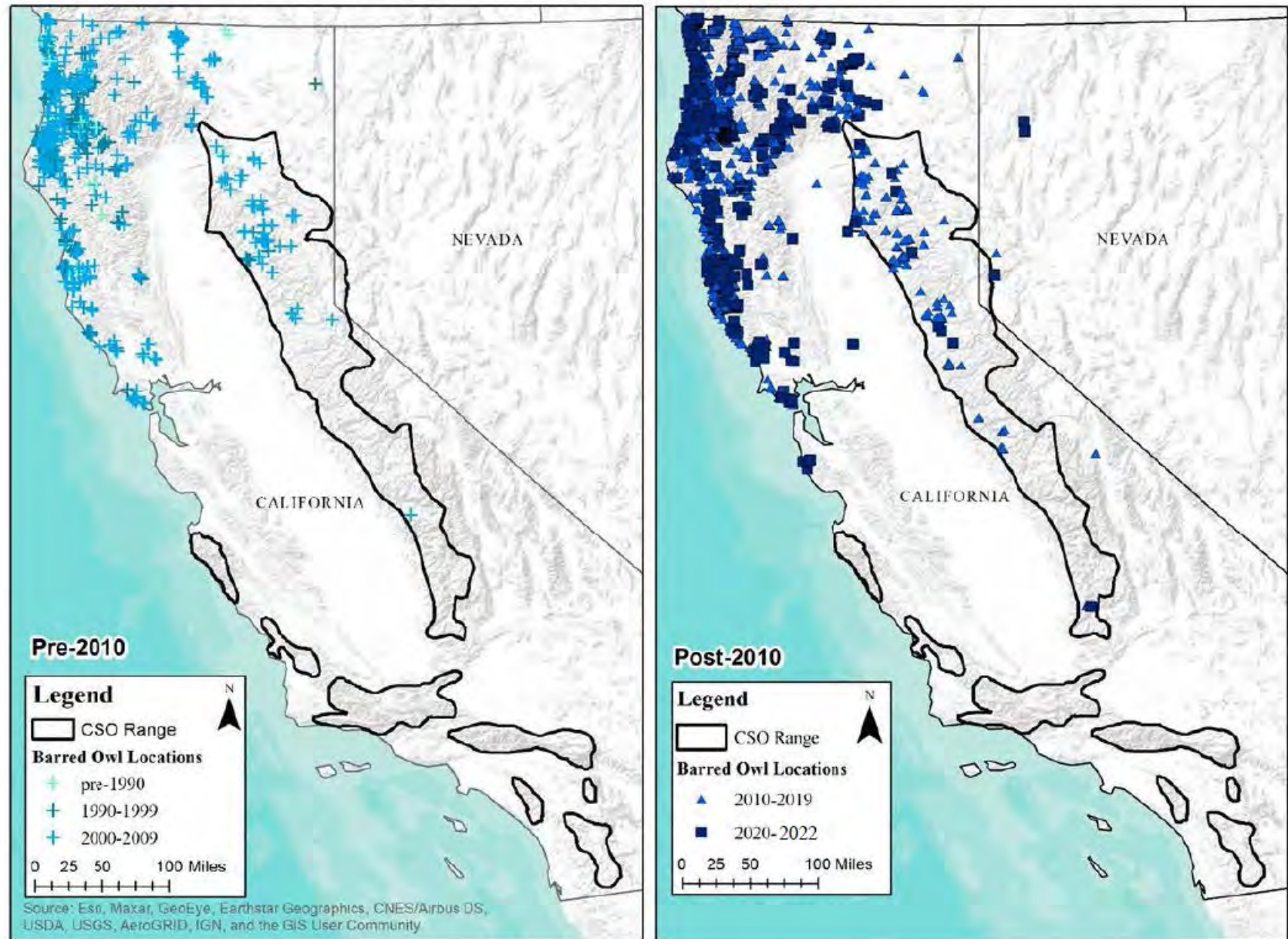


Figure 11: Barred owl detections within the California spotted owl range (eBird 2022; CNDDB 2022). Each point does not necessarily represent a unique individual, but rather a separate detection.

experimental removals of barred owls within the CSO range in the Sierra Nevada has dampened the urgency of this threat, but the potential for continued and persistent expansion into the range remains. Funding is currently available to continue barred owl removal experiments in the California extent of the Sierra Nevada through 2024 (Peery in litt. 2022). However, continued barred owl monitoring and experimental removal would likely need to continue into the future (Hofstadter et al. 2022, p. 6). Management options are currently being evaluated for potential future implementation.

Regulatory mechanisms and management actions that are providing or could potentially provide some protection from the effects of barred owl expansion include management teams, management plans, and Habitat Conservation Plans (HCPs) that coordinate, fund, and implement the experimental removals described above. For more information about the management teams, management plans, and HCPs that ensure these efforts occur, see 4.9 Regulatory Mechanisms and Management Actions. However, barred owls are a significant threat to the persistence of California spotted owls, and the magnitude of this threat is expected to increase into the foreseeable future, particularly if management efforts are not continued.

4.7 Rodenticides

Exposure of nontarget wildlife to anticoagulant rodenticides threatens many species, including CSO, likely because of ingestion of prey animals that have been exposed (Gabriel et al. 2018, p. 5; Franklin et al. 2018, p. 2). Secondary exposure to anticoagulant rodenticides in predators such as raptors can be lethal, with higher exposure levels causing severe blood loss and internal hemorrhaging that can result in organ failure and death (Gomez et al. 2022, p. 147). Although this threat has potential impacts to individuals, because CSO is a long-lived species with low reproductive rates, the loss of just a few individuals may reduce survival and the population growth rate. This threat would be particularly detrimental if a parent were exposed during breeding season because hatchlings and juveniles rely on parental care to survive, so the loss of just one parent would likely result in the loss of offspring as well. Rates of mortality in free-living wild birds due to anticoagulant rodenticides are often unknown due to the difficulty of linking exposure to death and the lack of understanding of toxicity thresholds in different species (Gomez et al. 2022, pp. 147–148). Documentation of anticoagulant rodenticides in ovaries of female barred owl suggests the possibility for in-utero transfer to chicks (Hofstadter et al. 2021, pp. 7–8). Sub-lethal effects of anticoagulant rodenticides in other owl species include reduced clutch size, brood size, fledging success, slower clotting time, residual transfer to eggs, anemia, and impaired mobility; however, these impacts have not yet been documented in spotted owls (Rattner et al. 2012, p. 832; Salim et al. 2014, p. 113; Gabriel et al. 2018, p. 7; Gomez et al. 2022, p. 148).

Although there is little information specific to CSO regarding the exposure rates and resulting impacts of rodenticides, available literature on other species suggests the potential for widespread exposure. Exposure of nontarget species to anticoagulant rodenticides is commonly associated with agricultural or urban settings, but exposure in forest settings in northern California has recently been documented as detrimental to northern spotted owls and barred owls in northern California (Gabriel et al. 2018, p. 5; Franklin et al. 2018, p. 2). Seven out of ten northern spotted owl carcasses tested positive for anticoagulant rodenticides, and 40% of 84 barred owls tested in the northern spotted owl range had been exposed (Gabriel et al. 2018, pp. 4–5). In another study using barred owls as a proxy for spotted owls, Wiens et al. (2019, p. 4) demonstrated exposure to

anticoagulant rodenticides in almost half of barred owls sampled (n=40) and one northern spotted owl sampled opportunistically. Exposure did not vary based on proximity to developed and agricultural areas, or among different study areas, age-classes, and sexes in the study. High rates of exposure were also demonstrated in barred owls and barred owl/spotted owl hybrids in California, with females having higher rates of exposure than males (Hofstadter et al. 2021, pp. 6–7). Despite some differences in diet between barred owls and spotted owls (generalist vs. specialist), comparison of space use by tagged barred owl, northern spotted owl, and CSO in areas with high barred owl anticoagulant rodenticide exposure supports the use of barred owls as a proxy for spotted owls (Hofstadter et al. 2021, pp. 7–8). Large amounts of rodenticides and other pesticides have been found on Forest Service land in the southern Sierra Nevada (Thompson et al. 2013, pp. 95–99). Studies examining rodenticide exposure rates of fisher (*Martes pennanti*), a carnivorous predator with similar habitat requirements as CSO, found 83% to 85% of carcasses studied in the Sierra National Forest had been exposed to rodenticides (Gabriel et al. 2012, pp. 1–14; Thompson et al. 2013, p. 91). These data also suggest potential exposure to CSO.

Anticoagulant rodenticide use has increased throughout California with increases in illegal marijuana cultivation since anticoagulant rodenticides are used to control rodent damage to the plants (Franklin et al. 2018, p. 1). Figure 12 presents marijuana grow sites that have been found in California within the CSO range and MAXENT model results that were developed to predict likelihood of locations of marijuana grow sites (Gabriel et al. 2017, p. 32). Modeling to compare marijuana cultivation site likelihood with northern spotted owl suitable habitat found almost 50% overlap between the two (Wengert et al. 2021, p. 10). Although the exact number of illegal marijuana growing operations within the CSO range is unknown, considering the number of illegal marijuana growing operations found throughout the state, there are likely thousands within the CSO range (Gabriel et al. 2012, pp. 12–13, 2018, p. 6; Thompson et al. 2013, pp. 95–99).

In 2014, the California Department of Pesticide Regulation restricted the purchase, possession and use of anticoagulant rodenticides to only be purchased and used by a certified pesticide applicator with a permit issued by the county agricultural commissioner in order to protect wildlife; however, anticoagulant rodenticides associated with illegal marijuana grows are more likely the source of contaminants. If illegal marijuana grows are found, law enforcement will shut the operations down, but there is currently no standardized clean-up protocol and a limited amount of funding to ensure removal of all rodenticides. Recently there has been an increased effort to locate and shutdown illegal marijuana grows on public lands in California called Operation Forest Watch (DOJ 2018, p. entire). For more information about efforts to address illegal use of rodenticides, see 4.9 Regulatory Mechanisms and Management Actions. Overall, anticoagulant rodenticides are likely affecting CSO across their range, and this threat is expected to continue into the foreseeable future.

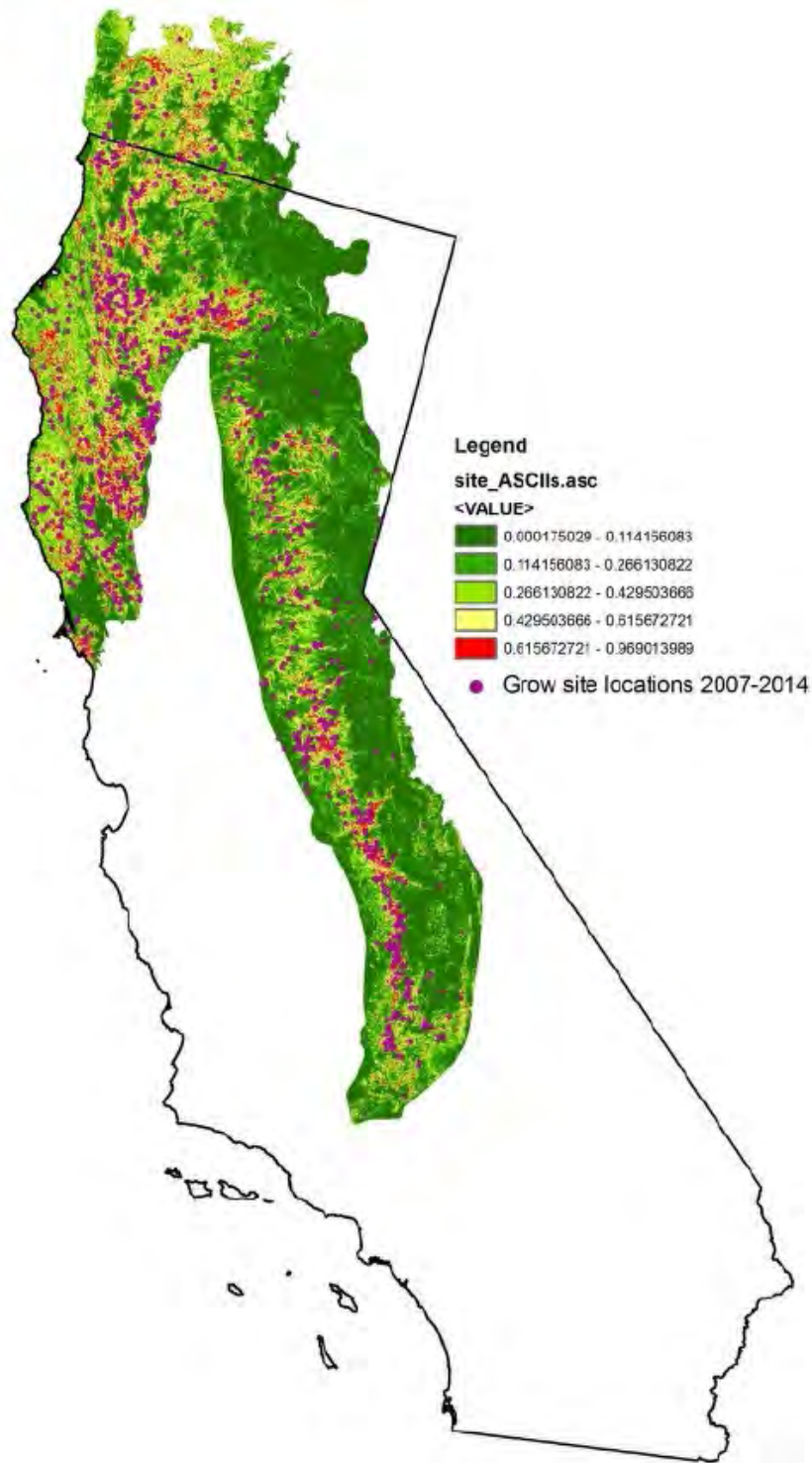


Figure 12: Figure from the Service's Endangered Species Act (Section 6) Grant-in-Aid Program Administered by CDFW, *Science with Solutions: Documentation, Reclamation and Monitoring of the Ecological Impacts of Marijuana Cultivation on Endangered Species* (Gabriel et al. 2017, p. 32). Map of likelihood of marijuana grow site presence based on MAXENT predictions using known grow site localities and several biotic and abiotic features as predictors. Red areas represent highest relative likelihood of grow sites presence, while yellow is moderate likelihood, and green is low-likelihood.

4.8 Development

Anthropogenic land use (including both cultivation and development) in California is expected to increase 28% by 2100 with a projected 3% decrease in overall forest land cover (Sleeter et al. 2017, pp. 1068, 1075). Urbanization is projected to be a primary driver of land use and land cover change in California over this time frame (Sleeter et al. 2017, p. 1076). Urban development is a threat throughout the range of CSO; however, the threat is more substantial in the coastal and southern California areas (Sleeter et al. 2017, pp. 1081, Figure 6, Figure 7). A majority of CSO habitat occurs on public lands (~71% of total range); therefore, this threat is primarily relegated to a small amount of private lands. Future projections for development are unknown within the CSO range because much of the current range occurs on public lands.

In southern California, there are high development demands with specific threats of wind farms and large reservoirs impacting connectivity within the CSO range (Gutiérrez et al. 2017, pp. 253–254). Loss of riparian areas due to water diversion in southern California has created barriers to dispersal among small populations (Gutiérrez et al. 2017, pp. 253–254). The southern California area of the CSO range is fragmented, with low dispersal between populations, so more development could further exacerbate fragmentation (LaHaye et al. 2001, p. 692; Barrowclough et al. 2005, p. 1116; Gutiérrez et al. 2017, pp. 253–254).

In the Sierra Nevada, low to mid elevation development is considered a threat to CSO and its habitat (Verner et al. 1992, pp. 264–265). Low and mid elevation zones in the Sierra Nevada continue to experience human population growth, which may increase the demand for development. Fifty percent of known CSO sites on the west slope of the Sierra Nevada are considered wildland-urban interface and may be vulnerable to further development (Gutiérrez et al. 2017, p. 207). Spotted owls living near the wildland-urban interface may be at a higher risk for exposure to anticoagulant rodenticides, as is the case for barred owls and hybrids (Hofstadter et al. 2021, p. 8); see 4.7 Rodenticides). The northern Sierra Nevada is expected to have a higher level of forest harvest compared to other parts of the CSO range (Sleeter et al. 2017, pp. 1081, Figure 7). Overall, development is likely affecting owls across their range, and we expect this threat will continue into the foreseeable future.

4.9 Regulatory Mechanisms and Management Actions

In this section we include information about regulatory mechanisms in place that provide protection for CSO or reduce or eliminate impacts to habitat. We describe each mechanism or action and how it relates to the species or its habitat, noting that some mechanisms do not actually carry formal legal status or provide formal regulatory protections. Mechanisms and actions include state and federal codes, designations, or acts, federal incidental take permits, and forest management on Forest Service lands. Other conservation or management actions are described under the relevant viability influence (e.g., barred owl removal research is described in 4.6 Competition and Hybridization with Barred Owls). Below we summarize the current conservation efforts and regulatory mechanisms that provide benefits specifically for CSO and its habitat.

U.S. Forest Service Management

The U.S. Forest Service has been a part of ongoing conservation efforts for CSO including the 2004 Sierra Nevada Forest Plan Amendment, which includes Forest Service land in the Lassen, Plumas, Tahoe, Humboldt-Toiyabe, Eldorado, Stanislaus, Sierra, Inyo, and Sequoia CSO analysis units, and the 2005 Southern California National Forest Land Management Plans, which includes the Los Padres, Los Padres-Angeles, San Bernardino, and Cleveland CSO analysis units. In 2019, the Inyo National Forest completed its own Land Management Plan and revised Forest Plans for the Sierra and Sequoia National Forests are expected to be final in 2023 (Miller in litt. 2022.). Once these Plans are finalized, the Inyo, Sierra, Sequoia National Forests will no longer follow the 2004 Sierra Nevada Forest Plan Amendment. All of these are regulatory documents that provide conservation measures for CSO on Forest Service lands (Forest Service 2004, 2005, p. entire, 2019a, pp. 43–47, 2022b, pp. 59–68, c, pp. 59–68). The main goals of these conservation measures include protection and management of CSO activity centers and home range core areas, increasing the frequency of large trees on the landscape, and increasing structural habitat diversity. The goals relate to increasing the condition of the species' ecological needs to increase resiliency and provide conservation efforts related to the threats of large-scale high-severity fire, clearcutting, mechanical thinning, and salvage logging.

The 2004 and 2005 Forest Service land management plans and the 2019 Inyo National Forest and 2022 version of the Sierra and Sequoia National Forest Plans maintain the designation of PACs for CSO, which encompass the best available 121 ha (300 ac) of habitat in as compact of a unit as possible around a nest tree (Forest Service 2004, p. 37; Forest Service 2005, p. 109; Forest Service 2019a, p. 43; Forest Service 2022b, p. 61; Forest Service 2022c, pp. 61–62). There are special considerations for any land management activities or projects that may take place within a PAC. Depending on the plan, management standards and guidelines can include conducting surveys during the planning process of vegetation treatments where appropriate (i.e., in areas of suitable habitat for CSO), limiting activities to reducing surface and ladder fuels through prescribed fire, limiting mechanical treatments to only allow fuel reduction treatments in some wildland urban defense zones where prescribed fire is not feasible, identifying maximum size of canopy gaps created within CSO territories, requiring a limited operating period for when vegetation treatments can occur, and limiting the impacts a vegetation treatment can have on a PAC per year (Forest Service 2004, pp. 54, 60–61, 2022b, p. 64, c, p. 64). The limited operating period is March 1 through August 15 or August 31, unless surveys confirm CSO are not nesting or the treatment is limited such that it would not disturb breeding (Forest Service 2004, p. 60, 2019a, p. 46). Under the 2004 Sierra Nevada Forest Plan Amendment, the limited operating period may also be waived when early season prescribed fire is necessary, but in only up to 5% of PACs per year on a forest (Forest Service 2004, p. 61). Under the 2019 Inyo National Forest and 2022 version of the Sierra and Sequoia National Forest Plans this waiver applies to up to 10% of the PACs per year on a forest (Forest Service 2019, p. 47; Forest Service 2022b, p. 67; Forest Service 2022c, p. 67). The Sierra Nevada Forest Plan Amendment specifies vegetation treatments cannot be conducted in more than 5% per year and 10% per decade of the acres in PACs for each Sierra Nevada area national forest (Forest Service 2004, p. 61); however, this is not described in the 2019 Inyo National Forest Plan or the 2022 version of the Sierra and Sequoia National Forest Plans. In addition to protections, the 2004 Sierra Nevada Forest Plan Amendment and the 2022 version of the Sierra and Sequoia National Forest Plans outline desired conditions for PACs and other large habitat blocks within the home range that include at least two tree canopy layers, dominant and co-dominant trees with average diameters of at

least 61 cm (24 in) dbh, at least 60% to 70% canopy cover, some very large snags (greater than 114 cm (45 in) dbh), and snag and coarse woody debris levels that are higher than average (Forest Service 2004, pp. 37, 39–40). As discussed below, in April 2019, the Forest Service finalized a new CSO conservation strategy for the Sierra Nevada (Forest Service 2019b). The intention of the strategy is to be used for adaptive management and to be incorporated into future Forest Plan updates, although it is not legally enforceable and does not commit and agency action or inaction.

There is disagreement about whether or not measures in these plans, such as mechanical thinning, are beneficial or detrimental to CSO, and whether or not protections afforded by PACs are sufficient to ameliorate impacts to CSO (John Muir Project of Earth Island Institute and The Wild Nature Institute 2014, pp. 70–71, 98, 108; Sierra Forest Legacy and Defenders of Wildlife 2015, pp. 39–40). However, a meta-analysis of CSO occupancy and forest management practices indicated that mechanical thinning treatments that maintain canopy cover at 40% or greater would not substantially reduce CSO occupancy, though canopy cover at 50% or above is more strongly correlated with CSO occupancy (Tempel et al. 2016, pp. 761–762). Forest management practices from the 2004 Sierra Nevada Framework generally maintain at least 50% canopy cover as well as large trees within PACs, and in the 2005 Southern California plan, 40–50% canopy cover must be maintained. The 2019 Conservation Strategy also maintains a minimum of 50% canopy cover within PACs (Forest Service 2019b). Overall, PACs are designated to preserve key habitat used by CSO, and some researchers have concluded that PACs are a key conservation tool that should continue to be implemented (Berigan et al. 2012, pp. 300, 303). In contrast, other research has shown that PACs can be more susceptible to the effects of high-severity fire due to the relatively larger amounts of surface fuel (North et al. 2012, p. 395). A recent study of GPS tagged CSO in the northern Sierra Nevada demonstrated little overlap between PACs and roost or foraging locations, though PACs were not designed to protect foraging habitat (Blakey et al. 2019, p. 920).

In addition to these regulatory documents, the Forest Service has been engaged in four of the five demography studies since 1986 on Lassen, Eldorado, Sierra, and San Bernardino National Forests to increase understanding of CSO ecology and conservation needs. The Forest Service fully funded the four demography studies from 1990–1998, and although they have started to transition to a new monitoring method that covers the species', the Forest Service continued to fund three demography studies on Lassen, Eldorado, and Sierra National Forests, with the Service contributing funding to continue the Lassen and Sierra National Forests through 2024. Due to the transition to the new monitoring method, the Eldorado study area is currently unfunded for 2022 and beyond (Peery 2022, pers. comm.). The San Bernardino demography study was also discontinued in 1998 due to funding constraints. Data collected from these studies have been used to calculate population and occupancy trends, habitat selection and suitability, life history strategies, genetics and phylogeny, and post-fire and post-disturbance distribution. In lieu of continuing these demography studies, the Forest Service is working with the University of Wisconsin Madison to deploy Autonomous Recording Units throughout the Sierra Nevada to determine species presence (Keane and Peery 2022, pers. comm.). Utilizing this newly emerging technology will hopefully allow researchers to identify individual owls on the landscape in the future (Zhou et al. 2020).

In April 2019, the Forest Service completed an updated CSO conservation strategy for the Sierra Nevada national forests (Forest Service 2019b, p. entire). The updated strategy includes new

scientific understanding since the 2004 Sierra Nevada Forest Plan Amendment and will be incorporated into the National Forest Land Management Plans as they are updated in the coming years according to the Forest Service 2012 Planning Rule as amended (36 CFR Part 219). Until the revised National Forest Land Management Plans can be completed, a letter of direction was sent to the Sierra Nevada national forests on April 19, 2019 to provide guidance on implementing the new conservation strategy in the interim (Forest Service 2019c, p. entire). The new conservation strategy gives direction for increased pace and scale of ecological restoration to provide more resilient habitat for CSO, while simultaneously continuing to protect the most important habitat attributes and areas for CSO. The three main goals for the 2019 conservation strategy include: (1) maintain a well-distributed and stable CSO population across the Sierra Nevada by minimizing impacts from non-habitat threats (i.e., barred owls and contaminants); (2) promote and maintain well-distributed CSO habitat by developing key habitat elements and connectivity; and (3) promote CSO persistence by enhancing habitat resilience to multiple disturbances, considering climate change. This increased habitat resilience will lead to improved conditions on the landscape, and greater population resiliency. The new strategy provides adaptive management and metrics for success in order to ensure the conservation measures outlined in the plan are beneficial to CSO. In addition to the conservation strategy, the Forest Service is planning to implement a new monitoring plan using acoustic recording units to cover the Sierra Nevada portion of the CSO range. The goal is to use the information from the new monitoring plan to allow the Forest Service to conduct a future CSO occupancy modeling effort to provide information over a larger portion of the CSO range, and allow greater potential for inference on broad scale effects of restoration and disturbance (Forest Service 2019d, pp. 14–15). There are elements of the strategy that may entail some short-term, localized reduction in occupancy. These elements allow for more forest management flexibility in application of fuels reduction and other landscape treatment projects as compared to the 2004 Sierra Nevada Forest Plan Amendment both within PACs and on the landscape, as well as more flexibility in the retirement of PACs when they are no longer occupied. Additional flexibility in these landscape treatments provides access to additional tools to maintain and restore CSO habitat (Forest Service 2019b, p. entire). We anticipate that the short-term impacts that may occur for the purpose of fuel reduction and forest health will be outweighed by the long-term benefit as more sustainable and dynamic habitat is developed through active management (Forest Service 2019b, p. 2).

On August 30, 2017, a Memorandum of Understanding (MOU) was signed by Sierra Pacific Industries (SPI), California Department of Forestry and Fire Protection (CAL FIRE), National Fish and Wildlife Foundation (NFWF), and U.S. Department of Agriculture, U.S. Forest Service Pacific Southwest Region (hereafter referred to as the Fire MOU), which will impact all lands from Lassen National Forest south through Stanislaus National Forest. The purpose of the MOU is to document the agreement between the parties to coordinate on certain actions to reduce the risk of large-scale high-severity wildfire through forest fuels reduction to benefit CSO conservation. The MOU involves establishing a strategic conservation framework to help restore and protect areas where CSO are threatened by habitat degradation due to uncharacteristically extensive and severe adverse fire effects. The MOU is designed for signatories to engage in collaborative landscape-level fuels and fire risk reduction treatments to: 1) minimize potential fire-related impacts to CSO activity centers on federal, state and private lands; and 2) better coordinate implementation of fuels reduction work on federal, state, and private lands to maximize the effectiveness of this work. Sites for fuels treatment are selected to minimize risk to known occupied CSO activity centers. Measures

associated with the Fire MOU include fire management activities such as increased mechanical thinning that may benefit CSO by decreasing risk of large-scale high-severity fire. If mechanical thinning is planned in consideration of CSO habitat needs, there may be some negative impacts, but these would be outweighed by reducing the risk of large-scale high-severity fire in CSO activity centers (Jones et al. 2016a, p. 305, 2021a, p. 6; Service 2017, pp. 24–25; Chiono et al. 2017, p. 1).

The Forest Service, SPI (a private corporation), and CAL FIRE manage forest lands in California that are frequently adjacent to each other, and have ongoing programs to protect and enhance habitat for fish and wildlife and also manage forest fuels to reduce fire risk and its potential impacts on wildlife species. Under state law, SPI has the authority to participate in fire suppression on its own lands while CAL FIRE, contract counties, Forest Service, and other government agencies have primary fire suppression responsibility for all federal, state, and private wildlands in California. The parties also have responsibilities and interests in the inventory of their respective lands for federally- and state-recognized threatened, endangered, proposed, candidate, and sensitive species and in the development of appropriate protection measures for these species. Due to these natural resource challenges, the Fire MOU parties believe it is important to establish a coordinated, multi-stakeholder agreement to help protect and enhance forest resources.

Though the Fire MOU was initially set to expire on December 2019, an amendment was signed in April 2019 to extend the terms of the MOU through December 2024. In March 2020, a new MOU that supersedes the 2017 MOU and 2019 amendment was signed by the same parties. An amendment to the 2020 MOU was signed in September 2020 to add a number of new commercial forest landowners. The terms of the 2020 MOU are effective through December 2024. The Service is actively engaged with the signatory parties to discuss fuels reduction efforts and associated monitoring.

Barred owls (*Strix varia*) have expanded into western North America over the past several decades, first through the Pacific Northwest and more recently into the Sierra Nevada (see 4.6 Competition and Hybridization with Barred Owls). The Service and the Forest Service are funding researchers at the University of Wisconsin-Madison to carry out an ongoing barred owl removal study. The project grant was signed in August of 2018 and funding has been secured from the Service and potentially University of Wisconsin-Madison through 2025 (Keane and Peery 2022, pers. comm.). The project addresses several key questions related to the range expansion of barred owls in the Sierra Nevada and will inform the development of a scientifically-based barred owl management plan. Specifically, this project: (1) assesses the current distribution and density of barred owls; (2) conducts experimental barred owl removals; (3) tests for reductions in barred owl site occupancy rates; 4) quantifies spatio-temporal patterns of barred owl recolonization; and 5) characterizes barred owl dispersal into and within the Sierra Nevada. This project takes place primarily in the northern and central Sierra Nevada, including Lassen National Forest, Lassen National Park, Plumas National Forest, Tahoe National Forest, and Eldorado National Forest, Yosemite National Park, and Sequoia-Kings Canyon National Park.

Additionally, on July 22, 2022, the Service published a Notice of Intent to prepare an Environmental Impact Statement (EIS), initiating a 30-day public scoping period seeking input on barred owl management in the northern spotted owl and CSO range (87 FR 43886). Preventative barred owl management for CSO will likely be considered in the EIS. Northern spotted owl are the

main focus right now, but barred owl have expanded into northern California into the CSO range and are expected to continue to expand without continued management.

Migratory Bird Treaty Act

The CSO is currently protected in part under the Migratory Bird Treaty Act (MBTA) which is intended to ensure the sustainability of populations of all protected migratory bird species (16 U.S.C. 703–712). These protections make it “illegal for anyone to take, possess, import, export, transport, sell, purchase, barter, or offer for sale, purchase, or barter, any migratory bird, or the parts, nests, or eggs of such a bird except under the terms of a valid permit issued pursuant to Federal regulations.” The MBTA provides regulatory protection to individuals that could be targeted via trapping, shooting, or direct poisoning.

The level of protection a migratory bird species has received under the MBTA has changed based on varying memorandums. The U.S. Department of the Interior’s Office of the Solicitor (solicitor) issued a memorandum opinion (M-Opinion 37050) to the Director of the Service on December 22, 2017, providing a legal analysis for the interpretation of the MBTA to only include purposeful take and not incidental take. Based on this analysis, M-Opinion 37050 concluded that the MBTA’s prohibition on take “applies only to direct and affirmative purposeful actions that reduce migratory birds, their eggs, or their nests, by killing or capturing, to human control”. However, on March 8, 2021, the Principal Deputy Solicitor of the Interior issued a memorandum withdrawing Solicitor’s Opinion M-37050. Therefore, the incidental take of eggs and/or nestlings during timber harvest activities and during the destruction of active nest trees are a violation of the MBTA.

Fish and Wildlife Conservation Act

Under the Fish and Wildlife Conservation Act, the Service considers CSO a Bird of Conservation Concern and a Bird of Management Concern; however, neither of these designations offers regulatory protection. Inclusion as a Bird of Conservation Concern is “intended to stimulate coordinated and collaborative conservation actions among Federal, State, Tribal, and private partners...” for the species and “...to prevent or remove the need for additional...bird listings...” under the Endangered Species Act. Birds of Management Concern are species which are protected under the MBTA and “warrant management or conservation attention.”

Habitat Conservation Plans

The Service may issue incidental take permits to non-federal applicants pursuant to section 10(a)(1)(B) of the Endangered Species Act. Incidental take is defined as take that is incidental to, and not the purpose of, the carrying out of an otherwise lawful activity (50 CFR 402.02). Habitat conservation plans (HCPs) are planning documents required as part of an application for an incidental take permit; HCPs can apply to both listed and non-listed species, including those that are candidates or have been proposed for listing. They describe the anticipated effects of the proposed taking; how those impacts will be minimized or mitigated to the maximum extent practicable; and how the HCP is to be funded. There are currently two HCPs that include CSO.

Sierra Pacific Industries

Sierra Pacific Industries (SPI) is the largest private forest land owner in California, with approximately 1.84 million acres of timberland in northern California (SPI 2021, p. 1). Sierra Pacific Industries' Habitat Conservation Plan for both northern spotted owl and CSO cover all areas on SPI-managed property where covered activities will occur within the range of the two spotted owl subspecies, which is over 1.5 million acres ([SPI] Sierra Pacific Industries 2021, p. 2). The plan area for CSO includes approximately 1,188,265 acres of modeled habitat in the Modoc Plateau, Cascade Mountains, and Sierra Nevada Mountains in the northern and eastern portions of California; however, the plan area may increase or decrease somewhat over time due to the sale, purchase, or exchange of SPI lands (Service 2020, p. 7).

Sierra Pacific Industries manages their forestlands for the primary purpose of growing and harvesting timber. Some logging has occurred on all of SPI's lands and there is no old growth forest present. These forestlands are harvested using primarily even-aged silvicultural methods. Covered activities under the HCP include timber operations and other forest management activities. Major activities associated with the HCP include growing, harvesting, and transporting timber; timber stand regeneration and improvements; road and landing construction and maintenance; fuel break construction and maintenance; and monitoring and research (e.g., for spotted owls) (Service 2020, p. 8).

Implementation of the HCP is not expected to result in direct injury or mortality of CSO due to the implementation of conservation measures. To meet the HCP goals, SPI outlines eight conservation measures that will be implemented throughout the 50-year permit term. These measures include: increase aggregations of CSO habitat across the landscape; establish protection zones around all known and recently discovered activity centers; retain important habitat elements during salvage harvesting to accelerate the development of future habitat for spotted owls in sites that are reforested following salvage logging; reduce the risk of catastrophic fire by establishing fuel breaks and other fuel reductions strategies; conduct pre-operational surveys for spotted owls when conducting covered activities and protect active nests with a 0.25 acre buffer from March 15 to August 31; implement land access control activities and cooperate with local, state and federal law enforcement agencies to eradicate illegal marijuana plantations and prevent illegal firewood cutting that could remove habitat for the spotted owl or its prey; retain and manage habitat standards identified for spotted owl; and address barred owl expansion (Service 2020, pp. 10–13).

In 2015, SPI began studying barred owls via removal experiments. In 2018, the study was revised to include the following objectives: 1) assess the genetic differentiation of barred owl populations across northern and central California, 2) analyze allele frequency changes on the front of the range expansion, 3) estimate the amount of spotted owl – barred owl interbreeding (admixture) in each population, and 4) identify what barred owls are preying on in California. These efforts are ongoing and SPI has committed to continue these efforts during the term of the permit, as feasible. For more information about SPI's barred owl removal research, see 4.6 Competition and Hybridization with Barred Owls. Ongoing research and monitoring efforts for CSO on SPI land have indicated that some CSO populations in mixed-ownership landscapes have higher occupancy,

density, and probability of reproduction compared to CSO populations on public land (Roberts et al. 2017, p. 113; Hobart et al. 2019, p. 1987; [SPI] Sierra Pacific Industries et al. 2022, pp. 9, 17).

Western Riverside County Multiple Species Habitat Conservation Plan

The Western Riverside County Multiple Species Habitat Conservation Plan (MSHCP) is one of the largest habitat conservation plans in the United States covering 500,000 acres. Acreage includes 347,000 acres of public/quasi-public (PQP) lands that were conserved prior to the MSHCP, and 153,000 acres of Additional Reserve Lands that have been or will be acquired to complete the MSHCP. Collectively, 146 listed and unlisted species are Covered Species under the MSHCP, including CSO. The CSO is currently listed as a Species Not Adequately Conserved under the MSHCP until a Memorandum of Understanding (MOU) is executed with the U.S. Forest Service that addresses management of CSO on Forest Service lands. As of January 21, 2022, which was the latest update on the Status of Covered Species Not Adequately Conserved under the MSHCP, the MOU with the Forest Service had not yet been executed for CSO (<https://www.wrc-rca.org/document-library/>).

The MSHCP Plan Area includes 54,119 acres of modeled habitat for CSO. If the MOU with the Forest Service is signed, the loss of 12,905 acres (24%) of this modeled habitat is anticipated over the 75-year permit term. With the low density of CSO in the Plan Area, loss of these 12,905 acres is not anticipated to result in direct mortality of adult birds. However, loss of foraging and nesting habitats to development will cause CSO in impacted areas to disperse in search of other habitats. Birds forced to disperse may experience increased competition for the remaining suitable habitat or decreased fitness due to increased energy and time spent locating new habitats. They may also be subjected to increased rates of predation and injury. Further, if clearing of habitat occurs near the initiation of the breeding season, the search for and establishment of a new breeding site may result in an overall reduction in reproductive output. Thus, loss of breeding and foraging habitat may impact overall population numbers of CSO within the Plan Area over the long term by reducing the number of areas suitable for use as foraging and nesting sites (Service 2004, p. 449).

In order to offset these impacts, the MSHCP will conserve and manage 1,321 acres (2%) of modeled habitat for CSO within Additional Reserve Lands. Another 39,894 acres (74%) of modeled habitat will remain in PQP Lands. In total, 41,214 acres (76%) of the modeled habitat for CSO will be included in the MSHCP Conservation Area. If the MOU with the Forest Service is signed, additional monitoring and management would occur in habitat for CSO within Forest Service lands included in the MSHCP Conservation Area. Surveys for CSO will be conducted at least every eight years to verify occupancy at a minimum of 75% of the known and future-identified locations. If a decline in the distribution of CSO is documented below this threshold, management measures will be triggered, as appropriate, to meet the species-specific objectives identified in the MSHCP (Service 2004, p. 450).

Clean Air Act

The Clean Air Act of 1970 (42 U.S.C. 7401 et seq.) provides the platform for the Environmental Protection Agency (EPA) to develop and enforce regulations to protect the general

public from exposure to airborne contaminants known to be hazardous to human health. In 2007, the Supreme Court held that gases such as carbon dioxide fit within the Clean Air Act's definition of "air pollutant," and thus that EPA has the authority to regulate the emissions of such gases from new motor vehicles (*Massachusetts et al. v. EPA*, 549 U.S. 497, 532 (2007)).

California Fish and Game Codes

There are several California Fish and Game Codes that are relevant to the CSO. These codes limit take or destruction of CSO individuals and their nests. California Fish and Game Codes applicable to CSO, and their definitions, include:

§355: "The commission may, annually, adopt regulations pertaining to migratory birds to conform with or to further restrict the rules and regulations prescribed pursuant to the Migratory Bird Treaty Act."

§3503: "It is unlawful to take, possess, or needlessly destroy the nest or eggs of any bird, except as otherwise provided by this code or any regulation made pursuant thereto."

§3503.5: "It is unlawful to take, possess, or destroy any birds in the orders Falconiformes or Strigiformes (birds-of-prey) or to take, possess, or destroy the nest or eggs of any such bird except as otherwise provided by this code or any regulation adopted pursuant thereto."

§3513: "It is unlawful to take or possess any migratory nongame bird as designated in the Migratory Bird Treaty Act or any part of such migratory nongame bird except as provided by rules and regulations adopted by the Secretary of the Interior under provisions of the Migratory Treaty Act."

California Species of Special Concern

California spotted owls are considered a California Species of Special Concern, designated by the CDFW, because declining population levels, limited ranges, and/or continuing threats have made them vulnerable to extinction (California Department of Fish and Wildlife, Natural Diversity Database 2018). The designation is administrative and does not carry formal legal status. However, the California Environmental Quality Act (CEQA; California Public Resources Code §§ 21000-21177) requires state agencies, local governments, and special districts to evaluate and disclose impacts from "projects" in the state. Section 15380 of the CEQA Guidelines clearly indicates that species of special concern should be included in an analysis of project impacts if they can be shown to meet the criteria of sensitivity outlined therein.

California Global Warming Solutions Act

The state of California passed Assembly Bill 32 (AB 32), the California Global Warming Solutions Act of 2006, to reduce the amount of greenhouse gas emissions within the state to 1990 levels by 2020. AB 32 requires the California Air Resources Board to adopt regulations for reporting and verifying statewide greenhouse gas emissions and for monitoring and enforcing compliance with the program.

Nevada Wildlife Codes

The Nevada Administrative Code (NAC) and Nevada Revised Statutes (NRS) contain several permanent regulations set forth by the Nevada Department of Wildlife (NDOW) that are relevant to CSO. These codes limit take, possession, or destruction of CSO individuals and their nests. Regulations applicable to CSO, and their definitions, include:

NRS 503.585: A species or subspecies of native fish, wildlife and other fauna must be regarded as threatened with extinction when the Commission, after consultation with competent authorities, determines that its existence is endangered and its survival requires assistance because of overexploitation, disease or other factors or its habitat is threatened with destruction, drastic modification or severe curtailment. Any animal so declared to be threatened with extinction must be placed on the list of fully protected species, and no member of its kind may be captured, removed or destroyed at any time by any means except under special permit issued by the Department.

NAC 503.050: Protected birds:

1. Are all species of wild birds protected by the Migratory Bird Treaty Act, as amended, 16 U.S.C. §§ 703 et seq., and listed in 50 C.F.R. § 10.13
2. Include the following species which are further classified as endangered:

(c). California spotted owl (*Strix occidentalis occidentalis*)

Applicable federal law is the Migratory Bird Treaty Act, as amended, 16 U.S.C. §§ 703 et seq. and federal regulations adopted pursuant thereto.

NAC 503.090.1: There is no open season on those species of wild mammals, wild birds, fish, reptiles or amphibians classified as protected.

NAC 503.093.1: A person shall not hunt or take any wildlife which is classified as protected, or possess any part thereof, without first obtaining the appropriate license, permit or written authorization from the Department.

Nevada Species of Conservation Priority

California spotted owls are considered a Nevada Species of Conservation Priority, designated by NDOW, because low numbers, limited availability of suitable habitat, uncertain population status, and threats such as improper forest management, catastrophic wildfire, and drought-related conifer mortality make them vulnerable to extinction within the state (NDOW 2022, Appendix E, pp. 96–98). The designation is administrative and does not carry formal legal status.

4.10 Potential Threats Not Carried Forward in Analysis

We also include a brief discussion here of potential influences to viability that were not carried forward within this SSA Report because there is either no evidence that the factors are negatively impacting the species, negative effects are expected to be minimal, or the known negative impacts are low and not having a population level impact. There is no evidence of overutilization of

the species for commercial or recreational purposes. There have been no documented changes in predator communities that would affect predation rates beyond those naturally experienced by CSO and we do not anticipate any changes in the future. Similarly, although there are known CSO parasites (including hematozoans, haemosporidians, and the flagellated protozoan parasite *Trichomonas gallinae*), and ectoparasites found on the species (including fleas, ticks, mites, and lice) (Gutiérrez 1989, p. 614; Hunter et al. 1994, p. 232; Ishak et al. 2008, p. 1; Rogers et al. 2016, p. 305), the expected current and future impacts from parasites are minor. There is limited information about disease impacts to the species: some hypotheses as to the impacts of parasites include reduced competitive advantage to barred owls due to infection and avian trichomonosis, a disease caused by a protozoan parasite that has caused mortality in other bird species (Ishak et al. 2008, p. 1; Rogers et al. 2016, pp. 305–306). Another disease of potential concern is West Nile Virus because it has had detrimental effects to other species of owls, including barred owls (Fitzgerald et al. 2003, pp. 602, 605; Komar 2003, pp. 190, 193, 195, 217–218, 223; Gancz et al. 2004, p. 2135; Nemeth et al. 2006, p. 2). However, there is currently no evidence West Nile Virus is having negative impacts on CSO (Hull et al. 2010, p. 168). There are some concerns that recreation within CSO habitat may cause degradation of habitat and behavioral disturbance, but little is known about this potential threat (LaHaye and Gutiérrez 2005, p. 204; Gutiérrez et al. 2017, pp. 217–218, 255). Northern spotted owls exposed to continuous traffic had higher corticosterone levels, a measure of physiological stress (Hayward et al. 2011, p. 1). Although Mexican spotted owl behavior activity budgets did not change markedly during a controlled hiking experiment, there was some evidence that high levels of recreational hiking could be detrimental (Swarthout and Steidl 2001, p. 312). In summary, over-utilization of the species for commercial or recreational purposes and predation are not discussed in the current condition and future condition sections of this SSA Report, although additional information could change this assessment in the future. Parasites, disease, and recreation are discussed in the future condition sections as we expect potential changes in these influences in the future. We will consider all threats in our summary of the species status now and in the future.

4.11 Interaction Between Threats

The threats discussed above not only act independently, but also interact with each other. It is important to assess the relationship between threats because there may be new or exacerbated impacts that are not considered when a threat is assessed alone. There are a vast number of ways threats may be interacting with each other, but the SSA Report will only focus on what is currently most relevant to the viability of the species. Figure 13 shows the relationships between threats, CSO habitat needs, CSO population needs, and ultimately CSO viability.

For example, climate change intensifies the threats of large-scale high-severity fire, drought, tree mortality, and increases interannual climate variability (Kadir et al. 2013, pp. 132, 137; Stephens et al. 2018, p. 77). Development in wildland-urban interfaces also increases the likelihood of large-scale high-severity fire (Mann et al. 2016, pp. 14–18). An increase of large-scale high-severity fires with changing climate conditions can lead to accelerated fire-facilitated conversion of forest edge to non-forested habitat (Parks et al. 2019, pp. 1, 7). The impacts to CSO would likely range from direct physiological impacts to indirect habitat and prey impacts. The loss of trees due to high-severity fire, drought, and tree mortality would likely lead to increased salvage logging on the landscape, further reducing CSO habitat. Additionally, the expansion of barred owls outcompeting CSO in

combination with timber harvest outside of PACs further worsens the outlook for habitat availability.

Where the different threats are occurring on the landscape simultaneously is also important to consider. Many of the threats are range-wide, but some may be more significant or more concentrated in particular parts of the range. Barred owls are moving south into the CSO range, so the northern portion of the Sierra Nevada will likely experience a greater magnitude of this threat, and earlier in time. Tree mortality is more concentrated in the Sierra Nevada than other parts of the landscape and may experience more significant impacts from this threat. The threat of wildfire in California has a higher likelihood in southern California than other portions of the CSO range. Considering the temporal, spatial, and interactive components of all the threats together is important for understanding the viability of CSO now and into the future.

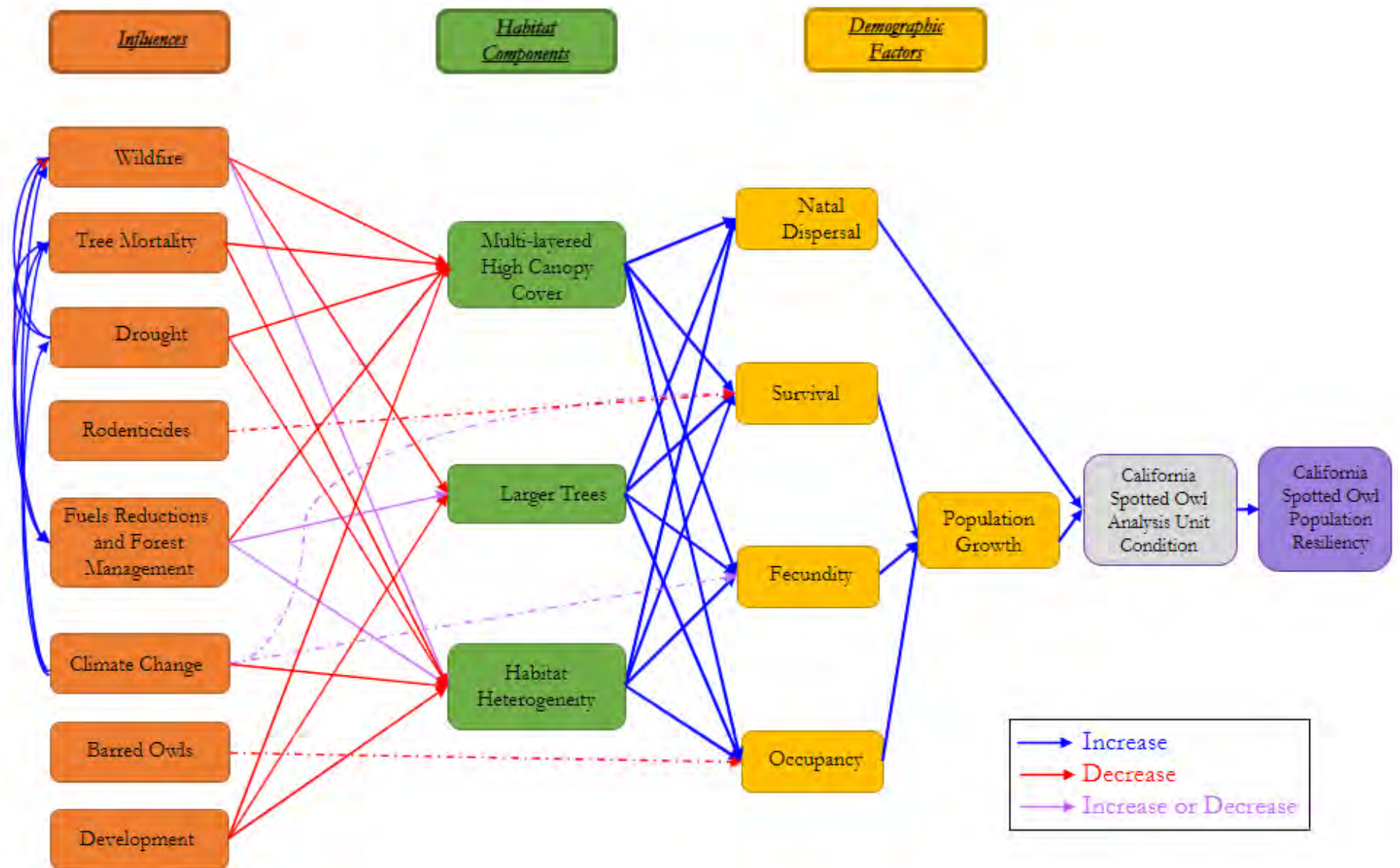


Figure 13: Conceptual model showing the interactions among influences, the species ecological needs, and how they interact to impact resiliency of California spotted owl populations. Blue arrows indicate a relationship where there is an increase; for example, an increase can mean one threat may increase or intensify the likelihood of another threat or an increase can mean that an individual need increases or promotes a population need. Red arrows indicate a decreasing relationship, where it can mean a decrease or reduction in the likelihood of another threat, or it can mean a decrease or reduction in an individual or population need. Purple arrows indicate that a threat may either increase (improve) or decrease (diminish) an individual or population need. Dotted lines indicate influences that not only impact habitat components, but also have direct impacts on demographic factor.

CHAPTER 5: CURRENT CONDITION

Current condition may be described in terms of past and ongoing changes in a species' habitat, demographics, and distribution (Smith et al. 2018, p. 306). To assess the current condition of CSO, we used the best scientific and commercial data available to analyze and describe, both quantitatively and qualitatively, past and ongoing changes in the species' habitat, demographic parameters, and distribution across the two populations and 15 analysis units described in Chapter 3 (see 3.2.1 Definition of a Population and an Analysis Unit). The methods and results of our assessment of current condition are described in the subsequent sections.

5.1 Current Condition Summary of Methods

For our current condition analysis, we consider two populations of CSO: one occupying the Sierra Nevada and the other coastal-southern California. To analyze these populations in more detail, we further divided them into analysis units; however, we recognize that these units do not function independently and in areas where the species distribution is continuous, like the Sierra Nevada, impacts to one unit may result in impacts to an adjacent unit. We assessed the condition of all CSO ecological needs where information was available for each analysis unit, including the demographic factors of survival, fecundity, occupancy, and population growth, and habitat components of large trees and canopy cover. In addition, because high-severity fire has significant effects on the condition of habitat within an analysis unit, we also incorporated results from our fire analysis in Chapter 4.1. For each population, we present an overview of the available information on ecological conditions and threats across the entire population, our analysis of the demographic factors and habitat components within each analysis unit to determine current condition, and a summary assessing population resiliency. We then assess CSO redundancy and representation under the current condition analysis. Additional information about our analysis of demographic and habitat condition is presented here.

To assess current condition, when available, we used demographic information available from partner reports and peer-reviewed literature. Researchers have been studying the demography of CSO in the Sierra Nevada since 1986. This research has focused on the Lassen National Forest, Eldorado National Forest, Sierra National Forest, and Sequoia/Kings Canyon National Parks. The San Bernardino National Forest in southern California was initially included, but mark-recapture studies there stopped in 1998. However, researchers have continued to collect occupancy and reproduction data within the San Bernardino analysis unit. These demography studies have provided consistent survival, fecundity, and occupancy data, and have been used to model occupancy and population growth changes in analysis units over time. For the analysis units that have been a part of demography studies, occupancy and population growth data were used to assess the current condition. Only one other analysis unit, Yosemite, had information available to assess occupancy, but the information is based on only three years of survey data, so we did not incorporate this information into our demographic analysis. Table 4 presents how we categorized the available demographic data to determine analysis unit demographic condition, with data presented as narrative for each analysis unit when available. Our assessment also discusses the amount of connectivity between analysis units.

Table 4: Demographic condition of analysis units.

Condition	Demographic data
Increasing	Increasing population trend over >10 years
Stable	Occupancy and/or population stable over >10 years, or increasing over <10 years
Declining	Occupancy reduced by up to 50% or population trend decreasing over >10 years
Strongly declining	CSO absent, or occupancy reduced by over 50% over >10 years
Unknown	No demographic data

For all analysis units, we also assessed current condition of an analysis unit using habitat components based on the assumption that high quality habitat supports stable or increasing populations and low quality habitat could only support declining or strongly declining populations. To assess current habitat condition, we looked at spatial information relevant to habitat components as well as information from our fire analysis described in Chapter 4.1. For large trees and multi-layered canopy cover we gathered optimal or normal values from a variety of resources, which are described below, and then conducted a quantitative habitat analysis calibrated using the known demographic information. We used updated Gradient Nearest Neighbor (GNN) forest structure maps (LEMMA 2020) for tree size from 2017. Plot data used to calculate all GNN habitat metrics ranged from 2000–2017 at a 30-meter resolution scale. These methods followed similar methods as (Jones et al. 2018, pp. 342–345). GNN data (including, but not limited to, large and medium trees with dense and medium cover) were also used to map habitat suitability for CSO across the Sierra Nevada (Keane in litt. 2022, p. 7). We used the attribute QMD_DOM, quadratic mean diameter of dominant and codominant trees in each pixel, to map tree size class. We defined large trees as >61 centimeters dbh. We also conducted an analysis specific to the coastal-southern California population assessing smaller size classes of hardwood and conifers because stick or platform nests are more common in this part of the range (LaHaye et al. 1997, pp. 42, 47; Tanner 2022, in litt.). We considered trees >33 centimeters dbh to evaluate the availability of trees that could potentially support a stick or platform nest. We used canopy cover data (“horizontal cover fraction occupied by tree canopies”) from California Forest Observatory representing conditions on the ground in 2020 using satellite imagery at a 10-meter spatial resolution (Salo Sciences, Inc. 2020, pp. 1–3). We defined moderate canopy cover as >40% and did not use areas with <40% canopy cover in the analysis below. Further, because CSO in Yosemite National Park had territory centers with average values of 40% canopy cover in burned forests it further supports using this value to assess potential habitat (Schofield et al. 2020, pp. 4–5). We also calculated the area of overlap for each analysis unit between large trees and moderate canopy cover and incorporated the overlap values into our analysis. Because these sources use habitat data from earlier time periods, we removed areas that have burned at high-severity from fires that occurred after the time period represented by the available habitat data (e.g., areas that burned at high-severity in 2021 were excluded from the canopy cover dataset and areas that burned at high-severity after 2017 were excluded from the tree size dataset). Any fires that burned in 2022 were excluded from the dataset as the information was not available at the time this analysis was conducted (e.g., Oak and Washburn Fires near Yosemite National Park).

We used zonal statistics and tabulate area functions in ArcMap 10.8.1 to determine the proportion of large trees and moderate canopy cover within each CSO analysis unit. Proportions were calculated for the broad landscape scale of each analysis unit within the CSO range and within

the two CSO populations (Sierra Nevada and coastal-southern California). Results are shown in Table 5 (and by analysis unit in Tables 9 and 13 in the Sierra Nevada and coastal-southern California population sections 5.3.1 and 5.3.2). Maps showing the habitat components, including overlap, are presented in Figure 14. We also completed these calculations for the northern and southern Sierra Nevada as the northern Sierra Nevada tends to have more dense forests and higher precipitation, thus, resulting in potentially different CSO habitat conditions (Van Wagtendonk et al. 2006, p. 250; Climate Engine 2017). Tree mortality was also less severe in the northern Sierra Nevada (see Figure 9 in section 4.2 Tree Mortality). We considered the northern Sierra Nevada to include the Lassen, Plumas, Tahoe, Eldorado, and northern portion of the Humboldt-Toiyabe analysis units. The southern Sierra Nevada included the southern portion of the Humboldt-Toiyabe, Stanislaus, Yosemite, Sierra, Sequoia-Kings Canyon, Sequoia, and Inyo analysis units.

Table 5: Habitat component percentages for large trees and moderate canopy cover for the entire CSO range, the two CSO populations, and portions of the Sierra Nevada population.

CSO Population or Range	Large trees	Moderate Canopy cover
Range-wide	5%	46%
Sierra Nevada	7%	50%
<i>Sierra Nevada North</i>	5%	52%
<i>Sierra Nevada South</i>	9%	46%
Coastal-Southern California	1%	37%

Habitat condition within each analysis unit was assessed using different scoring systems depending on the habitat component being considered (see Table 6). For large trees and moderate canopy cover, we considered four separate categories to determine current condition, with less points assigned to decreasing habitat percentages. For our fire analysis, which is described in more detail in Chapter 4, we considered only two categories to determine current condition and we limited our analysis to high severity fires that have occurred between 2011–2021. To incorporate the fire information into our habitat analysis we only want to consider whether high-severity wildfires have had a negative impact to the overall unit. We consider high-severity wildfire values up to 4% of the unit area to have a negative impact on the overall unit and assign those values -1 point to reflect their negative impact to habitat. High-severity wildfire values of 4% or less are assigned no point value.

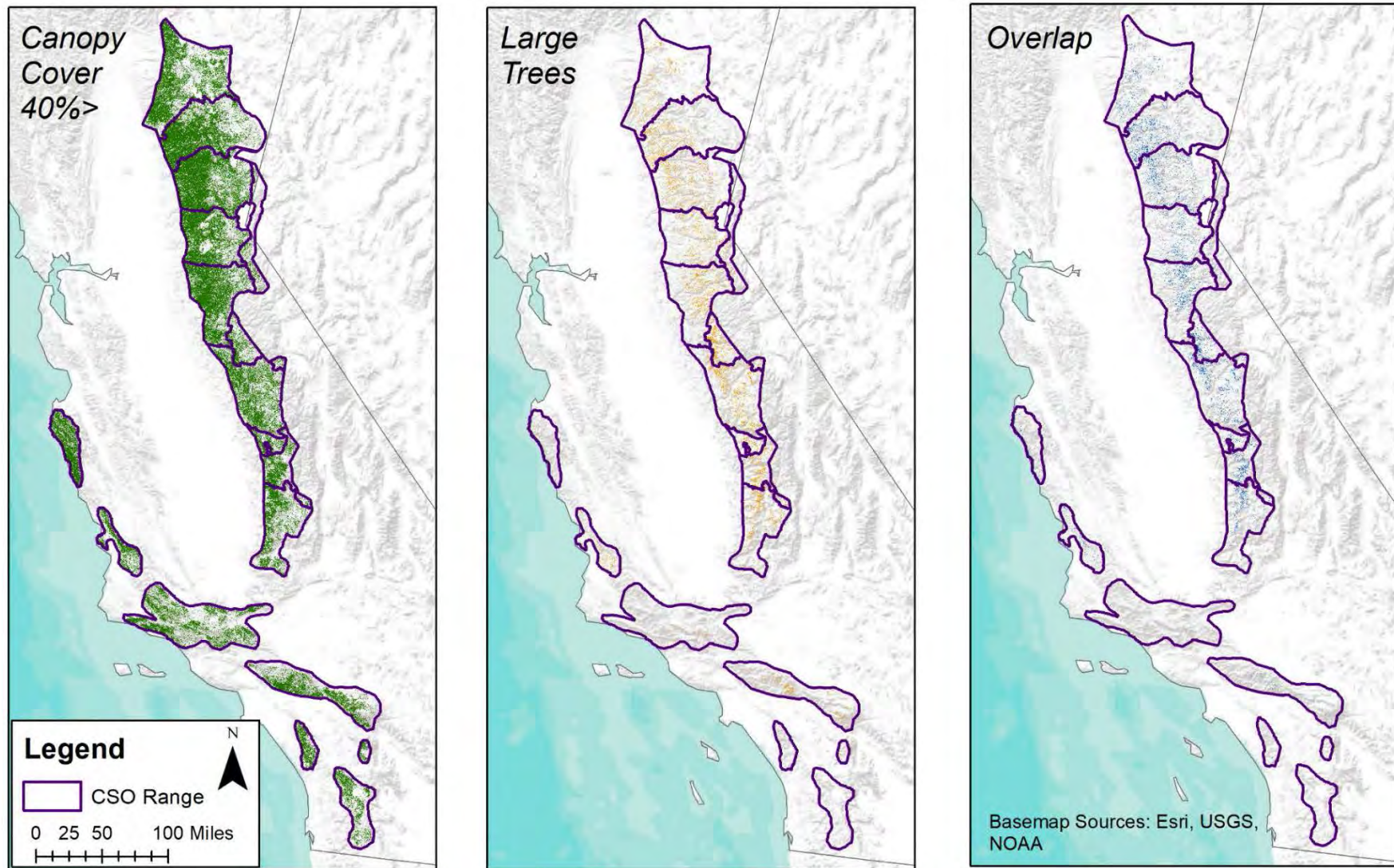


Figure 14: Moderate canopy cover, large trees, and the overlap between the two habitat needs in CSO range. Overlap values are presented by analysis unit in the Sierra Nevada and coastal-southern California population sections 5.3.1 and 5.3.2.

Table 6: Summary of habitat component scoring for large trees, high canopy cover, moderate canopy cover, and the proportion of the analysis unit burned at high-severity.

Score	Large Trees	Moderate Canopy Cover	Large Trees and Moderate Canopy Cover	Proportion burned at high-severity (2011-2021)
3	>15%	>60%	--	--
2	10-15%	41-59%	--	--
1	2-9%	27-40%	>7%	--
0	<2%	0-26%	0-6%	0-4%
-1	--	--	--	>4%

We add the scores across each of the four categories to assign a habitat condition for each analysis unit. We used the available demographic information to help calibrate our habitat assessment, and then used the results of our habitat analysis to determine analysis unit condition. Analysis units with final habitat scores of 6–7 were considered to have the highest habitat suitability, units with habitat scores of 4–5 were considered to have suitable habitat, scores of 2–3 were considered to have less suitable habitat, and units with scores of 0–1 are considered to have the lowest suitability. If an additive score for an analysis unit was -1, we would consider that unit to have no habitat suitability (see Table 7). Note that the individual scores of each habitat component are not associated with overall condition (e.g., an analysis unit with moderate canopy cover above 30% would have 1 point added to habitat condition score, but it does not necessarily mean that the analysis unit is in low or declining condition, and an analysis unit that was >4% burned at high-severity between 2011 and 2021 is not necessarily in declining condition or extirpated, but the condition of the habitat would have been reduced from that burn). We also incorporated overlap values between moderate canopy cover and large trees in our scoring. Although values were low across all analysis units, these findings are consistent with those from other habitat analyses for CSO (e.g., Table 1 in Jones et al. 2018, p. 5) and reinforce the complexity of assessing CSO habitat. The threat of barred owls is not considered in the analysis of current condition because of the success of recent and aggressive removal experiments as described in Chapter 4.6, but is considered in the future as described in the next chapter because of evidence documenting their ability to recolonize and expand rapidly.

Table 7: Habitat analysis based on adding habitat component scores across an analysis unit.

Habitat Score	Habitat Suitability	Overall Condition
-1	No suitability	Extirpated
0–1	Lowest suitability	Strongly Declining
2–3	Less suitable	Declining
4–5	Suitable	Stable
6–7	Highest suitability	Increasing

If demographic data are available for an analysis unit, we provide both the demographic condition as presented in Table 4 and the habitat analysis results to describe the current condition for that analysis unit. For analysis units where no demographic data are available, or where demographic data are only available for a small section of the area within that unit, we only present

our habitat analysis to describe current condition. Our habitat analysis will be used in the assessments of future condition in Chapter 6.

As mentioned in the previous paragraph, we took the average of habitat scores for all analysis units within a population to determine a population score and corresponding population condition; population condition is compared to population resiliency in Table 8. For populations that have an increasing condition, we expect them to have high resiliency at that time period (i.e., they have stable or increasing survival, fecundity, and occupancy, and available habitat has high suitability and is well connected). Populations in increasing condition are expected to persist into the future and have the ability to withstand stochastic events that may occur. Populations in stable condition, which are less resilient than those in high condition, are expected to maintain moderate resiliency with the majority (approximately 70–90 percent) of these populations expected to persist beyond 40–50 years. Populations in stable condition may have some declines in individual or population needs but would likely still be able to support a population. Using this definition, we would not consider a population with very low numbers of individuals, even if those low numbers were stable, to be in stable condition. Because the numbers being maintained are at a very low abundance, we would consider this population to be in declining condition. Populations in declining condition have low resiliency and may not be able to withstand stochastic events because of significant declines in occupancy, survival, fecundity, or habitat suitability. Populations with a declining condition are less likely to persist for 40–50 years, but a population in a declining condition does not automatically mean it will become extirpated. Populations that have a strongly declining condition have very low resiliency and are likely not to withstand stochastic events because of significant declines in occupancy, survival, fecundity, or habitat suitability. Populations in strongly declining condition may not persist for 40–50 years and have the potential to be extirpated. Populations in extirpated condition will not persist for 40–50 years. Populations that have an extirpated condition have no resiliency and cannot withstand stochastic events. To assess the current condition of redundancy we consider the size and distribution of the two CSO populations throughout the species' range, and the plausible catastrophic events to which the species may be exposed. To assess the current condition of representation, we consider the ecological setting and genetic diversity among the two populations.

Table 8: Population condition based on averaging scores across analysis units within a population and how population condition relates to population resiliency

Population Score	Population Condition	Resiliency Definition
<0	Extirpated	None
0–1	Strongly declining	Very Low
2–3	Declining	Low
4–5	Stable	Moderate
6–7	Increasing	High

5.2 Current Condition Uncertainty

We do not have an estimate of CSO abundance throughout the range of the species. Historically the number of CSO territories was used as an index to illustrate the range of the species

and areas in which it occurs. This number includes PACs and other estimates of territories available in the literature. It is a cumulative total of all territories known to be historically or currently occupied by at least one CSO through 2002, so the total increased over time as CSO moved to new territories and as researchers surveyed new areas. Because the number of historical CSO territories was additive rather than reflective of current occupancy, and is outdated by 20 years, these data do not accurately reflect current condition for the species, and should not be viewed as a current population estimate for the taxon. For PACs specifically, they are only retired when the habitat is no longer suitable (i.e., due to wildfire) or they have been reliably documented to lack occupancy or breeding activity in consecutive recent years (Forest Service 2019b, p. 27). Many territories with sufficient suitable habitat may not be occupied in the years following their initial discovery and some historical territories may no longer have sufficient suitable habitat to support CSO due to logging or fires. Moreover, the most recent number of CSO territories was last updated in 2002; since that time, we have not received updated estimates of the total number of territories range-wide. At that time, a total of 2,306 CSO territories had been documented, 1,865 (81%) of which are in the Sierra Nevada (71 FR 29886). Most territories are monitored opportunistically as funding or specific projects arise (e.g., timber harvest project, fuels reduction project, post-fire monitoring, etc.), so without a systematic survey effort, it is challenging to determine the exact number of CSO territories.

While there are extensive and detailed data for many CSO analysis units, not all analysis units have demographic information available to analyze the demographic conditions of occupancy, survival, and fecundity. Additionally, optimal values for large tree and multi-layered moderate canopy cover conditions were largely based upon values from the Sierra Nevada. These values could be different for the coastal-southern California population analysis units, but very little data are available to make this comparison (although we did incorporate an additional analysis using smaller trees for coastal-southern California, as described in the section above). There are limitations to using both GNN and California Forest Observatory data layers to map current CSO habitat conditions, including the scale of analysis and changes in habitat since the layers were published. We attempted to account for some of these changes in habitat by removing areas that have experienced high-severity wildfire since the data layers were published. The scale at which these habitat data are most relevant is larger than the scale at which CSO select nest or roost sites, and the characteristics at the nest tree itself are likely the most important. For example, canopy cover at a nest tree could be due solely to the clumping of several large trees and thus be considered very high at the nest tree, but this detail is lost when the available data are averaged at a larger spatial resolution. We also acknowledge that the presence of a large tree alone (or the smaller tree sizes specific to coastal-southern California) does not ensure that CSO will initiate nesting. Platform and stick nests are often created and abandoned by other wildlife species or features associated with the tree like mistletoe brooms, which we are unable to measure with the data available for this SSA Report. However, there are likely other changes in habitat that have also not been accounted for in our analysis. Although using our habitat analysis as a proxy for condition when demographic information is unavailable leaves the possibility of underestimating or overestimating condition, we think that using the presence of habitat features (large trees and canopy cover) is more likely to overestimate condition by assuming CSO presence in potential habitat. Further, we used the available demographic information to calibrate the categories for our habitat analysis. It is unlikely

that CSO in numbers that might constitute a stable or increasing population in any of the analysis units for which we do not have demographic data have gone undetected by community science (i.e., eBird data), which we would have uncovered while searching available data. Even if we are underestimating habitat due to the scale of our analysis not picking up enough canopy cover, we still cannot assume CSO presence. Further, specific to the coastal-southern California population, available literature (Gutiérrez et al. 2017, p. 242; Tempel et al. 2022, pp. 20–21) suggests that demographics in areas without recent survey data are reduced compared to those with demographic information.

The Geographic Distribution section (Chapter 2.3) of this SSA Report describes available information about potential CSO occurrences in Baja California Norte, Mexico, and the reasons for considering CSO to be only a rare visitor of this area and for not including these areas as part of the species range. However, we acknowledge the uncertainty surrounding CSO in Baja and the lack of information on CSO habitat and/or breeding status in this area. Updated information could change our understanding of the species range to include additional areas besides those currently described in this SSA Report.

5.3 Current Analysis Unit Condition and Population Resiliency

5.3.1 Sierra Nevada Population

Until recently, CSO and suitable habitat were relatively well-distributed in the Sierra Nevada with few barriers to dispersal (Gutiérrez et al. 2017, p. 94): as of 2017, an estimated 1.98 million hectares (4.9 million acres) of suitable habitat for CSO was available in the Sierra Nevada, primarily on federal lands (Gutiérrez et al. 2017, pp. xx, 123). Of that land, 75% is managed by the Forest Service, 7% is managed by the National Park Service (Park Service), and 18% is either privately owned or managed by other government agencies (Gutiérrez et al. 2017, p. xx). The suitable habitat in Gutiérrez et al. (2017) was determined using the California wildlife habitat relationships existing vegetation classification and mapping using tree size classified as ≥ 30 cm (12 in) in combination with canopy cover $\geq 40\%$. However, recent large, catastrophic fires have reduced available habitat and have likely created new barriers for CSO dispersal (see Chapter 4.1 Wildfire). Other barriers to dispersal include urban and suburban development, large reservoirs, physiographic features such as non-forested or unsuitable habitat or vegetation communities, or lack of riparian areas to act as corridors through unsuitable extents (Gutiérrez et al. 2017, pp. 94–95, 253–254). Specific information about habitat and demographic conditions, when available, is incorporated below for each of the Sierra Nevada analysis units.

From our habitat analyses, we found that the Sierra Nevada has higher canopy cover and tree size values than coastal-southern California, which was not unexpected (see Tables 5, 9, and 13). When comparing the northern to the southern Sierra Nevada, the north contains higher canopy cover which aligns with historical forest structure data that tends to show more dense forests in the northern Sierra Nevada (Van Wagtendonk et al. 2006, p. 250), with the exception being are on the east side of the Sierra Nevada (i.e., Humboldt-Toiyabe and Inyo analysis units) which contain more open and disjunct habitat than the west side. Higher canopy cover combined with higher precipitation levels tend to result in lower tree mortality in the northern Sierra Nevada (see Figure 9 in section 4.2 Tree Mortality) which may have helped reduce the potential for megafires in the

northern Sierra Nevada in past years, but climate change impacts of reduced snowpack and increased temperatures show that increased fire risk is also occurring in the northern Sierra Nevada (see 4.4 Climate Change). We also found the two units mostly containing National Parks (e.g., Yosemite and Sequoia-Kings Canyon) contain the largest tree size percentages. Overall, the overlap values between canopy cover and large trees was low across all analysis units (see Table 9)

Table 9: Habitat component (large trees, moderate canopy cover, and their overlap) analysis results for analysis units within the Sierra Nevada population.

Analysis Unit	Large trees	Moderate Canopy cover	Moderate Canopy Cover & Large Trees Overlap
Lassen	4%	48%	2%
Plumas	5%	51%	4%
Tahoe	7%	64%	5%
Eldorado	6%	57%	4%
Humboldt-Toiyabe	4%	24%	2%
Stanislaus	7%	62%	5%
Yosemite	18%	36%	9%
Sierra	9%	47%	6%
Sequoia-Kings Canyon	11%	44%	8%
Sequoia	7%	37%	3%
Inyo	7%	26%	3%

The threats that are currently impacting the Sierra Nevada population include large-scale high-severity fire, tree mortality, drought, climate change, various impacts from fuels reductions and forest management, competition with barred owls, and rodenticides. As described in the descriptions of the analysis units below, these threats are not equivalent across all analysis units within the Sierra Nevada population. For example, competition with barred owls is more pronounced in the northern part of this population than in the southern portion, and the threat from rodenticides is more pronounced at the wildlife-urban interface. However, some threats, like fire, are considered a threat across the population, and there is a general increasing trend in the annual acreage and relative proportion of high-severity fires in the Sierra Nevada (Keane in litt. 2022, p. 3). In 2020–2021, the percent of habitat that burned at high-severity within CSO PACs in the Sierra Nevada was almost twice as that from 1993–2019; in 1993–2019, 35% of fire burned at high-severity, compared to 65% of fire being high-severity in 2020–2021. (Keane in litt. 2022, p. 5). We conducted a separate fire analysis for the entire CSO range which includes PACs as well as additional acreage outside PACs. Our fire analysis shows similar results, with approximately 42% of the CSO range in the Sierra Nevada burned between 1984 and 2021, with 7% and 12% of that total from acreages burned in 2020 and 2021, respectively. Of the 42% of CSO range burned within the Sierra Nevada, approximately 13% was burned at high-severity. In our supplemental analysis which analyzes habitat and fire metrics along a documented ecological boundary between the northern and southern Sierra Nevada, we found that both portions of the Sierra Nevada burned at similar amounts between 1984 and 2021. However, the majority of burned acreage in the northern Sierra Nevada occurred in 2021 (18% burned with 9% at high-severity compared to 5% or less in all other years and 2% or less for

high-severity from 1984 to 2021). In the southern Sierra Nevada 11% burned in 2020 with 2% at high-severity in 2020 and 2021, compared to 5% or less total burned and 1% or less for high-severity from 1984 to 2021. These results are presented in Appendix I and suggest higher levels of disturbance to the species and increased recovery time for habitat conditions to improve post-fire because such a large acreage burned over a relatively concentrated period of time. Fire severity information by analysis unit is described below for each of our Sierra Nevada analysis units from 1984 through 2021 and is shown in Table 10. Data from 2011 through 2021 is shown in Table 11 (see Appendix I for tables of fire severity by year for each analysis unit).

Table 10: Proportion of analysis unit burned at low-, moderate-, and high-severity for the Sierra Nevada analysis units from 1984 to 2021.

Analysis Unit	Low-Severity	Moderate-Severity	High-Severity	Total
Lassen	15.63%	11.65%	16.29%	43.57%
Plumas	20.63%	19.51%	30.92%	71.06%
Tahoe	2.97%	2.70%	2.64%	8.31%
Eldorado	9.57%	7.84%	13.85%	31.26%
Humboldt-Toiyabe	5.42%	5.22%	5.66%	16.30%
Stanislaus	14.80%	14.23%	9.35%	38.38%
Yosemite	32.88%	14.80%	8.93%	56.61%
Sierra	21.07%	15.24%	7.27%	43.58%
Sequoia-Kings Canyon	16.70%	8.44%	6.85%	31.99%
Sequoia	24.32%	19.47%	16.41%	60.20%
Inyo	18.34%	10.91%	7.11%	36.36%

Table 11: Proportion of analysis unit burned at low-, moderate-, and high-severity for the Sierra Nevada analysis units from 2011 to 2021.

Analysis Unit	Low-Severity	Moderate-Severity	High-Severity	Total
Lassen	10.89%	8.61%	13.58%	33.0%
Plumas	14.72%	15.03%	26.89%	56.34%
Tahoe	0.74%	0.76%	0.59%	2.09%
Eldorado	8.33%	6.47%	11.85%	26.65%
Humboldt-Toiyabe	2.45%	2.21%	3.83%	8.49%
Stanislaus	7.60%	7.41%	5.10%	20.11%
Yosemite	13.58%	8.14%	4.93%	26.65%
Sierra	18.24%	13.28%	6.52%	38.04%
Sequoia-Kings Canyon	10.15%	5.55%	5.66%	21.36%
Sequoia	15.05%	11.77%	10.29%	37.11%
Inyo	8.01%	4.45%	0.49%	12.95%

In addition to common threats acting on all analysis units within this population, there are also common management actions taking place within the Sierra Nevada. For example, the Forest

Service designates PACs around known CSO nest trees, so analysis units containing national forests (e.g., all Sierra Nevada population analysis units except for Yosemite and Sequoia-Kings Canyon) include these protections (see 4.9 Regulatory Mechanisms and Management Actions). Further, barred owl removal experiments have so far been successful in avoiding the catastrophic impacts that could have occurred in the absence of any management (see 4.6 Competition and Hybridization with Barred Owls and 4.9 Regulatory Mechanisms and Management Actions).

Lassen Analysis Unit Condition

The Lassen analysis unit includes the Lassen National Forest, Lassen National Park, and other private lands that are within the CSO range. Forest Service lands and Park Service lands were combined within this one analysis unit due to the fact that Lassen National Park is completely surrounded by and within Lassen National Forest.

The Lassen analysis unit has been part of an ongoing CSO demography study, with consistent data ranging back to the early 1990s (Jones et al. 2018, p. entire); most of the area within this study is on public land managed by the Forest Service. This analysis unit has high apparent adult survival (Blakesley et al. 2010, pp. 13–14; Conner et al. 2016, p. 11). Blakesley et al. (2010, p. 12) found male adult survival in the Lassen analysis unit to be 0.840 (± 0.017) and female adult survival to be 0.848 (± 0.016). Reproductive output, measured in both number of female young fledged per territorial female and total number of young fledged per territorial female, have varied over time (Franklin et al. 2004, p. 24; Blakesley et al. 2010, pp. 17–19). Models of the probability of territory occupancy show reductions of 21% (95% Confidence Interval -34% to -9%) from 1993 to 2013 (Conner et al. 2016, p. 15). When taking into account all demographic parameters, a population decline of -44% has been observed (95% Confidence Intervals -61% to -21%) over that same time period (Conner et al. 2016, p. 15).

Our habitat analysis found the Lassen analysis unit contains 4% large trees, a moderate canopy cover value of 48%, and a large tree and moderate canopy cover overlap value of 2%. Although this unit has a relatively high canopy cover percentage compared to other analysis units within the Sierra Nevada population, the low percentage of large trees suggests the habitat has been degraded from historical conditions. Our fire analysis supports this, with approximately 44% of the unit burned between 1984 and 2021, 16% of which was at high-severity. Between 2011 and 2021, 14% of the unit burned at high-severity. Protected Activity Center data from the Forest Service from 1993–2021 reveals wildfires have burned 57% of PAC acreage in the Lassen National Forest, which is part of the Lassen analysis unit. Wildfires have burned 62% of PAC acres within fire perimeters at high- or moderate-severity (Keane in litt. 2022, p. 6). Most recently, the Dixie fire burned almost 850,000 acres, including habitat containing 168 PACs (Keane in litt. 2022, p. 13).

Current condition for the Lassen analysis unit was determined using available demographic information and our habitat analysis. Our habitat analysis found this unit has less suitable habitat with an overall score of 2. Considering population declines through 2013 and substantial reduction in habitat from wildfire within this analysis unit, the current condition of the Lassen analysis unit is declining (see Table 12).

Plumas Analysis Unit Condition

The Plumas analysis unit includes the Plumas National Forest as well as private lands in the area within the CSO range. The CSO demography study described for the Lassen unit also covers a large portion of the Plumas analysis unit; therefore the results of that demographic study (i.e., survival, fecundity, occupancy, or population growth) also applies to the Plumas unit.

For the Plumas analysis unit, our habitat analysis found the unit contains 5% large trees, 51% moderate canopy cover, and a large tree and moderate canopy cover value of 4%. Similar to the Lassen unit, the Plumas unit has a relatively high canopy cover percentage, but a low percentage of large trees, suggesting the habitat has been degraded from historical conditions. Since our fire analysis reveals approximately 71% of this analysis unit has burned between 1984 and 2021, 31% at high-severity, the habitat condition of this unit has been degraded since historical conditions. Further, 27% of the unit has burned at high severity between 2011 and 2021.

Between 1993 and 2021, wildfires have burned 65% of PAC acreage in the Plumas National Forest portion of this analysis unit. Considering only PAC acres within fire perimeters, wildfires have burned 68% at high or moderate-severity during this same time period (Keane in litt. 2022, p. 6). Available suitable habitat has decreased from over 303,000 ha (pre-2017) to under 200,000 ha in 2022 (removing areas burned with 50% basal area mortality) (Chudek in litt. 2022, p. 2). These wildfires have affected many PACs in the Plumas National Forest, in some cases resulting in complete habitat loss or retirement of the PAC designation, and in other cases leading to minor to significant boundary revisions of the PACs (Chudek in litt. 2022, p. 1). Since 2000, 177 out 319 PACs have had a change in status or boundary: 55 have been retired (all but 1 of these due to wildfires), an additional 20 pending retirement, and 102 PAC boundaries have been revised. Border revisions may remain within fire scars and revisions may be redrawn in areas with lower quality or degraded habitat in areas burned at lower-severity. In some cases, PACs were redrawn into areas with no previous history of CSO use (Chudek in litt. 2022, p. 2). Wildfire effects to CSO in the Plumas National Forest have accelerated between 1993 and 2021, and wildfires have impacted 146 PACs in the last three years alone (Chudek in litt. 2022, p. 1). A gap in the distribution within the Plumas analysis unit, mainly on private land, extends east-west which may limit dispersal within this analysis unit (Gutiérrez et al. 2017, pp. 204–206).

Our habitat analysis found this unit has less suitable habitat with an overall score of 2. Overall, the current condition of the Plumas analysis unit is declining based on available demographic information and our habitat analysis, which is further supported by available information on PAC retirement and PAC boundary revisions (see Table 12).

Tahoe Analysis Unit Condition

The Tahoe analysis unit includes the Tahoe National Forest, a portion of the Forest Service's Lake Tahoe Basin Management Unit, as well as private lands in the area within the CSO range. No information is available to assess the current condition of survival, fecundity, occupancy, or population growth for the Tahoe analysis unit.

The results of our habitat analysis for the Tahoe analysis unit found the unit contains 7% large trees, 64% moderate canopy cover, and 5% overlap of large trees and canopy cover. This unit

has the highest canopy cover percentage; however, the results for tree size suggest the habitat has been degraded from historical conditions. In contrast, our fire analysis finds only 8% of this unit has burned between 1984 and 2021, with only 3% at high-severity, suggesting the habitat in this unit is likely still relatively intact. Between 2011 and 2021, only 1% of this unit burned at high severity. From 1993–2021, wildfires have burned 13% of PAC acreage in the Tahoe National Forest, part of this analysis unit. Considering only PAC acres within fire perimeters, wildfires have burned 46% at high- or moderate-severity (Keane in litt. 2022, p. 6). Granite outcrops and red fir forest, both associated with low CSO density, give the habitat a checkerboard pattern of suitability which may limit CSO distribution within the analysis unit causing Verner et al. (1992, pp. 49–50) to label this an area of concern for the integrity of the range within the Sierra Nevada (Gutiérrez et al. 2017, pp. 204–206).

Our habitat analysis found this unit has suitable habitat with an overall habitat suitability score of 4. Overall, the current condition of the Tahoe analysis unit is stable based on our habitat analysis (see Table 12).

Eldorado Analysis Unit Condition

The Eldorado analysis unit includes the Eldorado National Forest, a portion of the Lake Tahoe Basin Management Unit, as well as other private lands in the area within the CSO range. The Eldorado analysis unit has been part of an ongoing demography study within the CSO range, with data ranging back to the early 1990s (Jones et al. 2018, p. entire); most of the area within this study was on public land managed by the U.S. Forest Service. This analysis unit has high apparent adult survival (Blakesley et al. 2010, pp. 13–14; Tempel et al. 2014b, p. 91). Blakesley et al. (2010, p. 12) found male adult survival in the Eldorado analysis unit to be 0.843 (± 0.020) and female adult survival to be 0.811 (± 0.021). Reproductive output has a decreasing trend (Franklin et al. 2004, p. 24; Blakesley et al. 2010, pp. 17–19). When only considering occupancy from 1993–2010, population declines have been modeled to be -30% (95% Confidence Interval -45% to -15%) (Tempel and Gutiérrez 2013, pp. 1091–1093). A follow-up study using an integrated population model (which took into account all demographic parameters, including occupancy data, reproduction data, and mark-recapture data) calculated a population decline of 50% (95% CI: -62% to -46%) from 1990–2012 (Tempel et al. 2014b, pp. 86, 90–92). A checkerboard pattern of lands and large private inholdings may limit distribution across this analysis unit; the checkerboard pattern of lands is associated with mixed habitat suitability, and lack of surveys on private lands (and therefore uncertainty about presence) also led Verner et al. (1992, pp. 49–50) to label this an area of concern (Gutiérrez et al. 2017, pp. 204–206).

Habitat values for this unit includes 6% large trees, 57% moderate canopy cover, and 4% overlap of large trees and canopy cover. These data suggest that the habitat is degraded. Our fire analysis finds between 1984 and 2021, 31% of this unit has burned, 14% at high-severity, and between 2011 and 2021 12% of the unit burned at high severity. From 1993–2021, wildfires have burned 57% of PAC acreage in the Eldorado National Forest, part of this analysis unit. Considering only PAC acres within fire perimeters, wildfires have burned 62% at high or moderate-severity (Keane in litt. 2022, p. 6). When considering the Caldor Fire that burned in 2021, 43.8% of PACs burned at over 50% high severity (Keane in litt. 2022, p. 13).

Our habitat analysis found this unit has less suitable habitat with an overall habitat suitability score of 2. Considering demographic information and our habitat analysis for this analysis unit, the current condition of the Eldorado analysis unit is declining (see Table 12).

Humboldt-Toiyabe Analysis Unit Condition

The Humboldt-Toiyabe analysis unit is a small analysis unit on the eastern edge of the CSO range that includes a portion of the Humboldt-Toiyabe National Forest, a portion of the Lake Tahoe Basin Management Unit, as well as state and private lands in the area within the CSO range. There are six PACs within the Humboldt-Toiyabe National Forest, most of which have experienced impacts from threats and reduced detections in recent years. The only confirmed active PAC was fully consumed by wildfire in 2021 (Forest Service 2022d). One CSO territory currently exists on state land at Lake Tahoe and has been active every year since it was first discovered in 2015. The territory has fledged 3 young during that time (Enders in litt. 2022). There are no PACs in the Lake Tahoe Basin Management Unit within this analysis unit. No further information is available to assess the current condition of survival or fecundity, for the Humboldt-Toiyabe analysis unit. There are no known barriers to limit dispersal within this analysis unit.

Habitat analysis for this unit only included habitat within California because there were no data available for Nevada that was comparable to the data for California used for the rest of this SSA Report. The results of our habitat analysis for this unit found 4% large trees, 24% moderate canopy cover, and a large trees and moderate canopy cover overlap value of 2%. These results suggest the habitat is less suitable for CSO, possibly due to a less productive system on the eastern edge of the Sierra Nevada (Dilts 2022, p. 5). For the northern and eastern portion of this analysis unit, which cover some of the Nevada extent not included in our habitat analysis, Dilts (2022, pp. 5–9) found that habitat for both nesting and foraging is extremely limited and more discontinuous compared to other parts of the Sierra Nevada including within the Lake Tahoe Basin.

Our fire analysis finds that between 1984 and 2021, 16% of the unit has burned with 6% of this at high-severity, which is relatively low compared to the other Sierra Nevada analysis units. Between 2011 and 2021, only 4% of the unit burned at high severity. However, in 2021, 2 of the 6 PACs on the Humboldt Toiyabe National Forest were partially or fully consumed by the Tamarack Fire (Forest Service 2022d, pp. 2–3).

Our habitat analysis found this unit has the lowest habitat suitability with an overall score of 1, which is at the upper limit of our scoring boundary for this habitat suitability category. Overall, the current condition of the Humboldt-Toiyabe analysis unit is strongly declining based on available PAC information and our habitat analysis (see Table 12).

Stanislaus Analysis Unit Condition

The Stanislaus analysis unit includes the Stanislaus National Forest as well as private lands in the area within the CSO range. No information is available to assess the current condition of survival, fecundity, or occupancy for the Stanislaus analysis unit. Dispersal may be constrained by two potential gaps in the distribution because of large private inholdings, where occupancy is unknown, and a burned area leaving the habitat highly fragmented (Verner et al. 1992, pp. 49–50; Gutiérrez et al. 2017, pp. 204–206).

This unit contains 7% large trees, 62% moderate canopy cover, and 5% overlap of large trees and moderate canopy cover based on the results of our habitat analysis. Between 1984 and 2021, approximately 38% of the unit has burned, with 9% at high-severity. Between 2011 and 2021, 5% of the unit burned at high severity. These values suggest some habitat degradation has occurred in this unit since historical conditions. From 1993–2021, wildfires have burned 36% of PAC acreage in the Stanislaus National Forest, which is part of this analysis unit. Considering only PAC acres within fire perimeters, wildfires have burned 43% at high- or moderate- severity (Keane in litt. 2022, p. 6).

Our habitat analysis found this unit has less suitable habitat with an overall habitat suitability score of 3, which is at the upper limit of our scoring boundary for this habitat suitability category. Overall, the current condition of the Stanislaus analysis unit is declining based on our habitat analysis (see Table 12).

Yosemite Analysis Unit Condition

The Yosemite analysis unit includes Yosemite National Park as well as private lands in the area within the CSO range. Based on data collected recently within Yosemite National Park, 36 historical CSO territories from 2004 and 2013 were monitored from 2015 through 2017 and 27 territories were documented (Schofield et al. 2020, pp. 2, 3, 5). Several nests were found in 2017, including eight nests within the 2013 Rim Fire perimeter and eight nests outside the perimeter (Schofield et al. 2020, p. 5), indicating occupancy and fecundity may have remained stable and largely unaffected by the Rim Fire and drought. Because the Yosemite analysis unit does not have the 20+ years of data that are available for the other analysis units that are part of the CSO demography study, it is hard to compare across timescale and protocols. There are no known barriers which may limit dispersal in this area.

Our habitat analysis found the Yosemite analysis unit contains 18% large trees, 36% moderate canopy cover, and an overlap value of 9%. Although this unit has a relatively low percentage of moderate canopy cover compared to other analysis units in this population, the high percentage of large trees suggests the habitat is not as degraded as other Sierra Nevada population units. Our fire analysis finds approximately 57% of the unit burned between 1984 and 2021, 9% of which was at high-severity. Between 2011 and 2021, 5% of the unit burned at high severity.

Although CSO in Yosemite were detected successfully reproducing using moderate canopy cover values, they may have been successful due to the presence of large trees in this analysis unit and overall high quality habitat prior to disturbance like wildfire, drought, and subsequent tree mortality (Schofield et al. 2020, pp. 5, 8). This unit also has the largest percentage of moderate canopy cover and large tree overlap, which may explain why this unit is doing so well (see Table 9). Our habitat analysis found this unit has suitable habitat with an overall habitat suitability score of 4. Overall, the current condition of the Yosemite analysis unit is stable based on our habitat analysis (see Table 12).

Sierra Analysis Unit Condition

The Sierra analysis unit includes both the Sierra National Forest and other private lands in the area within the CSO range. The Sierra analysis unit has been part of an ongoing demography

study within the CSO range, with data ranging back to the early 1990s (Jones et al. 2018, p. entire); most of the area within this study was on public land managed by the U.S. Forest Service. This area has high apparent adult survival with male adult survival found to be 0.890 (± 0.016) and female adult survival to be 0.885 (± 0.016) (Blakesley et al. 2010, p. 12). Reproductive output has varied over time (Franklin et al. 2004, p. 24; Blakesley et al. 2010, pp. 17–19). When only considering occupancy, population declines have been modeled to be -13% (95% Confidence Interval -26% to 0%) (Conner et al. 2016, p. 15). Over the same period, mark-recapture based population models showed a decline of 31% (95% CI: -50% to -4%) (Conner et al. 2016, p. 15). Natural and anthropogenic fragmentation due to low elevations, dry conditions, and accentuated logging may limit dispersal within this analysis unit (Gutiérrez et al. 2017, pp. 204–206).

The results of our habitat analysis for the Sierra analysis unit found the unit contains 9% large trees, 47% moderate canopy cover, and 6% overlap of large trees and moderate canopy cover. These results suggest the habitat has degraded from historical condition. Our fire analysis finds 44% of the Sierra analysis unit burned between 1984 and 2021, with only 7% at high-severity. Between 2011 and 2021, 7% of the unit burned at high-severity. From 1993–2021, wildfires have burned 45% of PAC acreage in the Sierra National Forest, part of this analysis unit. Including only PAC acres within fire perimeters, wildfires have burned 65% at high- or moderate-severity (Keane in litt. 2022, p. 6).

Our habitat analysis found this unit has less suitable habitat with an overall habitat suitability score of 2. Considering our habitat analysis, recent PAC information, and demographic data, the current condition of the Sierra analysis unit is declining (see Table 12).

Sequoia-Kings Canyon Analysis Unit Condition

The Sequoia-Kings Canyon analysis unit includes Sequoia and Kings Canyon National Parks as well as private lands in the area within the CSO range. This analysis unit has been part of an ongoing demography study within the CSO range, with data ranging back to the early 1990s (Jones et al. 2018, p. entire). This analysis unit has high apparent adult survival (Blakesley et al. 2010, pp. 13–14; Conner et al. 2016, p. 11). Blakesley et al. (2010, p. 12) found male adult survival in the Sequoia-Kings Canyon analysis unit to be 0.890 (± 0.016) and female adult survival to be 0.885 (± 0.016). Reproductive output, measured in both number of female young fledged per territorial female and total number of young fledged per territorial female, has increased through time (Franklin et al. 2004, p. 24; Blakesley et al. 2010, pp. 17–19). When only considering occupancy, a population change of -1% (95% Confidence Interval -15% to +15%; Conner et al. 2016, p. 15) has been calculated, indicating a relatively stable population. Results from mark-recapture population models show a possible population increase of 25%, though the confidence intervals in this case were wide (95% CI: -15% to +85%) (Conner et al. 2016, p. 15). Available summaries of ongoing monitoring in this study area show that high rates of CSO territory occupancy have been maintained through 2022 (Munton and Keane 2022, p. 2). There are no known barriers which may limit dispersal in the Sequoia-Kings Canyon analysis unit.

Our habitat analysis found the Sequoia-Kings Canyon analysis unit contains 11% large trees, 49% moderate canopy cover, and an overlap value of 8%. The high percentage of large trees and moderate canopy cover within this unit suggest the habitat is not as degraded as other Sierra Nevada

population units. Further, this unit has the second largest percentage of moderate canopy cover and large tree overlap, which may explain why this unit is doing so well (see Table 9). Our fire analysis finds that 32% of the unit burned between 1984 and 2021, with just 7% of this at high-severity. Between 2011 and 2021, 6% of this unit burned at high-severity. Most of the fire occurred in 2021 with 5% at high-severity.

Our habitat analysis found this unit has suitable habitat with an overall habitat suitability score of 4. Overall, the current condition of the Sequoia-Kings Canyon analysis unit is stable based on available demographic information and our habitat analysis (see Table 12).

Sequoia Analysis Unit Condition

The Sequoia analysis unit includes both the northern and southern portions of the Sequoia National Forest as well as private lands in the area within the CSO range. No information is available to assess the current condition of survival, fecundity, or occupancy for the Sequoia analysis unit. There are no known barriers which may limit dispersal in this analysis unit.

Habitat values for this analysis unit include 7% large trees, 37% moderate canopy cover, and a large trees and moderate canopy cover overlap of 3%. All these values are relatively low compared to the other Sierra Nevada population units. Our fire analysis finds that 60% has burned between 1984 and 2021, with 16% at high-severity. Between 2011 and 2021, 10% of the unit burned at high-severity. From 1993–2021, wildfires have burned 75% of PAC acreage in the Sequoia National Forest. Considering only PAC acres within fire perimeters, wildfires have burned 68% at high- or moderate-severity (Keane in litt. 2022, p. 6).

Our habitat analysis found this unit has the lowest habitat suitability with an overall score of 1, which is at the upper limit of our scoring boundary for this habitat suitability category. Based on our habitat analysis, which is further supported by recent PAC data, the current condition of the Sequoia analysis unit is strongly declining (see Table 12).

Inyo Analysis Unit Condition

The Inyo analysis unit is a small peripheral area that includes the Inyo National Forest as well as private lands in the area within the CSO range. This analysis unit encompasses historical spotted owl detections from 1992 and earlier. However, surveys in recent years (2019–2022) have not detected CSO (Schlick and Torres pers. comm. 2022). There are currently no known PACs within the Inyo analysis unit. The southern portion of this unit with historical detections is still considered suitable habitat, yet CSO were not detected during recent surveys (Schlick and Torres pers. comm. 2022). There are no known barriers which may limit dispersal in this analysis unit.

Habitat values for this unit includes 7% large trees, 26% moderate canopy cover, and an overlap value of 3%. This unit contains low habitat values compared to other Sierra Nevada population units. The very low percentage of canopy cover for this unit suggest degraded habitat. Our fire analysis finds that 36% of this unit has burned between 1984 and 2021, with 7% of this at high-severity. Between 2011 and 2021, none of the unit burned at high severity. In one portion of the analysis unit, a large wildfire and windstorm event dramatically altered canopy cover and the habitat no longer appears suitable (Schlick and Torres pers. comm. 2022; Torres in litt. 2022).

Our habitat analysis found this unit has the lowest habitat suitability with an overall score of 1, which is at the upper limit of our scoring boundary for this habitat suitability category. Overall, the current condition of the Inyo analysis unit is strongly declining based on our habitat analysis, which is supported by the lack of CSO detections in recent years (see Table 12).

Overall Resiliency for the Sierra Nevada Population

The current condition of analysis units throughout the Sierra Nevada population varies, with three analysis units currently considered stable, five declining, and three strongly declining (see Table 12). However, all three of the strongly declining units are at the upper boundary of our scoring system. Based on these results, the overall condition of the Sierra Nevada population is declining with an average overall habitat score of 2.4. Therefore, the Sierra Nevada population currently has low resiliency (see Table 8).

Table 12: Summary of habitat scores and overall current condition of analysis units in the Sierra Nevada population. Overall current condition is based on the demographic condition (when available), or the habitat condition for analysis units without demographic information. See Table 18 for the full habitat scoring analysis for all CSO analysis units.

Analysis Unit	Overall habitat score	Analysis unit condition
Lassen	2	Declining
Plumas	2	Declining
Tahoe	4	Stable
Eldorado	2	Declining
Humboldt-Toiyabe	1	Strongly declining
Stanislaus	3	Declining
Yosemite	4	Stable
Sierra	2	Declining
Sequoia-Kings Canyon	4	Stable
Sequoia	1	Strongly declining
Inyo	1	Strongly declining

5.3.2 Coastal-Southern California Population

Habitat within the coastal-southern California CSO population is considered to be naturally fragmented, with little dispersal occurring between subpopulations due to discontinuous mountain ranges (Gutiérrez et al. 2017, pp. 93–95). This natural fragmentation has been further fragmented by development/habitat loss in the greater southern California area. Specific information about habitat and demographic conditions, when available, is incorporated below for each of our coastal-southern California analysis units. We do not mention dispersal again within text for the specific analysis units, because as mentioned in Chapter 3.2.1, available evidence does not document successful dispersal between the San Bernardino, San Gabriel, and San Jacinto Mountains, which are adjacent mountain ranges, indicating that if dispersal does occur within this population, it is very rare (LaHaye et al. 2001, p. entire, 2004, p. entire; Gutiérrez et al. 2017, pp. 242, 250).

As previously discussed, within this population, occupancy data are only available for the San Bernardino Mountains. The San Bernardino Mountains have historically contained the largest

number of CSO, suggesting that information extrapolated from this area would lead to an optimistic view for the overall population (Gutiérrez et al. 2017, p. 242). Data from Tempel et al. (2022, pp. 20–21) showed higher occupancy in the San Bernardino Mountains than the San Jacinto and San Gabriel Mountains, and the authors suggest that other parts of coastal-southern California may also have experienced greater declines than this area.

As mentioned for the Sierra Nevada population, our habitat analyses found that habitat values for large trees and canopy cover were lower in coastal-southern California than in the Sierra Nevada (see Tables 5, 9, and 13). Overlap between canopy cover and large trees was also low (see Table 13). In southern California, high canopy cover is positively associated with CSO reproductive output, but large trees appeared to be more important than high canopy cover (Tempel et al. 2022, p. 22) and are also important for occupancy. Our analysis found large tree values for coastal-southern California are low, which may indicate lower habitat suitability in these analysis units. For this population, we conducted an additional analysis identifying the percentage of small trees within the overall population that could potentially support platform or stick nests (see Table 14). We did not conduct this analysis for each analysis unit, but show the distribution of small and large trees in Figure 15. We found that 14% of the coastal-southern California analysis units contain these small trees compared to an overall value of 1% for large trees when only trees larger than 61 cm are considered. When looking at the combined total of small trees and large trees, 16% of coastal-southern California contains potential trees that could support CSO ecological needs (see Table 14).

Table 13: Habitat component (large trees and moderate canopy cover) analysis results for analysis units within the coastal-southern California population.

Analysis Unit	Large trees	Moderate Canopy cover	Moderate Canopy Cover & Large Trees Overlap
Los Padres	3%	59%	2%
Los Padres-Angeles	1%	33%	0%
San Bernardino	2%	31%	0%
Cleveland	0%	34%	0%

Table 14: Proportion of small and large trees in coastal-southern California.

>33cm and <61cm (small trees)	>33cm (small and large trees)	>61cm (large trees)
14%	16%	1%

The threats that are likely currently impacting this population include large-scale high-severity fire, tree mortality, drought, climate change, various impacts from fuels reductions and forest management, and rodenticides. Competition with barred owls is not yet considered a current threat within this population. Impacts from these threats may not be equally distributed across the population and are not equivalent to the ways that these threats impact the Sierra Nevada population. For example, what might be considered a stochastic event in the Sierra Nevada population leading to the removal of one or a few individuals from the population, could instead be considered catastrophic if it were to occur in the coastal-southern California population because of the lower number of CSO within this population. Our fire analysis shows that 60% of the CSO

range in coastal-southern California burned between 1984 and 2021, 17% at high-severity, with 6% of the total area burned in 2020 and 1% at high-severity that year. There were no fires in 2021 within this population. Typically, 4% or less of habitat within this population burned per year with 1% or less burning at high-severity, although some years burned at higher percentages (2003 at 6% with 3% high-severity and 2007 at 8% with 4% high-severity; see Appendix I). Fire severity information by analysis unit is described below for each of our coastal-southern California analysis units and is shown in Tables 15 and 16. In addition to common threats acting on all analysis units within this population, there are also common management actions taking place throughout the analysis units comprising the coastal-southern California population. For example, analysis units containing national forests include PACs around known CSO nest trees (see 4.9 Regulatory Mechanisms and Management Actions).

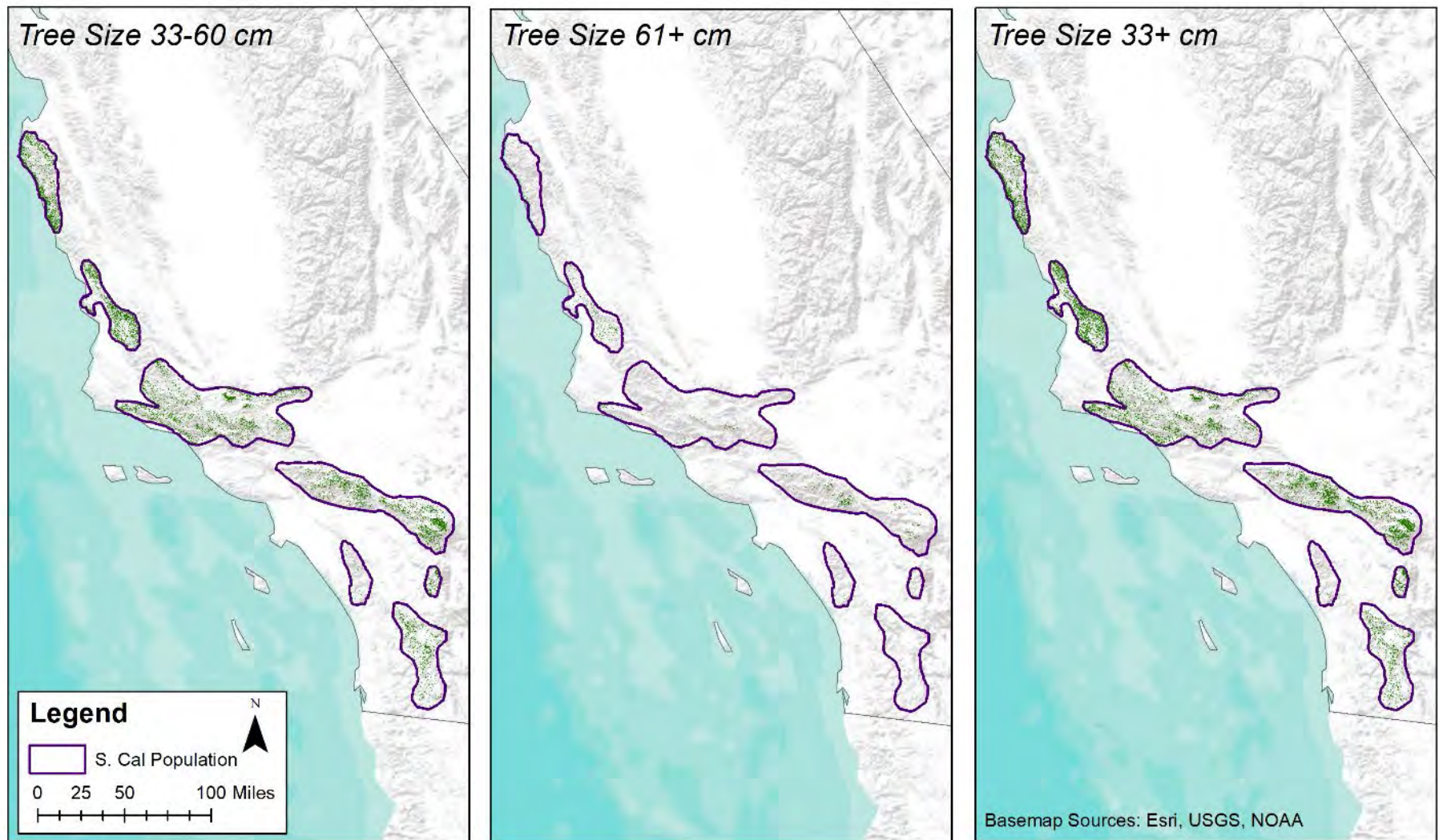


Figure 15: Tree size analysis for coastal-southern California units for large trees (61+ cm) and smaller trees (33+ cm). The first panel shows the tree sizes that are most likely to support platform nests based on data collected from platform nests on San Bernardino National Forest between 2015 and 2021 (nest type data was not available for earlier years).

Table 15: Proportion of analysis unit burned at low-, moderate-, and high-severity for the coastal-southern California population analysis units from 1984 to 2021.

Analysis Unit	Low- Severity	Moderate-Severity	High-Severity	Total
Los Padres	24.85%	24.49%	18.82%	68.16%
Los Padres-Angeles	16.94%	20.18%	17.68%	54.80%
San Bernardino	25.94%	27.61%	12.95%	66.50%
Cleveland	17.06%	16.84%	19.11%	53.01%

Table 16: Proportion of analysis unit burned at low-, moderate-, and high-severity for the coastal-southern California population analysis units from 2011 to 2021.

Analysis Unit	Low-Severity	Moderate-Severity	High-Severity	Total
Los Padres	10.36%	8.01%	5.58%	23.95%
Los Padres-Angeles	4.67%	7.58%	1.50%	13.75%
San Bernardino	10.32%	9.47%	3.20%	22.99%
Cleveland	3.02%	2.39%	0.76%	6.17%

Los Padres Analysis Unit Condition

The Los Padres analysis includes the Los Padres National Forest as well as private lands in the area within the CSO range. We do not have demographic or dispersal information about CSO in the Los Padres analysis unit.

The results of our habitat analysis for this unit found 3% large trees, 59% moderate canopy cover, and an overlap value of 2%. These percentages are higher than those in other coastal-southern California population analysis units. Our fire analysis shows between 1984 and 2021, 68% of the unit has burned with 19% at high-severity, which is relatively high compared to the other coastal-southern California analysis units. Between 2011 and 2021, 6% of this unit burned at high-severity.

Our habitat analysis found this unit has less suitable habitat with an overall habitat suitability score of 2. Overall, the current condition of the Los Padres analysis unit is declining based on our habitat analysis (see Table 17).

Los Padres-Angeles Analysis Unit Condition

The Los Padres-Angeles analysis unit includes the Angeles National Forest and a portion of the Los Padres National Forest, as well as private lands in this area. We have limited information about demographic condition from the Tempel et al. (2022, entire) long-term study (1991–2019), which is described in more detail in the San Bernardino analysis unit section. This study covered a total of 181 historical CSO territories, including ten from the eastern edge of the San Gabriel Mountains (Tempel et al. 2022, p. 4), which represents the eastern edge of the Los Padres-Angeles analysis unit. Occupancy was lower in the San Gabriel Mountains than in the San Bernardino Mountains (San Bernardino analysis unit), which included the majority of territories included in the study (Tempel et al. 2022, p. 20). In a supplemental figure showing territory occupancy, occupancy

in the San Gabriel and San Jacinto Mountains (San Bernardino analysis unit) in 2019 was about 20% (Tempel et al. 2022, Figure S1).

Habitat values for this analysis unit include 1% large trees, 33% moderate canopy cover, and 0% overlap of large trees and canopy cover. Our fire analysis shows that 55% has burned between 1984 and 2021, with 18% at high-severity. Between 2011 and 2021, 2% of the Los Padres-Angeles analysis unit burned at high severity.

Our habitat analysis found this unit has the lowest habitat suitability with an overall habitat suitability score of 1. Based on our habitat analysis and recent demographic data, the current condition of the Los Padres-Angeles analysis unit is strongly declining (see Table 17).

San Bernardino Analysis Unit Condition

The San Bernardino analysis unit includes the San Bernardino National Forest as well as private lands. Available demographic data shows a declining population over time. For the San Bernardino National Forest, discontinued studies suggested a population decline of 9% from 1987–1998 despite high apparent adult survival: $0.796 (\pm 0.012)$ (LaHaye et al. 2004, pp. 1056, 1062, 1064). A 30-year dataset (1991–2019), which includes the San Bernardino analysis unit, provides information about territory occupancy and reproduction, suggesting larger declines than the earlier studies (Tempel et al. 2022, p. entire). Population impact analyses simulated these demographic rates in comparison to variables including habitat, climate, and wildfires. Specifically, within this analysis unit, the study included the San Bernardino Mountains (149 historical CSO territories) and San Jacinto Mountains (22 historical CSO territories) (Tempel et al. 2022, p. 4). Mean occupancy in the study declined by over half, from 0.82 ± 0.01 in 1991 to 0.39 ± 0.00 in 2019 (Tempel et al. 2022, pp. 16, 18), and reproductive output fluctuated throughout the study period (mean reproductive output 0.65 young/occupied territory; Tempel et al. 2022, p. 16). However, it is important to note that equivalent reproductive outputs combined with declining occupancy corresponds to overall population declines. Although the San Bernardino Mountains and San Jacinto Mountains are both part of the San Bernardino National Forest, we are not aware of information about CSO moving between these mountain ranges, highlighting limited dispersal within this analysis unit and the coastal-southern California population overall.

Habitat values for this analysis unit include 2% large trees, 31% moderate canopy cover, and 0% overlap value, suggesting that the habitat in this unit has been degraded. Our fire analysis shows that between 1984 and 2021, 66% of this unit has burned, 13% at high-severity. Between 2011 and 2021, 3% of the unit burned at high-severity. Tempel et al. (2022, p. 22) found that high-severity wildfire had an adverse effect on occupancy; when high-severity fires had burned within a CSO territory in the previous 10 years, colonization declined to almost zero and territory extinction rates increased. Overall, simulations suggested that high-severity fire was responsible for approximately 10% of the observed decline in CSO occupancy (Tempel et al. 2022, p. 22), indicating that other threats are also impacting habitat condition within this analysis unit.

Our habitat analysis found this unit has less suitable habitat with an overall habitat suitability score of 2. Considering available demographic information and our habitat analysis, the current condition of the San Bernardino analysis unit is declining (see Table 17).

Cleveland Analysis Unit Condition

The Cleveland analysis unit includes the Cleveland National Forest as well as private lands in the area within the CSO range. There is little information available to assess the current demographic condition of the Cleveland analysis unit; however, non-systematic surveys of a couple of distinct territories indicate low reproduction rates, suggesting this population may not be doing well (information retrieved from U.S. Forest Service NRIS database).

Our habitat analysis found the Cleveland analysis unit contains 0% large trees, a moderate canopy cover value of 34%, and a large trees and canopy cover overlap value of 0%. These results suggest the habitat is degraded and that the large tree habitat component is not present on the landscape. Our fire analysis supports this, with approximately 53% of the unit burned between 1984 and 2021, 19% of which was at high-severity. Between 2011 and 2021, 1% of the unit burned at high-severity.

Our habitat analysis found this unit has the lowest habitat suitability with an overall habitat suitability score of 1. Considering our habitat analysis, the current condition of the Cleveland unit is strongly declining (see Table 17).

Overall Resiliency for the Coastal-Southern California Population

The current condition of analysis units within the coastal-southern California population are two units strongly declining and two units declining (see Table 17). Based on these results, the overall condition of the coastal-southern California population is strongly declining (average overall habitat score of 1.5), and therefore, has very low resiliency (Table 8).

Table 15: Summary of habitat scores and overall current condition of analysis units within the coastal-southern California population. Overall current condition is based on the demographic condition (when available), or the habitat condition for analysis units without demographic information. See Table 18 for the full habitat scoring analysis for all analysis units.

Analysis Unit	Overall habitat score	Analysis unit condition
Los Padres	2	Declining
Los Padres-Angeles	1	Strongly declining
San Bernardino	2	Declining
Cleveland	1	Strongly declining

5.3.3. Population resiliency

As described above, the current resiliency of the Sierra Nevada population is low and the coastal-southern California population is very low. Figure 16 shows the current condition of all CSO analysis units. A summary of demographic condition and our habitat analysis for all CSO analysis units is shown in Table 18. This information was used to inform the current condition of all analysis units, and overall condition of the two CSO populations, which is how we determine population resiliency.

Current Condition

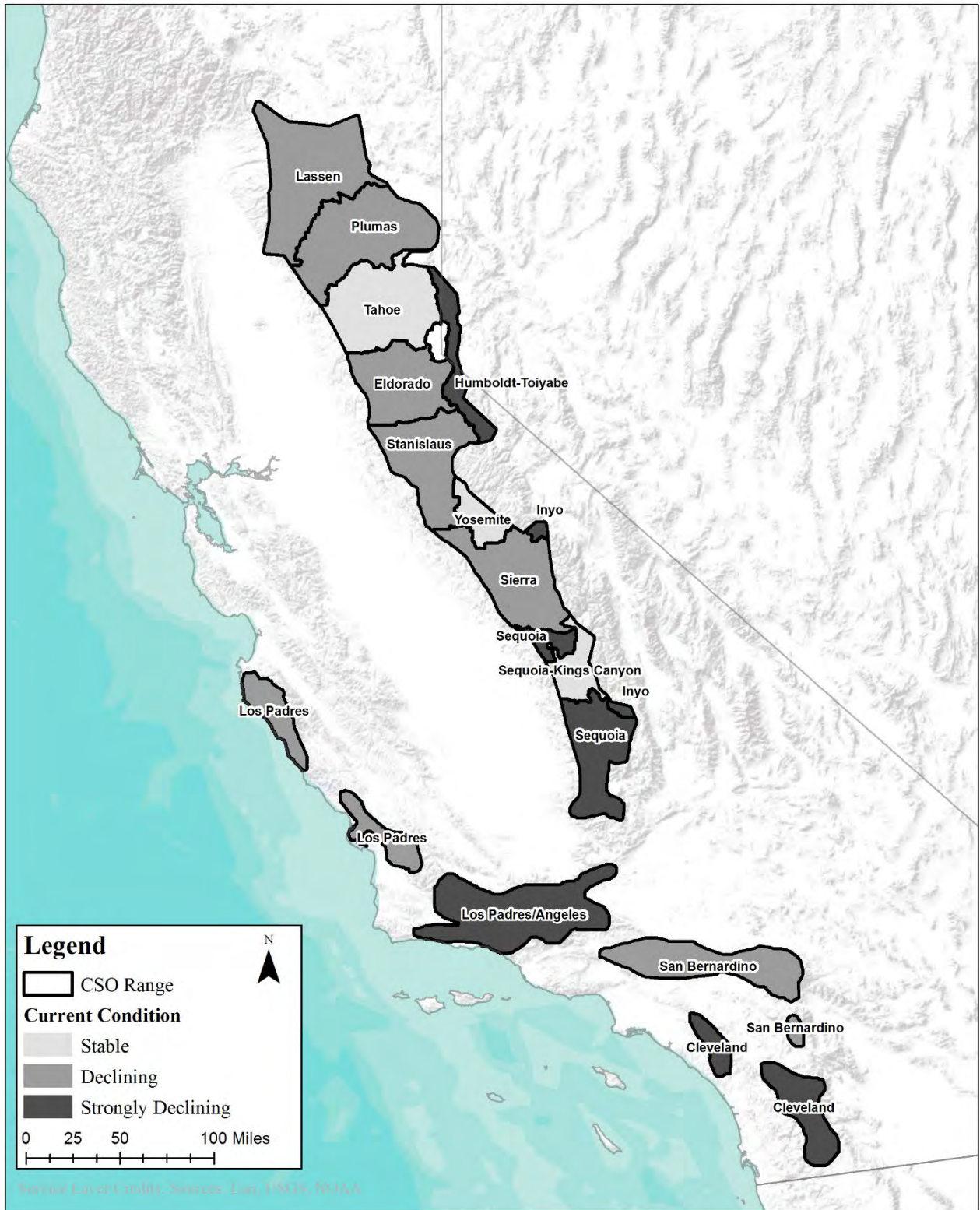


Figure 16: California spotted owl analysis units displaying the current condition

Table 16: Summary of demographic condition and our habitat analysis for all CSO analysis units. This information was used to inform the current condition for all units within the Sierra Nevada and coastal-southern California CSO populations, and population resiliency.

Analysis Unit	Large trees (LT)	LT score	Canopy cover (CC)	CC score	CC & LT	CC & LT score	Total habitat score	High severity fire	High severity score	Overall score	Habitat Suitability	Demographic condition	Overall Condition
Sierra Nevada													
Lassen	4%	1	48%	2	2%	0	3	14%	-1	2	Less suitable	declining	Declining
Plumas	5%	1	51%	2	4%	0	3	27%	-1	2	Less suitable	declining	Declining
Tahoe	7%	1	64%	3	5%	0	4	1%	0	4	Suitable	unknown	Stable
Eldorado	6%	1	57%	2	4%	0	3	12%	-1	2	Less suitable	declining	Declining
Humboldt-Toiyabe	4%	1	24%	0	2%	0	1	4%	0	1	Lowest suitability	strongly declining	Strongly declining
Stanislaus	7%	1	62%	3	5%	0	4	5%	-1	3	Less suitable	unknown	Declining
Yosemite	18%	3	36%	1	9%	1	5	5%	-1	4	Suitable	unknown	Stable
Sierra	9%	1	47%	2	6%	0	3	7%	-1	2	Less suitable	declining	Declining
Sequoia-Kings Canyon	11%	2	49%	2	8%	1	5	6%	-1	4	Suitable	stable	Stable
Sequoia	7%	1	37%	1	3%	0	2	10%	-1	1	Lowest suitability	unknown	Strongly declining
Inyo	7%	1	26%	0	3%	0	1	0%	0	1	Lowest suitability	strongly declining	Strongly declining
Coastal-Southern California													
Los Padres	3%	1	59%	2	2%	0	3	6%	-1	2	Less suitable	unknown	Declining
Los Padres-Angeles	1%	0	33%	1	0%	0	1	2%	0	1	Lowest suitability	unknown	Strongly declining
San Bernardino	2%	1	31%	1	0%	0	2	3%	0	2	Less suitable	declining	Declining
Cleveland	0%	0	34%	1	0%	0	1	1%	0	1	Lowest suitability	unknown	Strongly declining

5.4 Current Species Redundancy

To assess the current condition of redundancy, which is the species' current ability to withstand catastrophic events, this SSA Report considers the size and distribution of populations throughout the species' range, and the plausible catastrophic events to which the species may be exposed. Of the two populations throughout the species range, the Sierra Nevada population covers the most area and is the largest population, while the coastal-southern California population is small and fragmented. Catastrophic events that could impact CSO include very large high-severity wildfire, extreme drought, extreme weather events (e.g., excessive precipitation), or prolonged and persistent competition and displacement due to barred owl expansion. The difference in population structure between the Sierra Nevada and coastal-southern California population (i.e., one large relatively contiguous population compared to a fragmented population with gaps between occupied areas, respectively) could influence how CSO respond to these types of events.

California spotted owls are still distributed throughout the Sierra Nevada and this population makes up most of the spatial range of the species. This wide spread distribution throughout the Sierra Nevada offers some redundancy for the species. The coastal-southern California population is already highly fragmented and areas where demographic data are available demonstrate that declines have accelerated over the last 30 years. Further, Gutiérrez et al. (2017, p. 242) cautioned that information extrapolated from areas that historically contained the largest number of CSO would lead to an optimistic view for the overall population (Gutiérrez et al. 2017, p. 242), suggesting this population does little to contribute to redundancy for the species. A large high-severity wildfire within the San Bernardino National Forest, which historically contained the largest number of CSO in the coastal-southern California population, could have catastrophic impacts on this population, whereas a similar sized fire in the Sierra Nevada population may not have as catastrophic impacts. Overall, current CSO redundancy has declined from historical condition, making the species more vulnerable to extirpations due to a catastrophic event, especially in the coastal-southern California population.

5.5 Current Species Representation

To assess the current condition of representation, which is the species' current ability to adapt to change, this SSA Report considers the ecological setting and genetic diversity among the different populations. The California spotted owl has populations distributed across two areas: 1) the Sierra Nevada, and 2) coastal-southern California. In the Sierra Nevada, a majority of CSO occur within mid-elevation ponderosa pine, mixed-conifer, white fir, and mixed-evergreen forest types, with few CSO occurring in the lower elevation oak woodlands of the western foothills (Gutiérrez et al. 2017, p. xix). In coastal-southern California, CSO are found in riparian/hardwood forests and woodlands, live oak/big cone fir forests, and redwood/California laurel forests (Gutiérrez et al. 2017, p. xxvi). California spotted owls use stick nests more frequently in coastal-southern California compared to in the Sierra Nevada, showing diversity in nesting habitat. Historically there was evidence CSO nested in cliffs, but this has not been documented recently (Gutiérrez et al. 2020, "Breeding" section). Further, CSO in the northern portion of the range tend to have larger home range sizes than CSO in the southern portion of the range (Gutiérrez et al. 2017, p. xviii). The

climate of the Sierra Nevada is cooler and wetter compared to the more arid climate of southern California (Climate Engine 2017). Even within the Sierra Nevada, the northern portion of the range experiences more precipitation and lower mean temperatures than the southern portion of the range (Climate Engine 2017). The diversity in habitat and climate between and within the areas that we have data for suggests that the species has some flexibility to adapt to changing environmental conditions.

Of the three spotted owl subspecies (northern, California, and Mexican), CSO has the lowest genetic diversity when measured by unique haplotypes (Barrowclough et al. 1999, pp. 919, 927; Haig et al. 2004, p. 683). This suggests that CSO have lower genetic representation in general than either of the other two subspecies. However, whether the observed level of genetic diversity indicates low representation is unclear. Because the CSO has persisted throughout much of its historical range for an extended period of time, the relatively low genetic diversity may be a historical artifact rather than an indication of concern for representation. Within the CSO subspecies, genetic differences are found between CSO found in the Sierra Nevada and CSO found in southern California; this provides some degree of genetic representation, although not enough to be considered a separate subspecies (Barrowclough et al. 1999, p. 927; Gutiérrez et al. 2017, p. 101; Hanna et al. 2018, pp. 3946–3947, 3949). Whole-genome data indicates that there is greater genetic difference between CSO in the northern and southern extent of the range than between northern spotted owl and CSO in the northern portion of the range, which is consistent with isolation-by-distance (i.e., geographic differences increase with geographic scale) (Hanna et al. 2018, pp. 3946–3947). The genetic differences observed between populations, as well as the habitat and climate differences, may represent a moderate degree of adaptation and thus moderate representation. Although the species continues to inhabit different ecological settings throughout the range and shows some genetic differences within the subspecies, portions of the species range have become highly fragmented, reducing the amount of available habitat in those different ecological settings, and the overall condition of both populations have declined, which likely has resulted in reduced genetic diversity. Therefore, current CSO representation has declined from historical condition, suggesting that the ability for the taxon to adapt to change is decreased.

CHAPTER 6: FUTURE CONDITION

This chapter of the SSA Report forecasts the species' response to two plausible future scenarios. These two scenarios represent the extremes of a range of future changes in environmental conditions and success of implemented conservation efforts. The future scenarios project the influences to viability discussed in Chapter 4 into the future and consider the impacts those influences would potentially have on CSO viability. We apply the concepts of resiliency, redundancy, and representation to the future scenarios to describe the future viability of CSO. In this chapter, we describe two future scenarios and assess future resiliency for each CSO population. Scenario 1 assesses CSO future viability with an increase in the trend and magnitude of threats with implemented management efforts having mixed success. Scenario 2 assesses the viability of the species if the trend and magnitude of threats were to continue at the current trajectory into the future with implemented management efforts being fully successful. Table 19 provides a comparison of the assumptions made for each scenario. By using two scenarios representing the extremes of

plausible future projections for the species, it allows us to consider the full range of future possibilities for predicting the future viability of the species and incorporates any uncertainty regarding the impact of future environmental conditions and the success of implemented conservation efforts. For this SSA Report, the future was assessed at approximately 40–50 years. This range represents our best professional judgment of the projected future conditions related to climate change for California, CSO generation time, and regeneration time of large trees (likely only medium trees transitioning to large).

Table 17: Future scenario comparison table

Threats	Scenario 1: Increasing intensity of threats with mixed management success	Scenario 2: Current trajectory of threats with successful management efforts
Large-scale High-Severity Fire	Increase	Slight increase or stable
Tree Mortality	Increase	Stable or decrease slightly
Drought	Increase	Slight increase
Climate Change	Increase	Slight increase
Fuels Reductions and Forest Management	Increase (both positive and negative impacts)	Increase (both positive and negative impacts)
Barred Owls	Increase	Stable or decrease
Rodenticides	Increase	Remain stable
Disease and Parasites	Increase	Remain stable
Development	Increase	Remain stable
Recreation	Increase	Remain stable

6.1 Future Scenario Summary of Methods

We considered two potential future scenarios and assessed the viability of CSO under both. For each scenario (see 6.3 Scenario 1 and 6.4 Scenario 2), we include a description of the scenario assumptions, and explain expected changes in threats and how the threats would impact the species ecological needs. Current analysis unit condition and overall current population resiliency were determined as described in the current condition section of the SSA Report using demographic information and the results our habitat analysis (see 5.3 Current Analysis Unit Condition and Population Resiliency). Our future analysis uses the current condition of each analysis unit as a baseline and then incorporates future threat projections to determine whether analysis units will increase, decline, or remain stable (i.e., current condition level) into the future.

Our assumptions regarding barred owl expansion and the success of future management differ under the two scenarios. Under future scenario 1, we assume the significant threats of barred owl expansion will increase in magnitude into the future and that future management efforts, specifically barred owl removal efforts, are not successful such that barred owls have expanded throughout the entire range. To incorporate the large negative impacts barred owls would have on the demographic rates of all analysis units, we incorporated a barred owl score into our future condition analysis. In order to show how this threat will have impacts on demographic rates, we used the current condition analysis as a baseline to assign a demographic score from which to subtract the barred owl score. Baseline demographic scores for the future analysis are based on the

results of our current habitat analysis scores. Barred owl scores under scenario 1 are -1 for all analysis units to represent the large negative impacts to demographic rates that are projected to occur. Under scenario 2, all barred owl scores are 0 to represent the threat is being successfully addressed and there are no or very minimal impacts to the demographic condition of each analysis unit due to that specific threat. Barred owl scores are added to the baseline demographic score for a future demographic score.

Our assumption regarding high-severity wildfire risk differ under the two scenarios. Under scenario 1, so to incorporate an increased level of high-severity wildfire risk, we assume all units will have high-severity wildfire values of 4% or greater (as defined in 5.1 Current Condition Summary of Methods), so we adjusted the high-severity score included in the current condition analysis for all analysis units to -1. For scenario 2, we left the high-severity score the same as the current condition since we expect threats to continue at the current trajectory.

To represent future changes in habitat due to climate change and drought, we adjusted the current condition habitat analysis scores to represent the varying levels of impact to each habitat component. For scenario 1, we decreased the large tree values by 10%, the moderate canopy cover by 15%, and decreased the overlap values for all units to represent the largest likely negative impacts to habitat condition. For scenario 2, we decreased the large tree values by 5%, the moderate canopy cover by 10%, and maintained the current overlap score to represent the smallest likely negative impacts to habitat condition.

Habitat condition within each analysis unit was assessed using the scoring system in Table 6. As in the current condition analysis, for our future habitat analysis we sum all habitat scores across the analysis unit for a future habitat condition. Finally, to determine overall future habitat condition of a particular unit we average the habitat and demographic scores for that analysis unit, and then establish overall condition using the definitions in Table 7.

For population resiliency, we average scores for all analysis units within a population and then determine population resiliency using the definitions in Table 8. To assess the future condition of redundancy under both future scenarios, we consider the size and distribution of the two CSO populations throughout the species' range under the assumptions of that scenario, and the plausible catastrophic events to which the species may be exposed. To assess the future condition of representation for both scenarios, we consider the ecological setting and genetic diversity among the two populations in the future.

6.2 Future Scenario Uncertainty

As explained in 5.2 Current Condition Uncertainty, there are several ecological needs where data are not available to determine the condition for any analysis unit. Our two future scenarios represent the most plausible optimistic scenario and the most plausible pessimistic scenario in an infinite number of possible future scenarios. With many of the analysis units that do not have occupancy, survival, and fecundity data, we relied only on our current habitat analysis. However, we used the available demographic information to calibrate the categories for our habitat analysis.

There are several future climate projections that have been developed for different regions of California for California's Fourth Climate Change Assessment that take into account different scenarios of greenhouse gas emissions into the future (see 4.4 Climate Change). Although there is currently very little species-specific climate change information that exists to assess CSO and its future condition, the threats that interact synergistically with climate change (i.e., high-severity wildfire, drought, and tree mortality) are expected to grow in magnitude over time with increasing greenhouse gas emissions. The threat from wildfires is associated with the effects of climate change, such as increased drought, lower soil moisture, and decreased snowpack. Therefore, fire will continue to be a threat into the future with greater fire threat associated with increasing greenhouse emissions. We expect the pattern of increasing severity of fire and area burned in fires will continue to increase into the future under both future scenarios, with the largest increases under Scenario 1.

6.3 Scenario 1

Scenario 1 considers CSO viability if some of the significant threats were to increase in magnitude into the future and future management efforts have mixed success in addressing those threats. Under this scenario, climate change models under RCP 8.5 project temperature increases of 4.5–6°F, depending on the portion of the range. Increases in temperatures will likely increase extreme weather events including heat waves and drought conditions (Kadir et al. 2013, pp. 38, 48). With increased drought conditions, tree mortality and large-scale high-severity fire are likely to increase in frequency and size, especially if fuel loads in forests are not decreased (Westerling and Bryant 2008, pp. S244–S248; Abatzoglou and Williams 2016, pp. 11770, 11773; Young et al. 2017, p. 78). Extreme weather events or significant changes in interannual climate variability may have negative impacts on CSO survival and reproduction. Although there are some protections in place for CSO on public lands, timber harvest values can vary year to year. Therefore, it is possible that increases in timber harvest targets may reduce CSO habitat that is available now or that may be available in the future for CSO to establish new territories and disperse beyond the protected activity centers. Without continued ongoing experimental removals, barred owls will likely continue to expand their range into CSO habitat, eventually reaching a point of exponential increase and significantly displacing and outcompeting CSO on the landscape (Keane et al. 2018, pp. 8, 47). The timeline for barred owl expansion and replacement of CSO on the landscape is unknown; however, because they were able to expand so quickly within the northern spotted owl range, under future scenario 1 we assume barred owls would move beyond the Sierra Nevada and continue to expand into coastal-southern California. This expansion could be due to current experimental removal efforts becoming less successful over time (i.e., decreased experimental removal efforts) or the species being able to cross what was thought to be unsuitable habitat, like the Central Valley. Under scenario 1 it is also possible that rodenticide use could increase in California due to the legalization of marijuana in 2016. There will likely be an increase in demand of marijuana, which may increase illegal grow sites associated with the use of anticoagulant rodenticides in California if the cost of buying land and acquiring/maintaining permits to legalize a grow operation is too high (Soboroff and Koss 2017, p. entire; Yakowicz 2018, p. entire; Harrison 2018, p. entire). There is evidence that changing climate conditions could increase pathogen development and occurrence (Harvell et al. 2002, p. 2158), therefore there is a slight chance that disease and parasites may become a more significant issue in the future. Finally, development may continue to encroach upon CSO habitat as

the California human population continues to grow (California Economic Forecast 2016, pp. xii–xiii, 233–236).

6.3.1 Scenario 1 Future Analysis Unit Condition and Population Resiliency

Under future scenario 1, an increase in large-scale high-severity fire and full barred owl expansion into the CSO range will likely impact a majority of the CSO ecological needs. With an increase in large-scale high-severity fire, there may be some negative impacts to prey availability until the resources necessary to shelter and feed the prey return to the landscape (Roberts et al. 2015, pp. 107, 113; Service 2016b, pp. 60–61). However, it is only a minor impact, because although the overall abundance of prey may be reduced (Roberts et al. 2015, pp. 107, 113), some prey species are still able to persist even in areas burned at high-severity (Bond et al. 2013, pp. 114, 120; Roberts et al. 2015, pp. 107, 113). Some prey species, such as flying squirrels, may be more impacted by large-scale high-severity fire (Forsman 2018, in litt.). Large-scale high-severity fires greatly reduce multi-layered high canopy cover and large trees available on the landscape for CSO (Stephens et al. 2016, p. 1). A mosaic of fire severities in patches on the landscape can be beneficial for forest heterogeneity, but large-scale high-severity fires reduce heterogeneity that benefits CSO (Verner et al. 1992, pp. 247–248; Roberts et al. 2011, p. 610; Lee et al. 2012, p. 792; Bond et al. 2013, pp. 114, 122; Eyes et al. 2017, p. 384). With a decrease in large trees and multi-layered high canopy cover, available nest trees on the landscape will also be negatively impacted. Large-scale fires (>10,000 ha (24,711 ac)) are likely to reduce patch size at all scales for CSO within the fire area, and may even cause negative impacts to dispersal if the fire is large enough to inhibit movement. Large-scale high-severity fires likely only displace CSO from territories because they have the ability to fly and flee from a burning area, but there is evidence that fire can cause mortality to CSO (Jones et al. 2016a, p. 305), so there may be some negative impacts to survival with an increase in fires. With a reduction in some of the key habitat features due to large-scale high-severity fires, fecundity, occupancy, and population growth will likely decline under future scenario 1.

Under future scenario 1, an increase in tree mortality and drought will likely have strong impacts to canopy cover, occupancy, and population growth. Tree mortality and drought conditions significantly decreases the amount of canopy cover (Anderegg et al. 2013, pp. 30, 32); therefore, an increase of tree mortality events and drought conditions in the future will likely cause a decline in the condition of moderate canopy cover. California spotted owl occupancy sharply declines in habitat with less than 40% canopy cover (Tempel et al. 2016, pp. 747, 759); therefore, the significant decline in canopy cover from tree mortality and drought will likely negatively impact occupancy. California spotted owls can utilize large trees even if the trees are dead, and CSO are often found nesting in snags. However, CSO are less likely to nest in large trees without sufficient canopy cover. Tree mortality events and drought conditions may have slightly positive impacts on coarse woody debris and forest heterogeneity, but it will likely not improve the condition of an analysis unit. Increased drought alone may have negative impacts to survival if not enough water is available, but it is unlikely that a drought would be significant enough to have physiological impacts.

The future impacts of climate change are likely to impact a majority of CSO ecological needs. Climate change is likely to drive the increase in severity of many of the other threats discussed including large-scale high-severity fire, tree mortality, and drought. Climate change has other

potential impacts to the ecosystem, making it difficult to fully predict the specific impacts to CSO. Canopy cover and large trees will likely decline due to the multiple impacts of climate change and the potential shift in plant communities that may result (Gutiérrez et al. 2017, pp. 132, 215, 288). The significant decrease in both canopy cover and large trees will likely result in negative impacts to forest heterogeneity and available nest trees. With many of the habitat components degraded, dispersal will also likely be negatively impacted because there may be limited habitat remaining for an individual CSO to move across the landscape and establish a territory. Further, extreme weather events and heat waves associated with climate change will likely negatively impact survival. With a decline in habitat components and an increase in climate variability and extreme weather events, fecundity will likely decline. Also, climate change modeling predicts a decline in occupancy under multiple emission scenarios by 2052 (Jones et al. 2016b, p. 901). Finally, with a decrease in survival, fecundity, and occupancy, population growth will likely decline due to climate change under future scenario 1.

If the severity of interannual climate variability increases due to climate change, there may be strong negative impacts to fecundity. Significant variability of weather patterns under RCP 8.5 will likely result in a decline in fecundity. Survival may also be negatively impacted by an increase in interannual climate variability, but it is dependent on the nature of the variability and will likely be a weak impact. With a decrease in fecundity, there will likely be a decrease in population growth, but since CSO is a long-living species with generally low reproductive rates, the impacts of interannual climate variability may be reduced as long as there are occasional years with weather patterns suitable for reproduction.

Under future scenario 1, an increase in certain fuels reductions and forest management actions, like clearcutting, would have strong negative impacts on canopy cover, large trees, dispersal, fecundity, and occupancy. Clearcutting removes canopy cover, large trees, and nest trees from the landscape, which would significantly degrade habitat in the future. With a decrease in canopy cover and large trees, the habitat remaining for patch size would also decrease. In northern spotted owls, clearcutting has been shown to reduce dispersal and habitat use (Forsman et al. 1984, p. 25; Carey et al. 1990, p. 11; Miller et al. 1997, pp. 140, 145–148). The decrease in dispersal and habitat use would likely cause a decrease in fecundity, occupancy, and population growth.

Mechanical thinning would likely increase under future scenario 1, but current protections would likely remain in place within known CSO habitat. Current protections strictly limit the amount of habitat that can be thinned within known CSO territories. Mechanical thinning will likely have negative impacts on canopy cover and coarse woody debris. However, if mechanical thinning is done in a way that maintains owl habitat, the negative impacts are likely offset by the benefits of reducing fuel loads and reducing the potential of large-scale high-severity fire. For example, it is predicted that there would be little impact to CSO if multi-layered high canopy cover in a territory is reduced to 30% of the territory and the area thinned remains at moderate canopy cover (Tempel et al. 2016, p. 761). However, it is important to note that too much thinning can result in negative impacts to fecundity, occupancy, and population growth, so a balance must be maintained (Tempel et al. 2016, pp. 761–762).

An increase in salvage logging under future scenario 1 would likely result in a small decrease of prey abundance due to the loss of food and shelter. However, some prey species are able to

persist in more open habitat; therefore, some prey species will likely still be available (Bond et al. 2013, pp. 114, 120; Roberts et al. 2015, pp. 107, 113, 2017, p. 112). There would likely be little to no impacts on canopy cover because canopy cover would likely already be reduced by either fire or tree mortality for salvage logging to occur. Large trees and coarse woody debris would all likely be negatively impacted by the removal of trees resulting in degraded conditions. There would likely be no impact to survival. Fecundity, occupancy, and population growth would likely be negatively impacted with the loss of important habitat features.

Under future scenario 1, the increase of barred owls on the landscape would have a significant negative impact on CSO prey because barred owls consume the same prey species and establish 3–5 territories within the size of one CSO territory (Mazur and James 2000, "Diet and Feeding" section; Forsman 2018, in litt.). There would likely be no impacts to the quality of the species habitat components due to barred owls. However, it is important to note that barred owls inhabit the same habitat as CSO, thus the availability of many of the habitat components for CSO would likely be reduced. The amount of nest trees available for CSO would likely significantly decline due to barred owls outcompeting and using the available nest trees. Dispersal would also strongly decline because much of the available habitat would be occupied by barred owls. Barred owls outcompeting spotted owls, particularly for food, has the potential to have a significant negative impact on the survival of CSO (Forsman 2018, in litt.). Fecundity and occupancy would likely significantly decline due to barred owls displacing CSO and reducing the available habitat for spotted owls to occupy and reproduce. With decreased survival, fecundity, and occupancy, population growth would likely also decline significantly due to barred owl expansion and competition.

Under future scenario 1, rodenticides increasing on the landscape would have few impacts on the habitat, but likely detrimental effects on individuals. Rodenticides are ingested by prey species, which reduces the amount of prey available for CSO. Prey species that have ingested rodenticides and are then eaten by CSO may then result in the death of CSO. A threat that reduces survival in a population, such as rodenticides, has the potential to be highly detrimental to the species because CSO is long-lived with low reproductive rates. Rodenticides can also impact fecundity if a parent is contaminated during the breeding season, reducing the likelihood that the nest will be successful with only one parent left. An increase in rodenticides on the landscape will likely cause a decline in population growth, primarily due to a decrease in survival of CSO.

There is a small chance that under future scenario 1 disease and parasites could become a more significant threat for CSO viability. Given the limited information available, it is difficult to predict the impacts of disease/parasites; however, there would likely be some impact to survival and/or fecundity.

If development were to increase and encroach upon CSO habitat, there would likely be significant impacts to a majority of the species' ecological needs. Development would remove canopy cover, large trees, heterogeneity and coarse woody debris. There would likely be little to no impact to survival of CSO; however, fecundity, occupancy, and population growth would decline due to the loss of suitable habitat. Although development within CSO habitat is possible, it is unlikely throughout most of the range given the majority of land is federally owned.

Finally, if recreation were to increase under future scenario 1, there would likely be few impacts to CSO. Recreation activities have little to no impact on canopy cover, large trees, heterogeneity, coarse woody debris, survival, or population growth. Fecundity or occupancy may be impacted by recreation if noises or presence of people cause the individuals to leave a nest site or occupied territory. However, there is little evidence that this is a significant threat or that it could be in the future; therefore, the impacts would likely be small if any.

6.3.1.1 Sierra Nevada Population

Lassen Analysis Unit Condition

Under future scenario 1, the Lassen analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service and Park Service lands in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Lassen unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under future scenario 1, we anticipate demographic rates and habitat conditions to decline due to the increase of threats described above. The Lassen analysis unit will likely be strongly declining (overall score=1) in 40–50 years (see Table 20).

Plumas Analysis Unit Condition

Under future scenario 1, the Plumas analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Plumas unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2) and we anticipate demographic rates and habitat conditions to decline further due to the increase of threats described above for scenario 1. Under future scenario 1, the Plumas analysis unit will likely be strongly declining (overall score=1) in 40–50 years (see Table 20).

Tahoe Analysis Unit Condition

Under future scenario 1, the Tahoe analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Tahoe analysis unit is stable based on our habitat analysis (overall habitat analysis score=4), but we anticipate habitat conditions and demographic rates will decline due to the increase of threats described above. Under future scenario 1, the Tahoe analysis unit will likely be declining (overall score=2) in 40–50 years (see Table 20).

Eldorado Analysis Unit Condition

Under future scenario 1, the Eldorado analysis unit will likely be impacted by increases of large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Eldorado analysis unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under scenario 1, we anticipate demographic rates and habitat conditions will decline due to the increase of threats described above. Under future scenario 1, the Eldorado analysis unit will likely be strongly declining (overall score=1) in 40–50 years (see Table 20).

Humboldt-Toiyabe Analysis Unit Condition

The Humboldt-Toiyabe analysis unit is a small analysis unit on the eastern edge of the CSO range. Under future scenario 1, the Humboldt-Toiyabe analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service and Nevada State Park land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Recent PAC information and our current condition habitat analysis found the Humboldt-Toiyabe unit is strongly declining (overall habitat analysis score=1). Under scenario 1, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above and will no longer support the species. Under future scenario 1, the Humboldt-Toiyabe analysis unit will likely be extirpated (overall score=-1) in 40–50 years (see Table 20).

Stanislaus Analysis Unit Condition

Under future scenario 1, the Stanislaus analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Stanislaus unit is declining based on our habitat analysis (overall habitat analysis score=3). Under scenario 1, we anticipate the Stanislaus analysis unit will likely continue declining (overall score=2) in 40–50 years (see Table 20).

Yosemite Analysis Unit Condition

Under future scenario 1, the Yosemite analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, barred owls, and rodenticides. Clearcutting, mechanical thinning, and salvage logging will likely not be a threat because these activities do not occur on Park Service land. The current condition of the Yosemite analysis unit is stable based on our habitat analysis (overall habitat analysis score=4), but we anticipate demographic

rates and habitat conditions will decline due to the increase of threats described above. Under future scenario 1, the Yosemite analysis unit will likely be declining (overall score=2) in 40–50 years (see Table 20).

Sierra Analysis Unit Condition

Under future scenario 1, the Sierra analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service and Park Service lands in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the Sierra unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under scenario 1, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above. Under future scenario 1, the Sierra analysis unit will likely be strongly declining (overall score=1) in 40–50 years (see Table 20).

Sequoia-Kings Canyon Analysis Unit Condition

Under future scenario 1, the Sequoia-Kings Canyon unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, barred owls, and rodenticides. Clearcutting, mechanical thinning, and salvage logging will likely not be a threat because these activities do not occur on Park Service land. Our current condition analysis found the Sequoia-Kings Canyon unit is stable based on demographic information and our habitat analysis (overall habitat analysis score=4). Under scenario 1, we anticipate demographic rates and habitat conditions will decline due to the increase of threats described above. Under future scenario 1, the Sequoia-Kings Canyon analysis unit will likely be declining (overall score=2) in 40–50 years (see Table 20).

Sequoia Analysis Unit Condition

Under future scenario 1, the Sequoia analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition habitat analysis found the Sequoia unit is strongly declining (overall habitat analysis score=1). Under scenario 1, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above and will no longer support the species. Under future scenario 1, the Sequoia analysis unit will likely be extirpated (overall score=-1) in 40–50 years (see Table 20).

Inyo Analysis Unit Condition

The Inyo analysis unit is a small peripheral unit. Under future scenario 1, the Inyo analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, salvage logging, barred owls, and rodenticides. Although there

are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the Inyo analysis unit is strongly declining based on demographic information and our habitat analysis (overall habitat analysis score=1). Under scenario 1, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above and will no longer support the species. Under future scenario 1, the Inyo analysis unit will likely be extirpated (overall score=-1) in 40–50 years (see Table 20).

Overall Future Resiliency for the Sierra Nevada Population

Table 20 presents the future condition for each Sierra Nevada analysis unit with the assumptions described above for future Scenario 1. Under scenario 1 almost all analysis units degrade in condition, with four analysis units considered declining, four strongly declining, and three that will likely be extirpated (see Table 20). Two of the units that will likely be extirpated under scenario 1 are currently small, peripheral units. Based on these results, under scenario 1 the future overall condition of the Sierra Nevada population will be strongly declining (average overall future condition score of 0.82). Therefore, the Sierra Nevada population has very low resiliency under future scenario 1. Figure 17 is a map showing the overall future condition of all CSO analysis units under scenario 1.

Table 180: Summary of future condition scores and overall future condition for analysis units within the Sierra Nevada population under future scenario 1. See Tables 22 and 23 for the full scoring analysis for all CSO analysis units.

Analysis Unit	Overall future condition score	Future condition – scenario 1
Lassen	1	Strongly declining
Plumas	1	Strongly declining
Tahoe	2	Declining
Eldorado	1	Strongly declining
Humboldt-Toiyabe	-1	Extirpated
Stanislaus	2	Declining
Yosemite	2	Declining
Sierra	1	Strongly declining
Sequoia-Kings Canyon	2	Declining
Sequoia	-1	Extirpated
Inyo	-1	Extirpated

6.3.1.2 Coastal-Southern California Population

Los Padres Analysis Unit Condition

Under future scenario 1, the Los Padres analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, rodenticides, development, and barred owls. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of

large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Los Padres unit is declining based on our habitat analysis (overall habitat analysis score=2). Under future scenario 1, we anticipate demographic rates and habitat conditions to decline due to the increase in threats described above. The Los Padres analysis unit will likely be strongly declining (overall score=1) in 40–50 years (see Table 21).

Los Padres-Angeles Analysis Unit Condition

Under future scenario 1, the Los Padres-Angeles analysis unit will likely be negatively impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, rodenticides, development, and barred owls. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the Los Padres-Angeles unit is strongly declining based on our habitat analysis (overall habitat analysis score=1). Under scenario 1, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above and will no longer support the species. Under future scenario 1, the Los Padres-Angeles analysis unit will likely be extirpated (overall score=-1) in 40–50 years (see Table 21).

San Bernardino Analysis Unit Condition

Under future scenario 1, the San Bernardino analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, rodenticides, development, and barred owls. Although there are protections in place on the Forest Service and Park Service lands in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the San Bernardino analysis unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under scenario 1, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above. Under future scenario 1, the San Bernardino analysis unit will likely be strongly declining (overall score=0), with the potential of extirpation in 40–50 years (see Table 21).

Cleveland Analysis Unit Condition

Under future scenario 1, the Cleveland analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, rodenticides, development, and barred owls. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Cleveland analysis unit is strongly declining based on our habitat analysis (overall habitat analysis score=1). Under future scenario 1, we anticipate demographic factors and habitat conditions will continue to decline due to the increase of threats described above and will no longer support the species. Under future scenario

1, the Cleveland analysis unit will likely be extirpated (overall score=-1) in 40–50 years (see Table 21).

Overall Resiliency for the Coastal-Southern California Population

Table 21 presents the future condition for each coastal-southern California population analysis unit with the assumptions described above for future Scenario 1. Under scenario 1 all coastal-southern California analysis units degrade in condition, with two analysis units considered strongly declining and two that will likely be extirpated (see Table 21). Based on these results, the overall future condition of the coastal-southern California population under scenario 1 will likely be extirpated (average overall future condition score of -0.25), and therefore, will have no resiliency. Figure 17 is a map showing the overall future condition of all CSO analysis units under scenario 1.

Table 21: Summary of future condition scores and overall future condition for analysis units within the coastal-southern California population under future scenario 1. See Tables 22 and 23 for the full scoring analysis for all CSO analysis units.

Analysis Unit	Overall future condition score	Future condition – scenario 1
Los Padres	1	Strongly declining
Los Padres-Angeles	-1	Extirpated
San Bernardino	0	Strongly declining
Cleveland	-1	Extirpated

Table 22: Summary of our future condition analysis for all CSO analysis units under scenario 1. This information was used to inform the future condition for all units within the Sierra Nevada and coastal-southern California CSO populations, and population resiliency. The full habitat analysis for scenario 1 is shown in Table 23.

Analysis Unit	Current demographic score	Barred owls score	Total demographic score	Total habitat score	Overall score	Future condition Scenario 1
<i>Sierra Nevada</i>						
Lassen	2	-1	1	0	1	Strongly declining
Plumas	2	-1	1	0	1	Strongly declining
Tahoe	4	-1	3	1	2	Declining
Eldorado	2	-1	1	1	1	Strongly declining
Humboldt-Toiyabe	1	-1	0	-1	-1	Extirpated
Stanislaus	3	-1	2	1	2	Declining
Yosemite	4	-1	3	0	2	Declining
Sierra	2	-1	1	0	1	Strongly declining
Sequoia-Kings Canyon	4	-1	3	0	2	Declining
Sequoia	1	-1	0	-1	-1	Extirpated
Inyo	1	-1	0	-1	-1	Extirpated
<i>Coastal-Southern California</i>						
Los Padres	2	-1	1	1	1	Strongly declining
Los Padres-Angeles	1	-1	0	-1	-1	Extirpated
San Bernardino	2	-1	1	-1	0	Strongly declining

Analysis Unit	Current demographic score	Barred owls score	Total demographic score	Total habitat score	Overall score	Future condition Scenario 1
Cleveland	1	-1	0	-1	-1	Extirpated

Table 23: Full habitat analysis for future scenario 1.

Analysis Unit	Large trees (LT)	LT score	Canopy cover (CC)	CC score	CC & LT	CC & LT score	Total habitat score	High severity fire	High severity score	Total Habitat score	Overall score	Habitat Suitability	Overall Condition
<i>Sierra Nevada</i>													
Lassen	4%	0	48%	1	2%	0	1	14%	-1	0	1	Lowest suitability	Strongly declining
Plumas	5%	0	51%	1	4%	0	1	27%	-1	0	1	Lowest suitability	Strongly declining
Tahoe	7%	0	64%	2	5%	0	2	1%	-1	1	2	Less suitable	Declining
Eldorado	6%	0	57%	2	4%	0	2	12%	-1	1	1	Lowest suitability	Strongly declining
Humboldt-Toiyabe	4%	0	24%	0	2%	0	0	4%	-1	-1	-1	No suitability	Extirpated
Stanislaus	7%	0	62%	2	5%	0	2	5%	-1	1	2	Less suitable	Declining
Yosemite	18%	1	36%	0	9%	0	1	5%	-1	0	2	Less suitable	Declining
Sierra	9%	0	47%	1	6%	0	1	7%	-1	0	1	Lowest suitability	Strongly declining
Sequoia-Kings Canyon	11%	0	49%	1	8%	0	1	6%	-1	0	2	Less suitable	Declining
Sequoia	7%	0	37%	0	3%	0	0	10%	-1	-1	-1	No suitability	Extirpated
Inyo	7%	0	26%	0	3%	0	0	0%	-1	-1	-1	No suitability	Extirpated
<i>Coastal-Southern California</i>													
Los Padres	3%	0	59%	2	2%	0	2	6%	-1	1	1	Lowest suitability	Strongly declining
Los Padres-Angeles	1%	0	33%	0	0%	0	0	2%	-1	-1	-1	No suitability	Extirpated
San Bernardino	2%	0	31%	0	0%	0	0	3%	-1	-1	0	Lowest suitability	Strongly declining
Cleveland	0%	0	34%	0	0%	0	0	1%	-1	-1	-1	No suitability	Extirpated

Future Scenario 1 Condition

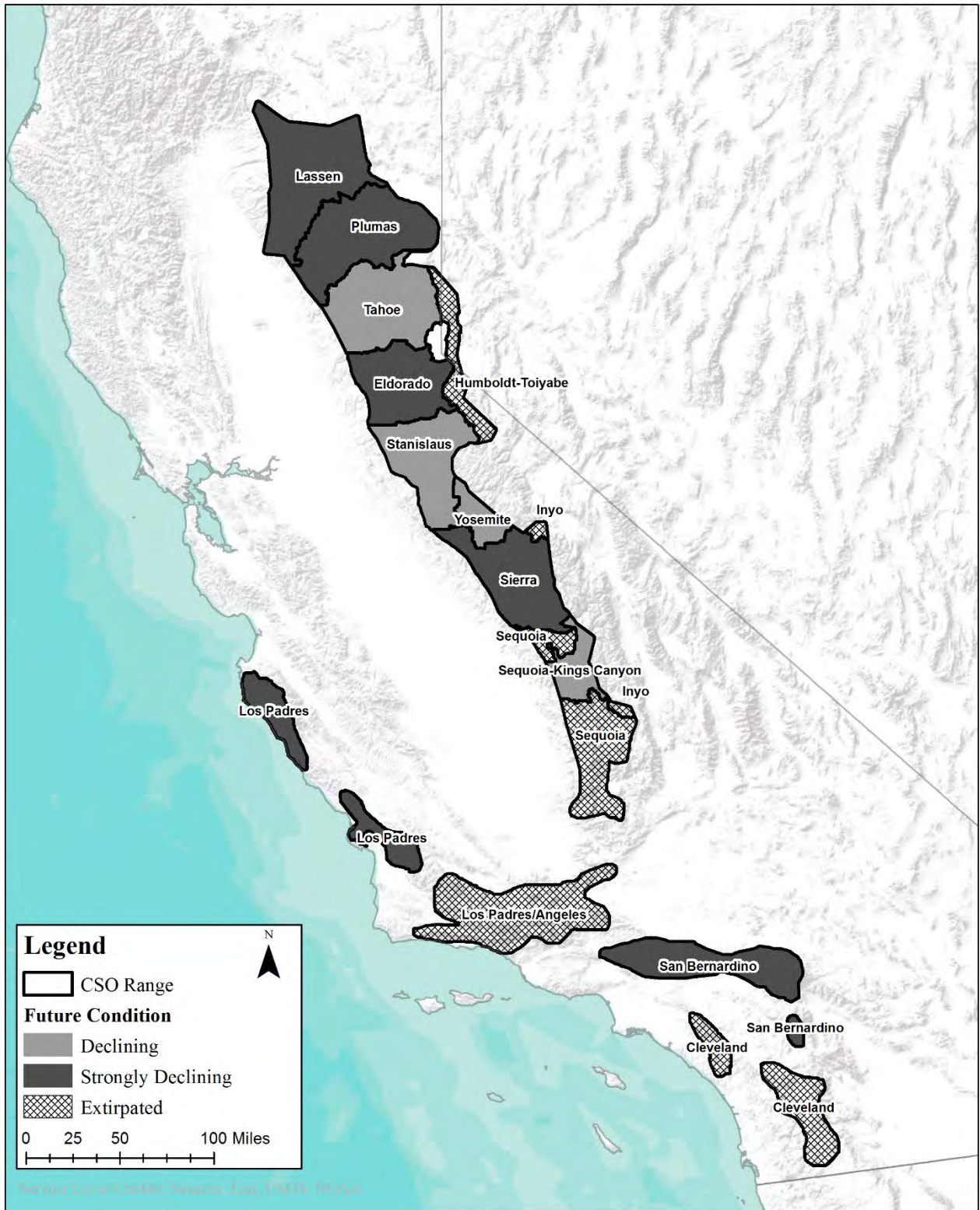


Figure 17: Map of CSO analysis units and their predicted condition under future scenario 1.

6.3.2 Future Species Redundancy

Under future scenario 1, we anticipate both populations would be less resilient compared to current condition. Because the coastal-southern California population will likely be extirpated under future scenario 1, the southern California population will contribute nothing to redundancy. The species will likely maintain a wide distribution throughout the Sierra Nevada; however, because the condition of almost all analysis units within the Sierra Nevada population are declining, the Sierra Nevada population will contribute less to redundancy under this scenario than it currently does. Therefore, under scenario 1 redundancy would decline compared to the current condition as the species would be less likely to withstand catastrophic events with only one population contributing to redundancy.

6.3.3 Future Species Representation

Predictions for future scenario 1 are that many of the habitat components identified for CSO will likely have a limited ability to withstand predicted changes and are likely to further decline in condition in the future. This would indirectly cause a decrease in representation for CSO if the diversity in habitat and climate that is currently documented declines. Further, with continued declines in occupancy, fecundity, and survival, population growth will decline and will likely further reduce genetic diversity. Under scenario 1, representation would decline compared to current condition as the species would have less flexibility to adapt to changing environmental conditions.

6.4 Scenario 2

Scenario 2 considers a future where the threats continue at the current trajectory and on-going management efforts are successful at addressing those threats. Under this scenario, climate change models under RCP 4.5 project temperature increases of 3.5–5°F, depending on the portion of the range. Under future scenario 2, drought conditions, tree mortality events, and high-severity fire will likely continue at the current trajectory. Currently, there are research actions in place to experimentally limit barred owl expansion within study areas, which have so far been successful (see 4.6 Competition and Hybridization with Barred Owls and 4.9 Regulatory Mechanisms and Management Actions) and we project will continue to be successful in limiting their expansion under this scenario. Protections would continue to stay in place for CSO on public lands, and timber harvest would remain at reduced levels on public lands. Rodenticide use would either remain the same or decrease due to continued law enforcement activity shutting down illegal marijuana grows. Under scenario 2, the current rate of human population growth will continue, leading to steadily increasing development, specifically in areas that are not on public land.

6.4.1 Scenario 2 Future Analysis Unit Condition and Population Resiliency

Under future scenario 2, large-scale high-severity fire will likely impact a majority of the CSO ecological needs. With continued large-scale high-severity fire on the landscape, there may be some negative impacts to prey availability until the resources necessary to shelter and feed the prey return to the landscape (Roberts et al. 2015, pp. 107, 113; Service 2016b, pp. 60–61). However, it is only a minor impact, because although the overall abundance of prey may be reduced (Roberts et al. 2015,

pp. 107, 113), some prey species are still able to persist even in areas burned at high-severity (Bond et al. 2013, pp. 114, 120; Roberts et al. 2015, pp. 107, 113). Large-scale high-severity fires reduce canopy cover and large trees available on the landscape for CSO (Stephens et al. 2016, p. 1). A mosaic of fire severities in patches on the landscape can be beneficial for forest heterogeneity; however, large-scale high-severity fires reduce heterogeneity that benefits CSO (Verner et al. 1992, pp. 247–248; Roberts et al. 2011, p. 610; Lee et al. 2012, p. 792; Bond et al. 2013, pp. 114, 122; Eyes et al. 2017, p. 384). With a decrease in large trees and multi-layered high canopy cover, available nest trees on the landscape will also be negatively impacted. Large-scale high-severity fires likely only displace CSO from territories because they have the ability to fly and flee from a burning area. However, there is evidence that fire can cause mortality to CSO (Jones et al. 2016a, p. 305), so there may be some negative impacts to survival with an increase in fires. With a reduction in some of the key habitat components due to large-scale high-severity fires fecundity, occupancy, and population growth will likely decline under future scenario 2.

Under future scenario 2, continued tree mortality and drought will likely have negative impacts to canopy cover, occupancy, and population growth. Tree mortality and drought conditions significantly decrease the amount of canopy cover (Anderegg et al. 2013, pp. 30, 32); therefore, continued tree mortality events and drought conditions in the future will likely reduce canopy cover. California spotted owl occupancy sharply declines in habitat with less than 40% canopy cover (Tempel et al. 2016, pp. 747, 759); therefore, the reduction in canopy cover from tree mortality and drought will likely negatively impact occupancy. Large trees, and fecundity also have the potential to be negatively impacted. California spotted owls can utilize large trees even if those trees are dead, and CSO are often found nesting in snags. However, CSO are less likely to use large trees if sufficient amount of canopy cover is not present. Tree mortality events and drought conditions may have slightly positive impacts on coarse woody debris, but those positive impacts are likely not great enough to improve the condition of individual analysis units. Drought conditions alone may have negative impacts to survival if not enough water is available, but it is unlikely that a drought would be significant enough to have physiological impacts.

The future impacts of climate change are likely to impact a majority of CSO ecological needs. Climate change is likely to drive the increase in severity of many of the other threats discussed including large-scale high-severity fire, tree mortality, and drought, even if they continue at the current trajectory. The global scale of this threat into the future will likely have other impacts that have the potential to disrupt the entire ecosystem, making it difficult to fully predict the impacts of climate change specifically to CSO. Canopy cover and large trees will likely decline due to the multiple impacts of climate change and the potential shift in plant communities that may result (Gutiérrez et al. 2017, pp. 132, 215, 288). The significant decrease in both canopy cover and large trees will likely result in negative impacts to forest heterogeneity and available nest trees. Climate change may negatively impact survival of CSO with an increase in extreme weather events and heat waves, but it will likely only be a minor impact and not affect the overall condition of any analysis unit. With a decline in habitat and an increase in climate variability and extreme weather events, fecundity will likely decline into the future. Climate change modeling predicts a decline in occupancy under even low emission scenarios by 2052 due to the impacts that climate change will likely have on habitat quality (Jones et al. 2016b, p. 901). Finally, with a decrease in survival, fecundity, and occupancy, population growth will likely decline due to climate change under future scenario 2.

If interannual climate variability changes due to projected climate change, there may be negative impacts to fecundity. Survival may also be negatively impacted by even a small increase in interannual climate variability, but it is dependent on the nature of the variability and will likely not have a significant impact. With a decrease in fecundity, there will likely be a decrease in population growth; however, since CSO is a long-lived species with generally low reproductive rates, the impacts of interannual climate variability may be minor as long as there are occasional years with weather patterns suitable for reproduction.

Under future scenario 2, continued clearcutting, primarily on private lands, would have negative impacts on canopy cover, large trees, fecundity, and occupancy. Clearcutting removes canopy cover and large trees from the landscape, which would decrease analysis unit condition in the future. In northern spotted owls, clearcutting has been shown to reduce dispersal and habitat use (Forsman et al. 1984, p. 25; Carey et al. 1990, p. 11; Miller et al. 1997, pp. 140, 145–148). The decrease in dispersal and habitat use would likely cause a decrease in fecundity, occupancy, and population growth.

Mechanical thinning would continue under future scenario 2, but current protections would likely remain in place in known CSO habitat. Current protections strictly limit the amount of habitat that can be thinned within known CSO territories. Mechanical thinning will likely have negative impacts on canopy cover and coarse woody debris. However, if mechanical thinning is done in a way that maintains CSO habitat, the negative impacts are likely offset by the benefits of reducing fuel loads and reducing the potential of large-scale high-severity fire. For example, it is predicted that there would be few impacts to CSO if multi-layered high canopy cover in a territory is reduced to 30% of the territory and if the area thinned remains at moderate canopy cover (Tempel et al. 2016, p. 761). However, it is important to note that too much thinning can result in negative impacts to fecundity, occupancy, and population growth, so a balance must be maintained (Tempel et al. 2016, pp. 761–762).

Continued salvage logging under future scenario 2 would likely result in a small decrease of prey abundance due to the loss of food and shelter. However, some prey species are able to persist in more open habitat; therefore, some prey species will likely still be available (Bond et al. 2013, pp. 114, 120; Roberts et al. 2015, pp. 107, 113, 2017, p. 112). There would likely be little to no impacts on canopy cover because canopy cover would likely already be reduced by either fire or tree mortality for salvage logging to occur. Large trees and coarse woody debris would likely be negatively impacted by the removal of trees. There would likely be no impact to survival. Fecundity, occupancy, and population growth would likely be negatively impacted with the loss of important habitat components.

Under future scenario 2, experimental removals continue to be successful in limiting the expansion of barred owls on the landscape. In areas where barred owls continue to occur in small numbers (northern Sierra Nevada population analysis units), there would likely be a small negative impact on CSO due to competition for the same prey species (Wiens et al. 2014, pp. 1–2). There would likely be no impacts to the suitability of canopy cover, large trees, or forest heterogeneity due to barred owls. Although barred owls outcompete spotted owls, particularly for food, under scenario 2 we assume that experimental removals continue to be successful and negative impacts from their temporary presence will be relatively short-lived and minor. Therefore, under scenario 2 we assume

barred owls are not having an analysis unit level impact and we do not reduce the current demographic scores to account for their impact on demographic factors.

Under future scenario 2, rodenticides would likely remain on the landscape, but they would not increase from current levels. Rodenticides have the potential to have detrimental effects to CSO, but there have been no documented cases impacting CSO; therefore, this threat is considered minor to survival, fecundity, and population growth.

Disease and parasites are also currently a minor threat to CSO. Given the limited information available, it is difficult to predict the impacts of disease/parasites. There would likely be some impacts to survival and/or fecundity. With little information available, these impacts are considered minor under future scenario 2.

If development continues and encroaches upon CSO habitat, there would likely be significant impacts to a majority of the ecological needs. California spotted owl habitat would likely decrease, as development would likely remove canopy cover and large trees. There would likely be little to no impact to survival of CSO; however, fecundity, occupancy, and population growth would significantly decline due to the loss of quality habitat.

Finally, if recreation remains at current levels under future scenario 2, there would likely be few impacts to CSO. Recreation activities have little to no impact on canopy cover, large trees, survival, or population growth. Fecundity or occupancy may be impacted by recreation if noises or presence of people cause the individuals to leave a nest site or occupied territory. However, there is little evidence that this is a significant threat or that it could be in the future; therefore, the impacts would likely be small if any.

6.4.1.1 Sierra Nevada Population

Lassen Analysis Unit Condition

Under future scenario 2, the Lassen analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, and salvage logging. With barred owls expanding from the north, this analysis unit will likely experience the most intense influx of barred owls; however, continued experimental removals under this scenario limits any further expansion from current condition. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO ecological needs in this analysis unit, but the impacts are likely to be minor. Although there are protections in place on Forest Service and Park Service lands in this unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Lassen unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under future scenario 2, we anticipate demographic rates and habitat conditions to decline due to the increase of threats described above, especially the threat of climate change and high-severity wildfire. The Lassen analysis unit will likely be strongly declining (overall score=1) in 40–50 years under scenario 2 (see Table 24).

Plumas Analysis Unit Condition

Under future scenario 2, the Plumas analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, and salvage logging. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Plumas unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under future scenario 2, we anticipate the Plumas analysis unit will likely continue declining (overall score=2) in 40–50 years (see Table 24).

Tahoe Analysis Unit Condition

Under future scenario 2, the Tahoe analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, and salvage logging. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available, even with the current protections in place. The current condition of the Tahoe analysis unit is stable based on our habitat analysis (overall habitat analysis score=4), but we anticipate habitat conditions and demographic rates will decline due to the increase of threats described above. Under future scenario 2, the Tahoe analysis unit will likely be declining (overall score=3) in 40–50 years (see Table 24).

Eldorado Analysis Unit Condition

Under future scenario 2, the Eldorado analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, and salvage logging. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Eldorado analysis unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under scenario 2, we anticipate the Eldorado analysis unit will likely continue declining (overall score=2) in 40–50 years (see Table 24).

Humboldt-Toiyabe Analysis Unit Condition

Under future scenario 2, the Humboldt-Toiyabe analysis unit will likely be impacted by continued threats of large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, and salvage logging. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on the Forest Service and Nevada State Park land in this analysis unit to ensure

that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Recent PAC information and our current condition habitat analysis found the Humboldt-Toiyabe unit is strongly declining (overall habitat analysis score=1). Under scenario 2, we anticipate the Humboldt-Toiyabe analysis unit will likely continue strongly declining (overall score=0) with the potential of extirpation in 40–50 years (see Table 24).

Stanislaus Analysis Unit Condition

Under future scenario 2, the Stanislaus analysis unit will likely be impacted by the continued threat of large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, and salvage logging. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Stanislaus unit is declining based on our habitat analysis (overall habitat analysis score=3). Under scenario 2, we anticipate the Stanislaus analysis unit will likely continue declining (overall score=3) in 40–50 years (see Table 24).

Yosemite Analysis Unit Condition

Under future scenario 2, the Yosemite analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, and climate change. Clearcutting, mechanical thinning, and salvage logging will likely not be a threat because these activities do not occur on Park Service land. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. The current condition of the Yosemite analysis unit is stable based on our habitat analysis (overall habitat analysis score=4), but we anticipate demographic rates and habitat conditions will decline due to the increase of threats described above. Under future scenario 2, the Yosemite analysis unit will likely be declining (overall score=3) in 40–50 years (see Table 24).

Sierra Analysis Unit Condition

Under future scenario 2, the Sierra analysis unit will likely be impacted by increases in large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, and salvage logging. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the Sierra unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under future scenario 2, we anticipate the Sierra analysis unit will likely continue declining (overall score=2) in 40–50 years (see Table 24).

Sequoia-Kings Canyon Analysis Unit Condition

Under future scenario 2, the Sequoia-Kings Canyon analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, and climate change. Clearcutting, mechanical thinning, and salvage logging will likely not be a threat because these activities do not occur on Park Service land. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Our current condition analysis found the Sequoia-Kings Canyon unit is stable based on demographic information and our habitat analysis supported (overall habitat analysis score=4). Under scenario 2, we anticipate demographic rates and habitat conditions will decline due to the increase of threats described above. The Sequoia-Kings Canyon analysis unit will likely be declining (overall score=3) in 40–50 years under scenario 2 (see Table 24).

Sequoia Analysis Unit Condition

Under future scenario 2, the Sequoia analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, clearcutting, mechanical thinning, and salvage logging. Rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition habitat analysis found the Sequoia unit is strongly declining (overall habitat analysis score=1). Under scenario 2, we anticipate the Sequoia analysis unit will likely continue strongly declining (overall score=1) in 40–50 years (see Table 24).

Inyo Analysis Unit Condition

Under future scenario 2, the Inyo analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, and salvage logging. Clearcutting, rodenticides, disease/parasites, development, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor. Although there are protections in place on Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the Inyo unit is strongly declining based on demographic information and our habitat analysis (overall habitat analysis score=1). Under scenario 2, we anticipate the Inyo analysis unit will likely continue strongly declining (overall score =1) in 40–50 years (see Table 24).

Overall Resiliency for the Sierra Nevada Population

Table 24 presents the future condition for each Sierra Nevada analysis unit with the assumptions described above for future Scenario 2. Under scenario 2 most analysis units degrade in condition, but some maintain their current condition. Overall, under scenario 2 we project the Sierra Nevada population will have seven analysis units declining and four strongly declining (see Table 24). Based on these results, under scenario 2 the future condition of the Sierra Nevada population will be strongly declining (average overall future condition score of 1.9), but to a lesser degree than

under scenario 1. An overall future condition score of 1.9 is at the very upper limit of our scoring boundary for population condition. Therefore, the Sierra Nevada population has very low resiliency under future scenario 2, but it is closer to the boundary of low resiliency. Figure 18 is a map showing the overall future condition of all CSO analysis units under scenario 2.

Table 24: Summary of future condition scores and overall future condition for analysis units within the Sierra Nevada population under future scenario 2. See Tables 26 and 27 for the full scoring analysis for all CSO analysis units.

Analysis Unit	Overall future condition score	Future condition – scenario 2
Lassen	1	Strongly declining
Plumas	2	Declining
Tahoe	3	Declining
Eldorado	2	Declining
Humboldt-Toiyabe	0	Strongly declining
Stanislaus	3	Declining
Yosemite	3	Declining
Sierra	2	Declining
Sequoia-Kings Canyon	3	Declining
Sequoia	1	Strongly declining
Inyo	1	Strongly declining

6.4.1.2 Coastal-Southern California Population

Los Padres Analysis Unit Condition

Under future scenario 2, the Los Padres analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, and development. Clearcutting, salvage logging, rodenticides, disease/parasites, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor or non-existent. Although there are protections in place on Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Los Padres unit is declining based on our habitat analysis (overall habitat analysis score=2). Under future scenario 2, we anticipate the Los Padres analysis unit will continue declining (overall score=2) in 40–50 years (see Table 25).

Los Padres-Angeles Analysis Unit Condition

Under future scenario 2, the Los Padres-Angeles analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, and development. Clearcutting, salvage logging, rodenticides, disease/parasites, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor or non-existent. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the Los Padres-Angeles unit is strongly declining based

on our habitat analysis (overall habitat analysis score=1). Under scenario 2, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above. Under future scenario 2, the Los Padres-Angeles analysis unit will likely continue strongly declining (overall score=0) with the potential of extirpation in 40–50 years (see Table 25).

San Bernardino Analysis Unit Condition

Under future scenario 2, the San Bernardino analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, and development. Clearcutting, salvage logging, rodenticides, disease/parasites, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor or non-existent. Although there are protections in place on Forest Service and Park Service lands in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. Our current condition analysis found the San Bernardino analysis unit is declining based on demographic information and our habitat analysis (overall habitat analysis score=2). Under scenario 2, we anticipate demographic rates and habitat conditions will continue to decline due to the increase of threats described above. Under future scenario 2, the San Bernardino analysis unit will likely be strongly declining (overall score=1) in 40–50 years (see Table 25).

Cleveland Analysis Unit Condition

Under future scenario 2, the Cleveland analysis unit will likely be impacted by the continued threats of large-scale high-severity fire, tree mortality, drought, climate change, mechanical thinning, and development. Clearcutting, rodenticides, disease/parasites, and recreation have the potential to affect CSO in this analysis unit, but the impacts are likely minor or non-existent. Although there are protections in place on the Forest Service land in this analysis unit to ensure that activity centers for CSO are protected, the threats of large-scale high-severity fire and climate change will likely reduce the amount of habitat available even with the current protections in place. The current condition of the Cleveland analysis unit is strongly declining based on our habitat analysis (overall habitat analysis score=1). Under future scenario 2, we anticipate demographic factors and habitat conditions will continue to decline due to the increase of threats described above and will no longer support the species. Under future scenario 2, the Cleveland analysis unit will likely be strongly declining (overall score=0) with the potential of extirpation in 40–50 years (see Table 25).

Overall Resiliency for the Coastal-Southern California Population

Table 25 presents the future condition for each coastal-southern California population analysis unit with the assumptions described above for future scenario 2. Under scenario 2 most coastal-southern California analysis units degrade in condition, with one analysis unit declining and three strongly declining (see Table 25). Based on these results, under scenario 2 the future condition of the coastal-southern California population will likely be strongly declining (average overall future condition score of 0.75). Therefore, the coastal-southern California population will have very low resiliency under scenario 2. Figure 18 is a map showing the overall future condition of all CSO analysis units under scenario 2.

Table 25: Summary of future condition scores and overall future condition for analysis units within the coastal-southern California population under future scenario 2. See Tables 26 and 27 for the full scoring analysis for all CSO analysis units.

Analysis Unit	Overall future condition score	Future condition – scenario 2
Los Padres	2	Declining
Los Padres-Angeles	0	Strongly declining
San Bernardino	1	Strongly declining
Cleveland	0	Strongly declining

Table 26: Summary of our future condition analysis for all CSO analysis units under future scenario 2. This information was used to inform the future condition for all units within the Sierra Nevada and coastal-southern California CSO populations, and population resiliency. The full habitat analysis for scenario 2 is shown in Table 27.

Analysis Unit	Current demographic score	Barred owls score	Total demographic score	Total habitat score	Overall score	Future condition Scenario 2
<i>Sierra Nevada</i>						
Lassen	2	0	2	0	1	Strongly declining
Plumas	2	0	2	1	2	Declining
Tahoe	4	0	4	2	3	Declining
Eldorado	2	0	2	1	2	Declining
Humboldt-Toiyabe	1	0	1	-1	0	Strongly declining
Stanislaus	3	0	3	2	3	Declining
Yosemite	4	0	4	2	3	Declining
Sierra	2	0	2	1	2	Declining
Sequoia-Kings Canyon	4	0	4	2	3	Declining
Sequoia	1	0	1	1	1	Strongly declining
Inyo	1	0	1	0	1	Strongly declining
<i>Coastal-Southern California</i>						
Los Padres	2	0	2	1	2	Declining
Los Padres-Angeles	1	0	1	-1	0	Strongly declining
San Bernardino	2	0	2	-1	1	Strongly declining
Cleveland	1	0	1	-1	0	Strongly declining

Table 27: Full habitat analysis for future scenario 2.

Analysis Unit	Large trees (LT)	LT score	Canopy cover (CC)	CC score	CC & LT	CC & LT score	Total habitat score	High severity fire	High severity score	Total Habitat score	Overall score	Habitat Suitability	Overall Condition
<i>Sierra Nevada</i>													
Lassen	4%	0	48%	1	2%	0	1	14%	-1	0	1	Lowest suitability	Strongly declining
Plumas	5%	0	51%	2	4%	0	2	27%	-1	1	2	Less suitable	Declining
Tahoe	7%	1	64%	2	5%	0	3	1%	-1	2	3	Less suitable	Declining
Eldorado	6%	0	57%	2	4%	0	2	12%	-1	1	2	Less suitable	Declining
Humboldt-Toiyabe	4%	0	24%	0	2%	0	0	4%	-1	-1	0	Lowest suitability	Strongly declining
Stanislaus	7%	1	62%	2	5%	0	3	5%	-1	2	3	Less suitable	Declining
Yosemite	18%	2	36%	0	9%	1	3	5%	-1	2	3	Less suitable	Declining
Sierra	9%	1	47%	1	6%	0	2	7%	-1	1	2	Less suitable	Declining
Sequoia-Kings Canyon	11%	1	49%	1	8%	1	3	6%	-1	2	3	Less suitable	Declining
Sequoia	7%	1	37%	1	3%	0	2	10%	-1	1	1	Lowest suitability	Strongly declining
Inyo	7%	1	26%	0	3%	0	1	0%	-1	0	1	Lowest suitability	Strongly declining
<i>Coastal-Southern California</i>													
Los Padres	3%	0	59%	2	2%	0	2	6%	-1	1	2	Less suitable	Declining
Los Padres-Angeles	1%	0	33%	0	0%	0	0	2%	-1	-1	0	Lowest suitability	Strongly declining
San Bernardino	2%	0	31%	0	0%	0	0	3%	-1	-1	1	Lowest suitability	Strongly declining
Cleveland	0%	0	34%	0	0%	0	0	1%	-1	-1	0	Lowest suitability	Strongly declining

Future Scenario 2 Condition

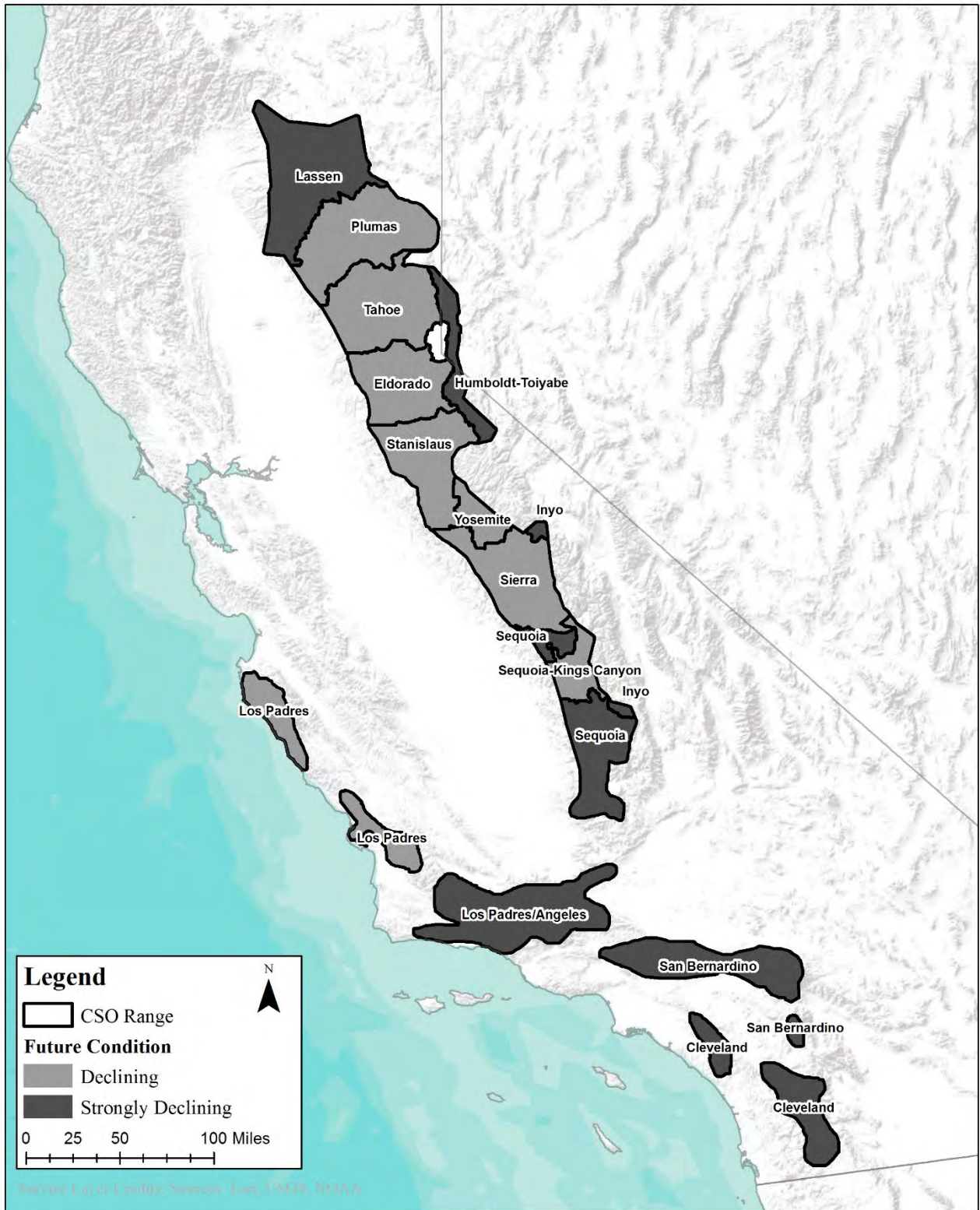


Figure 18: Map of CSO analysis units and their predicted condition under future scenario 2.

6.4.2 Future Species Redundancy

Under future scenario 2, both populations would be less resilient compared to the current condition. The species will likely maintain a majority of its current distribution throughout the Sierra Nevada, which will continue to offer some redundancy for the species. However, because the coastal-southern California population is already highly fragmented, which has accelerated over the last 30 years, the coastal-southern California population will contribute little or nothing to future redundancy for the species. Overall, the species would be less likely to withstand catastrophic events with both populations losing resiliency and a majority of analysis units declining or strongly declining with the potential to be extirpated under scenario 2. The outcome of scenario 1 and scenario 2 are very similar after 40–50 years. There are differences in how quickly the populations would decrease in condition, the likelihood of the impacts, and how many analysis units within a population may actually become extirpated. It is more likely that redundancy would be reduced, potentially from a catastrophic event, under scenario 1.

6.4.3 Future Species Representation

Under Scenario 2 many of the habitat components will likely degrade due to continued threats and the long-term impacts they cause. If the current conservation measures that are in place continue, there will be some protection for the species against certain ongoing threats; however, even with these protections in place the species is still vulnerable to large-scale high-severity fire and climate change impacts. Similar to scenario 1, under scenario 2 representation would decline compared to current condition as the species would have less flexibility to adapt to changing environmental conditions.

CHAPTER 7: OVERALL ASSESSMENT FOR SPECIES VIABILITY

The SSA Report describes the current condition as well as two plausible future scenarios that we considered important to determine the status of the species. The goal of the SSA Report is to describe the viability of the species in a manner that will address the individual, population, and species needs in terms of resiliency, redundancy, and representation. Table 28 provides a summary of the overall current condition as well as the predicted future conditions under scenario 1 and 2 for each analysis unit. Figure 19 is a side-by-side comparison map showing CSO analysis units and the current and predicted future scenario conditions.

Under the current condition, three of the 11 Sierra Nevada analysis units are in stable condition, five analysis units are declining, and three analysis units are strongly declining. In coastal-southern California, two analysis units are declining and two analysis units are strongly declining. Based on recent demographic information and our habitat analysis, we found the current resiliency of the Sierra Nevada population is low and the coastal-southern California population is very low. Overall, the species' current redundancy has declined from historical condition, reducing the species' ability to withstand a catastrophic event. Currently, the Sierra Nevada population covers the most area and has the largest population, contributing the most to species redundancy, while the coastal-southern California population is small and fragmented and contributes little to redundancy. Overall, current CSO redundancy has declined from historical condition, making the species more vulnerable

to extirpations due to a catastrophic event, especially in the coastal-southern California population where a large catastrophic event is likely to have devastating impacts to that population. Similarly, the species' current representation has also declined from historical condition, reducing the species' ability to adapt to changing conditions. The species maintains genetic differences observed between populations, as well as habitat and climate differences, which suggests some degree of adaptation; however, population declines and the lack of documented nesting in historical nesting locations suggest representation has declined.

Under future scenario 1, where the intensity of the threats increases over time and management actions are not fully effective at addressing threats, the condition of almost all analysis units would decline. Of the 15 total analysis units, no analysis units will be stable, four analysis units would likely be declining, six would likely be strongly declining, and five analysis units are likely to be extirpated. Overall, the resiliency of the Sierra Nevada would be very low under scenario 1 and because the condition of the coastal-southern California population would be extirpated, it would have no resiliency under scenario 1. Overall, redundancy and representation would decline as conditions degrade throughout the range and population resiliency declines, reducing the species' ability to withstand catastrophic events and adapt to changing environmental conditions.

Under future scenario 2, where the magnitude of the threats continues on the current trajectory and current management actions are fully effective in the future, the condition of analysis units and corresponding population resiliency decreases from current condition, although less than under future scenario 1. Of the 15 total analysis units, eight analysis units would likely be declining and seven would likely be strongly declining with the potential of extirpation. Overall, the resiliency of the Sierra Nevada would be very low under future scenario 2, although closer to the boundary of low resiliency, and the resiliency of the coastal-southern California population would be very low. Scenario 2 would likely lead to reduced redundancy and representation for the species, but to a lesser extent than scenario 1.

Table 28: Analysis Unit Current and Future Condition Comparisons (changes from current condition in **bold**).

Analysis Unit	Current Condition	Future Condition Scenario 1	Future Condition Scenario 2
<i>Sierra Nevada</i>			
Lassen	Declining	Strongly declining	Strongly declining
Plumas	Declining	Strongly declining	Declining
Tahoe	Stable	Declining	Declining
Eldorado	Declining	Strongly declining	Declining
Humboldt-Toiyabe	Strongly declining	Extirpated	Strongly declining
Stanislaus	Declining	Declining	Declining
Yosemite	Stable	Declining	Declining
Sierra	Declining	Strongly declining	Declining
Sequoia-Kings Canyon	Stable	Declining	Declining
Sequoia	Strongly declining	Extirpated	Strongly declining
Inyo	Strongly declining	Extirpated	Strongly declining

Analysis Unit	Current Condition	Future Condition Scenario 1	Future Condition Scenario 2
<i>Coastal-Southern California</i>			
Los Padres	Declining	Strongly declining	Declining
Los Padres-Angeles	Strongly declining	Extirpated	Strongly declining
San Bernardino	Declining	Strongly declining	Strongly declining
Cleveland	Strongly declining	Extirpated	Strongly declining

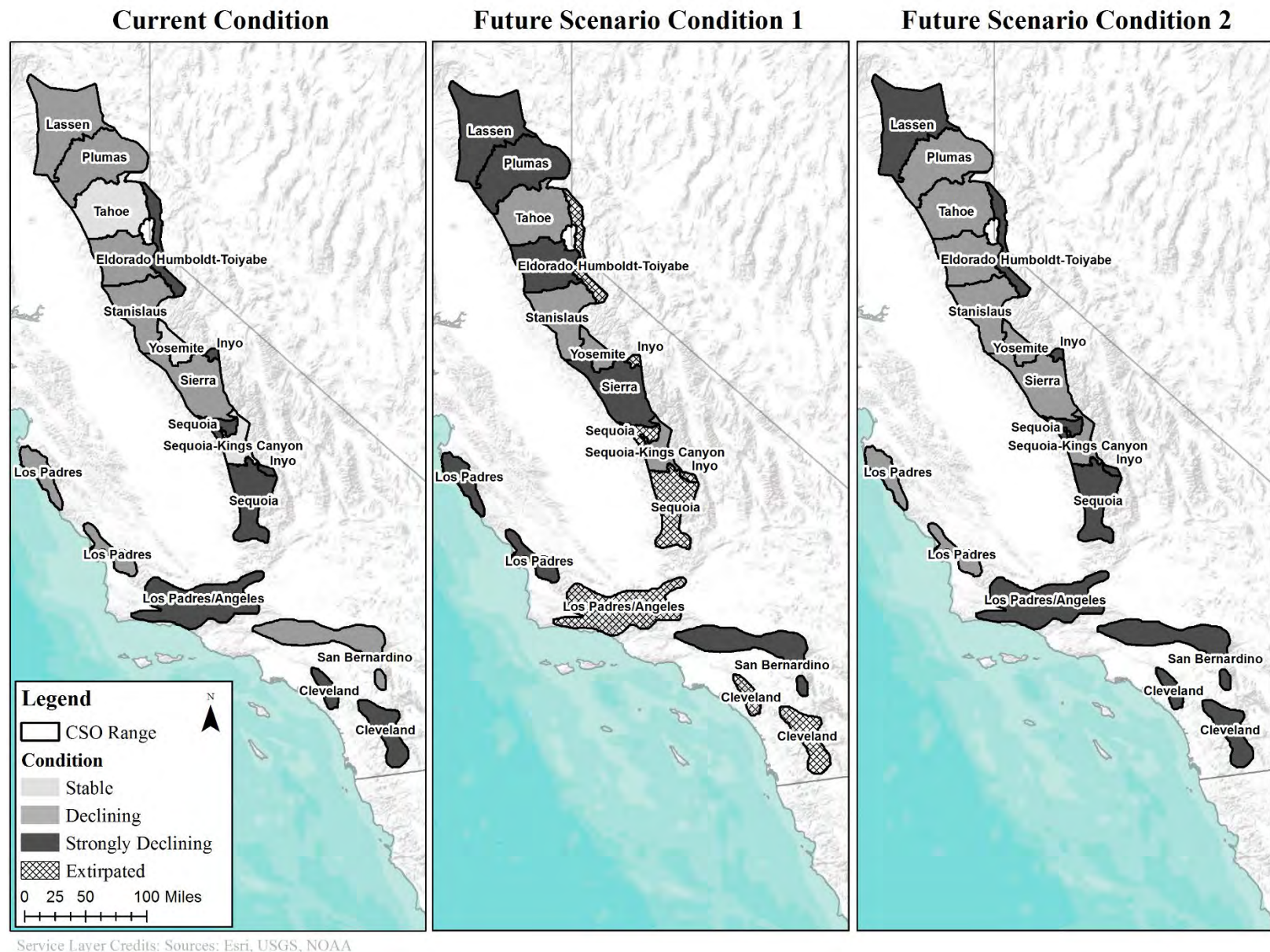


Figure 19: Maps showing the current condition of the CSO analysis units in comparison to predictions for CSO analysis units under future scenarios 1 and 2.

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APPENDIX 1

Table A-1. Coastal-southern California burn severity percentages between 1984 and 2021.

Year	Low Severity (ha)	Moderate Severity (ha)	High Severity (ha)	Total (ha)
1984	0.07%	0.08%	0.07%	0.22%
1985	1.07%	1.46%	1.18%	3.72%
1986	0.34%	0.06%	0.01%	0.41%
1987	0.36%	0.22%	0.09%	0.67%
1988	0.16%	0.16%	0.11%	0.43%
1989	0.20%	0.31%	0.37%	0.89%
1990	0.10%	0.08%	0.06%	0.25%
1991	0.02%	0.02%	0.02%	0.06%
1992	0.06%	0.04%	0.04%	0.14%
1993	0.45%	0.40%	0.09%	0.94%
1994	0.32%	0.33%	0.61%	1.26%
1995	0.23%	0.19%	0.08%	0.49%
1996	0.45%	0.40%	0.18%	1.03%
1997	0.25%	0.25%	0.18%	0.68%
1998	0.06%	0.06%	0.03%	0.15%
1999	0.82%	0.99%	0.68%	2.50%
2000	0.14%	0.13%	0.13%	0.40%
2001	0.01%	0.01%	0.01%	0.02%
2002	1.27%	0.97%	0.58%	2.82%
2003	1.14%	1.76%	2.70%	5.59%
2004	0.45%	0.35%	0.10%	0.91%
2005	0.03%	0.03%	0.01%	0.07%
2006	1.78%	1.83%	0.81%	4.42%
2007	1.50%	1.79%	4.36%	7.65%
2008	1.32%	1.50%	0.76%	3.58%
2009	1.25%	1.63%	1.13%	4.01%
2010	0.01%	0.01%	0.00%	0.03%
2011	0.19%	0.08%	0.01%	0.29%
2012	0.05%	0.06%	0.00%	0.11%
2013	0.20%	0.41%	0.30%	0.91%
2014	0.02%	0.03%	0.00%	0.06%
2015	0.44%	0.24%	0.05%	0.73%
2016	2.43%	1.39%	0.28%	4.10%
2017	1.23%	2.23%	0.17%	3.64%
2018	0.19%	0.32%	0.19%	0.70%
2019	0.05%	0.05%	0.01%	0.11%
2020	2.02%	2.37%	1.47%	5.86%
2021	0.01%	0.01%	0.04%	0.06%
TOTAL	20.70%	22.25%	16.91%	59.87%

Table A-2. Sierra Nevada burn percentages between 1984 and 2021.

Year	Low Severity (ha)	Moderate Severity (ha)	High Severity (ha)	Total (ha)
1984	0.09%	0.05%	0.03%	0.16%
1985	0.09%	0.02%	0.00%	0.11%
1986	0.07%	0.04%	0.02%	0.13%
1987	0.60%	0.55%	0.35%	1.51%
1988	0.12%	0.08%	0.05%	0.25%
1989	0.11%	0.08%	0.03%	0.21%
1990	0.17%	0.16%	0.21%	0.53%
1991	0.02%	0.01%	0.01%	0.04%
1992	0.15%	0.21%	0.34%	0.70%
1993	0.01%	0.00%	0.00%	0.02%
1994	0.31%	0.25%	0.15%	0.71%
1995	0.03%	0.01%	0.00%	0.04%
1996	0.47%	0.21%	0.10%	0.77%
1997	0.04%	0.03%	0.02%	0.08%
1998	0.03%	0.01%	0.00%	0.04%
1999	0.41%	0.22%	0.11%	0.73%
2000	0.24%	0.20%	0.15%	0.59%
2001	0.20%	0.21%	0.20%	0.60%
2002	0.45%	0.36%	0.34%	1.15%
2003	0.11%	0.06%	0.03%	0.20%
2004	0.11%	0.09%	0.08%	0.28%
2005	0.09%	0.04%	0.01%	0.13%
2006	0.13%	0.06%	0.03%	0.21%
2007	0.21%	0.22%	0.32%	0.76%
2008	0.69%	0.53%	0.38%	1.61%
2009	0.16%	0.08%	0.04%	0.28%
2010	0.13%	0.09%	0.04%	0.26%
2011	0.14%	0.03%	0.01%	0.18%
2012	0.40%	0.31%	0.23%	0.94%
2013	0.93%	0.80%	0.55%	2.29%
2014	0.35%	0.33%	0.49%	1.17%
2015	0.53%	0.45%	0.32%	1.31%
2016	0.14%	0.14%	0.18%	0.46%
2017	0.52%	0.27%	0.14%	0.93%
2018	1.00%	0.72%	0.31%	2.03%
2019	0.25%	0.15%	0.08%	0.48%
2020	2.86%	2.32%	2.14%	7.32%
2021	3.33%	3.08%	6.02%	12.42%
TOTAL	15.68%	12.45%	13.50%	41.63%

Table A-3. Sierra Nevada North burn percentages between 1984 and 2021.

Year	Low Severity (ha)	Moderate Severity (ha)	High Severity (ha)	Total (ha)
1984	0.07%	0.04%	0.01%	0.12%
1985	0.01%	0.00%	0.00%	0.01%
1986	0.03%	0.01%	0.00%	0.05%
1987	0.34%	0.27%	0.17%	0.78%
1988	0.02%	0.02%	0.03%	0.07%
1989	0.05%	0.04%	0.02%	0.11%
1990	0.11%	0.07%	0.04%	0.21%
1991	0.00%	0.00%	0.00%	0.00%
1992	0.11%	0.19%	0.47%	0.78%
1993	0.00%	0.00%	0.00%	0.00%
1994	0.39%	0.30%	0.24%	0.93%
1995	0.00%	0.00%	0.00%	0.00%
1996	0.08%	0.03%	0.01%	0.12%
1997	0.02%	0.01%	0.00%	0.04%
1998	0.01%	0.00%	0.00%	0.01%
1999	0.61%	0.32%	0.15%	1.08%
2000	0.27%	0.19%	0.16%	0.62%
2001	0.19%	0.24%	0.26%	0.69%
2002	0.02%	0.01%	0.00%	0.03%
2003	0.00%	0.00%	0.00%	0.00%
2004	0.13%	0.11%	0.10%	0.35%
2005	0.03%	0.01%	0.01%	0.05%
2006	0.08%	0.06%	0.03%	0.17%
2007	0.31%	0.35%	0.55%	1.21%
2008	0.80%	0.56%	0.43%	1.80%
2009	0.11%	0.05%	0.02%	0.18%
2010	0.02%	0.02%	0.01%	0.05%
2011	0.00%	0.00%	0.00%	0.00%
2012	0.65%	0.50%	0.38%	1.53%
2013	0.18%	0.18%	0.12%	0.48%
2014	0.44%	0.38%	0.75%	1.57%
2015	0.03%	0.02%	0.03%	0.08%
2016	0.05%	0.04%	0.03%	0.12%
2017	0.07%	0.04%	0.04%	0.15%
2018	0.77%	0.56%	0.25%	1.58%
2019	0.40%	0.21%	0.12%	0.74%
2020	1.30%	1.33%	2.40%	5.03%
2021	4.72%	4.48%	9.08%	18.27%
TOTAL	12.40%	10.64%	15.95%	38.99%

Table A-4. Sierra Nevada South burn severity percentages between 1984 and 2021.

Year	Low Severity (ha)	Moderate Severity (ha)	High Severity (ha)	Total (ha)
1984	0.11%	0.07%	0.05%	0.23%
1985	0.22%	0.04%	0.01%	0.26%
1986	0.13%	0.08%	0.04%	0.26%
1987	0.96%	0.95%	0.61%	2.52%
1988	0.26%	0.16%	0.08%	0.50%
1989	0.19%	0.12%	0.04%	0.35%
1990	0.25%	0.28%	0.44%	0.98%
1991	0.05%	0.03%	0.01%	0.09%
1992	0.22%	0.23%	0.15%	0.59%
1993	0.03%	0.01%	0.00%	0.05%
1994	0.20%	0.18%	0.04%	0.41%
1995	0.07%	0.02%	0.01%	0.09%
1996	1.01%	0.46%	0.22%	1.69%
1997	0.07%	0.05%	0.04%	0.15%
1998	0.07%	0.02%	0.00%	0.09%
1999	0.13%	0.08%	0.05%	0.26%
2000	0.20%	0.21%	0.13%	0.54%
2001	0.20%	0.16%	0.12%	0.48%
2002	1.05%	0.86%	0.80%	2.72%
2003	0.26%	0.14%	0.07%	0.48%
2004	0.08%	0.06%	0.04%	0.18%
2005	0.16%	0.07%	0.02%	0.25%
2006	0.19%	0.05%	0.01%	0.25%
2007	0.08%	0.03%	0.01%	0.12%
2008	0.54%	0.49%	0.31%	1.34%
2009	0.24%	0.12%	0.06%	0.42%
2010	0.28%	0.19%	0.08%	0.55%
2011	0.33%	0.06%	0.03%	0.42%
2012	0.05%	0.04%	0.02%	0.11%
2013	1.98%	1.68%	1.15%	4.81%
2014	0.22%	0.25%	0.13%	0.61%
2015	1.23%	1.05%	0.73%	3.01%
2016	0.27%	0.29%	0.38%	0.94%
2017	1.14%	0.60%	0.28%	2.03%
2018	1.31%	0.95%	0.40%	2.67%
2019	0.05%	0.06%	0.01%	0.11%
2020	5.05%	3.71%	1.77%	10.53%
2021	1.39%	1.12%	1.75%	4.26%
TOTAL	20.26%	14.98%	10.09%	45.32%

Table A-5. Yearly burn severity percentages for high severity for all Analysis Units.

Year	Los Padres-Angelos	Cleveland	Eldorado	Humboldt-Toiyabe	Inyo	Lassen	Los Padres	Plumas	San Bernardino	Sequoia	Sequoia Kings Canyon	Sierra	Stanislaus	Tahoe	Yosemite	TOTAL
1984	0.01%	0.24%	---	0.15%	---	0.01%	0%	---	0.08%	0.16%	0.03%	0%	0%	---	0%	0.04%
1985	1.88%	0.02%	---	---	---	0%	2.67%	---	---	---	0%	0.01%	0%	---	0.02%	0.35%
1986	---	---	---	0.06%	---	---	0.05%	---	0.01%	0%	0.02%	0.15%	---	---	0%	0.02%
1987	0.08%	0.29%	---	0.25%	---	0.02%	0.00%	0%	0.02%	---	0.15%	0%	2.30%	0.23%	0.06%	0.28%
1988	0.01%	0.02%	---	---	---	---	0.37%	---	0.14%	0.03%	0.10%	0.06%	0.12%	0.12%	0.23%	0.07%
1989	0.02%	1.83%	---	---	---	---	0.12%	0.08%	0.02%	---	---	0.13%	---	---	0.01%	0.13%
1990	0.02%	0.30%	---	---	---	0.13%	0.01%	0.01%	---	1.07%	0.06%	0.07%	0.27%	---	1.03%	0.17%
1991	0.05%	---	---	---	---	---	---	---	0.01%	---	---	---	---	---	0.18%	0.01%
1992	0.01%	---	0.99%	---	1.31%	1.06%	0.19%	---	---	---	0.01%	0%	0.46%	---	---	0.25%
1993	0.18%	0.11%	---	---	---	---	---	---	0.01%	---	0.03%	---	0.00%	---	---	0.03%
1994	0.01%	0.03%	0.03%	0.50%	---	0.04%	3.20%	0.01%	0.15%	0.03%	---	0.07%	0.02%	0.79%	0.05%	0.29%
1995	0.02%	0.18%	---	---	---	---	0.01%	---	0.15%	---	0.06%	---	---	---	---	0.02%
1996	0.09%	---	---	0.03%	---	---	0.68%	0.03%	0.11%	0.04%	0.37%	0%	0.28%	---	1.39%	0.12%
1997	0.10%	0%	---	---	---	0.01%	0.33%	---	0.31%	0.14%	0.01%	---	---	---	0.02%	0.06%
1998	0.08%	0.01%	---	---	---	0%	---	---	---	0%	0%	---	---	---	0%	0.01%
1999	0.00%	0.69%	---	---	---	0.13%	1.30%	0.39%	1.23%	0.06%	0.04%	---	0.12%	0.06%	0.02%	0.28%
2000	---	0.43%	---	---	---	0.19%	0.30%	0.43%	---	0.52%	---	---	---	---	---	0.15%
2001	---	0%	0.24%	0.63%	---	0.19%	---	0.07%	0.02%	0.05%	0%	0.05%	0.29%	0.43%	0.21%	0.14%
2002	0.39%	1.48%	0.01%	0.17%	5.28%	0.01%	---	---	0.59%	2.61%	0%	---	---	---	0.02%	0.41%
2003	0.96%	9.68%	---	---	0.03%	---	0.01%	---	2.04%	0.11%	0.05%	---	0.10%	---	0.17%	0.82%
2004	0.18%	0.07%	0.59%	---	---	0%	---	---	0.09%	0.07%	---	---	0.06%	---	0.14%	0.09%
2005	0%	---	---	---	---	0%	---	---	0.02%	0.01%	0.15%	---	---	0.05%	0.01%	0.01%
2006	1.78%	0.22%	0.03%	0.01%	---	0.02%	---	0.04%	0.35%	0.04%	---	0%	0%	0.06%	0.02%	0.26%
2007	9.78%	2.73%	0.11%	---	---	0.01%	---	2.07%	0.61%	0.03%	---	---	---	---	0%	1.51%
2008	0.07%	0.01%	---	---	---	0.84%	4.00%	0.52%	0.10%	0.82%	0.09%	0.19%	0.15%	0.27%	0.01%	0.49%
2009	0.45%	---	---	---	---	0.06%	---	---	3.67%	0.02%	---	---	0.09%	0.02%	0.40%	0.36%
2010	0.01%	---	---	0.03%	---	---	---	0.02%	---	0.30%	0.01%	---	---	0.01%	0.00%	0.03%
2011	0.02%	0.03%	---	---	---	---	---	---	0%	0.07%	0%	0.01%	0.04%	---	0%	0.01%
2012	0.56%	0.12%	---	---	---	0.05%	---	---	0.24%	0.03%	---	0.25%	3.16%	0.47%	3.61%	0.48%

Year	Los Padres- Angeles	Cleveland	Eldorado	Humboldt- Toiyabe	Inyo	Lassen	Los Padres	Plumas	San Bernardino	Sequoia	Sequoia Kings Canyon	Sierra	Stanislaus	Tahoe	Yosemite	TOTAL
2013	0.56%	0.12%	---	---	---	0.05%	---	---	0.24%	0.03%	---	0.25%	3.16%	0.47%	3.61%	0.48%
2014	---	---	3.75%	---	---	0.36%	---	---	0.01%	0.08%	0%	0.27%	0.03%	---	0.44%	0.35%
2015	---	---	---	0.18%	---	---	0.06%	0.03%	0.15%	1.33%	0.06%	0.63%	0.80%	0.06%	---	0.24%
2016	0.17%	---	0.13%	---	---	0.04%	0.73%	---	0.33%	1.48%	---	0%	---	---	0%	0.21%
2017	0.35%	0.02%	---	---	0.06%	---	0.03%	0.17%	0.12%	0.57%	---	0.27%	0.14%	---	0.39%	0.15%
2018	0%	0.57%	---	0.02%	0.08%	0.67%	---	0.20%	0.33%	0.02%	0.01%	0.45%	0.92%	0.04%	0.45%	0.28%
2019	0.01%	---	0.01%	---	---	---	---	0.47%	0.02%	---	---	0.04%	---	---	---	0.06%
2020	0.39%	0.03%	0.01%	0.24%	0.35%	0.50%	4.54%	8.76%	1.99%	1.77%	0.35%	4.61%	---	0%	0.03%	1.94%
2021	---	---	7.96%	3.39%	---	11.31%	0.23%	16.53%	---	4.90%	5.22%	---	---	---	---	4.09%

Table A-6. Yearly burn severity percentages for moderate severity for all Analysis Units.

Year	Los Padres-Angelos	Cleveland	Eldorado	Humboldt-Toiyabe	Inyo	Lassen	Los Padres	Plumas	San Bernardino	Sequoia	Sequoia Kings Canyon	Sierra	Stanislaus	Tahoe	Yosemite	TOTAL
1984	0.02%	0.21%	---	0.16%	---	0.07%	0.09%	0.02%	0.07%	0.21%	0.10%	0.01%	0.01%	---	0.04%	0.06%
1985	2.20%	0.09%	---	---	---	0%	3.49%	---	---	0.08%	0.03%	0.06%	0%	---	0.05%	0.44%
1986	0.01%	0.02%	---	0.19%	---	---	0.16%	---	0.09%	0%	0.03%	0.28%	---	---	0.05%	0.05%
1987	0.26%	0.49%	0%	0.40%	---	0.18%	0.01%	0.55%	0.11%	---	0.34%	0.08%	3.44%	0.19%	0.18%	0.45%
1988	0.08%	0.04%	---	---	---	0%	0.12%	---	0.38%	0.06%	0.21%	0.14%	0.27%	0.08%	0.23%	0.10%
1989	0.01%	1.50%	---	---	---	---	0.09%	0.16%	0.05%	---	---	0.44%	---	---	0.01%	0.15%
1990	0.06%	0.29%	---	---	---	0.21%	0.02%	0.02%	---	0.48%	0.12%	0.09%	0.32%	---	0.60%	0.13%
1991	0.03%	---	---	---	---	---	---	---	0.05%	0%	0%	---	---	---	0.35%	0.01%
1992	0.03%	---	0.44%	---	1.77%	0.42%	0.17%	---	---	0.01%	0.04%	0.02%	0.68%	---	---	0.16%
1993	0.61%	0.67%	---	---	---	---	---	---	0.17%	---	0.09%	---	0%	---	0.01%	0.12%
1994	0.06%	0.18%	0.03%	0.96%	---	0.14%	0.88%	0.02%	0.45%	0.45%	---	0.14%	0.04%	0.77%	0.13%	0.27%
1995	0.04%	0.22%	---	---	---	---	0.11%	0%	0.44%	0.01%	0.16%	---	---	---	---	0.06%
1996	0.61%	0.01%	---	0.20%	---	---	0.73%	0.07%	0.16%	0.15%	0.40%	0.02%	0.78%	---	2.57%	0.27%
1997	0.11%	0.02%	---	---	---	0.02%	0.16%	0.03%	0.68%	0.14%	0%	---	---	---	0.14%	0.09%
1998	0.10%	0.13%	---	---	---	0.01%	---	---	---	0.04%	0.04%	---	---	---	0.04%	0.02%
1999	0%	0.27%	---	---	---	0.29%	3.15%	0.86%	1.49%	0.06%	0.15%	---	0.15%	0.08%	0.13%	0.45%
2000	0.04%	0.47%	---	---	---	0.32%	0.16%	0.37%	---	0.82%	---	---	---	---	---	0.18%
2001	---	0%	0.13%	0.97%	---	0.21%	0%	0.08%	0.04%	0.09%	0.01%	0.10%	0.36%	0.30%	0.28%	0.15%
2002	0.64%	1.70%	0.02%	0.03%	4.48%	0.02%	0.01%	---	1.59%	2.93%	0.01%	---	---	---	0.07%	0.54%
2003	0.51%	2.51%	---	---	0.21%	---	0.04%	---	4.18%	0.18%	0.22%	---	0.21%	---	0.26%	0.56%
2004	0.34%	0.72%	0.62%	---	---	0.02%	---	---	0.34%	0.07%	---	---	0.08%	---	0.31%	0.17%
2005	0.05%	---	---	---	---	0.01%	---	---	0.04%	0.07%	0.50%	---	---	0.04%	0.06%	0.03%
2006	3.59%	0.92%	0.06%	0.04%	---	0.02%	---	0.07%	1.16%	0.14%	0.02%	0.01%	0.02%	0.09%	0.12%	0.58%
2007	2.26%	3.89%	0.07%	---	---	0.01%	---	1.32%	0.83%	0.13%	---	---	---	---	0.02%	0.68%
2008	0.28%	0.09%	---	---	---	0.96%	7.08%	0.82%	0.48%	0.80%	0.33%	0.60%	0.32%	0.35%	0.10%	0.82%
2009	0.64%	---	---	---	0%	0.15%	---	---	5.34%	0.08%	---	---	0.14%	0.04%	0.92%	0.54%
2010	0.04%	---	---	0.05%	---	0%	---	0.08%	---	0.71%	0.08%	---	---	0.01%	0%	0.07%
2011	0.13%	0.17%	---	---	---	---	---	---	0.01%	0.13%	0.01%	0.01%	0.08%	---	0.05%	0.04%

Year	Los Padres- Angeles	Cleveland	Eldorado	Humboldt- Toiyabe	Inyo	Lassen	Los Padres	Plumas	San Bernardino	Sequoia	Sequoia Kings Canyon	Sierra	Stanislaus	Tahoe	Yosemite	TOTAL
2012	---	0.08%	---	---	---	0.85%	---	0.97%	0.17%	0.09%	---	---	0.03%	0.05%	0.07%	0.23%
2013	0.58%	0.70%	---	---	---	0.11%	---	---	0.23%	0.06%	---	0.49%	4.44%	0.64%	5.38%	0.69%
2014	---	---	1.74%	---	---	0.28%	---	---	0.13%	0.22%	0.03%	0.46%	0.15%	---	0.39%	0.24%
2015	---	0%	0%	0.16%	---	---	0.09%	0.02%	0.87%	1.85%	0.32%	1.10%	0.95%	0.03%	---	0.39%
2016	0.73%	0%	0.14%	---	---	0.04%	3.40%	---	1.98%	1.02%	---	0.10%	---	---	0.02%	0.51%
2017	5.37%	0.08%	---	---	0.75%	---	0.29%	0.14%	0.51%	1.16%	---	0.44%	0.35%	0%	1.05%	0.85%
2018	0.01%	1.05%	---	0.05%	0.30%	1.57%	0%	0.41%	0.45%	0.07%	0.09%	1.75%	1.40%	0.02%	1.03%	0.60%
2019	0.04%	---	0.10%	---	---	---	---	0.76%	0.11%	---	---	0.21%	---	---	---	0.12%
2020	0.72%	0.30%	0.03%	0.58%	3.39%	0.47%	4.16%	4.56%	5.01%	4.27%	1.09%	8.72%	---	0.01%	0.14%	2.34%
2021	---	---	4.47%	1.41%	---	5.29%	0.07%	8.18%	---	2.92%	4.01%	---	---	---	---	2.05%

Table A-7. Yearly burn severity percentages for low severity for all Analysis Units.

Year	Los Padres- Angeles	Cleveland	Eldorado	Humboldt- Toiyabe	Inyo	Lassen	Los Padres	Plumas	San Bernardino	Sequoia	Sequoia Kings Canyon	Sierra	Stanislaus	Tahoe	Yosemite	TOTAL
1984	0.03%	0.14%	---	0.20%	---	0.18%	0.14%	0.03%	0.04%	0.27%	0.23%	0.02%	0.01%	---	0.17%	0.08%
1985	1.43%	0.11%	---	---	---	0.02%	2.89%	---	---	0.57%	0.20%	0.10%	0%	---	0.31%	0.38%
1986	0.12%	0.96%	---	0.38%	---	---	0.32%	---	0.22%	0%	0.06%	0.31%	---	---	0.52%	0.15%
1987	0.44%	0.68%	0%	0.44%	---	0.28%	0.30%	0.72%	0.07%	---	0.38%	0.15%	3.26%	0.20%	0.63%	0.53%
1988	0.12%	0.06%	---	---	---	0.04%	0.09%	---	0.34%	0.13%	0.24%	0.23%	0.41%	0.06%	0.46%	0.13%
1989	0.02%	0.94%	---	---	---	---	0.03%	0.19%	0.06%	---	---	0.70%	---	---	0.02%	0.14%
1990	0.08%	0.36%	---	---	---	0.35%	0.04%	0.02%	---	0.22%	0.15%	0.12%	0.34%	---	0.90%	0.15%
1991	0.01%	---	---	---	---	---	---	---	0.05%	0%	0.08%	---	---	---	0.56%	0.02%
1992	0.05%	---	0.28%	0.00%	3.06%	0.22%	0.22%	---	---	0.10%	0.11%	0.06%	0.38%	---	---	0.13%
1993	0.65%	0.80%	---	---	---	---	---	---	0.22%	---	0.15%	---	0.03%	---	0.17%	0.14%
1994	0.08%	0.27%	0.02%	0.76%	0%	0.47%	0.41%	0.06%	0.66%	0.34%	---	0.18%	0.11%	0.80%	0.41%	0.31%
1995	0.03%	0.32%	---	---	---	---	0.33%	0%	0.38%	0.13%	0.36%	---	---	---	---	0.09%
1996	0.81%	0.09%	---	0.39%	---	---	0.64%	0.18%	0.06%	0.34%	0.51%	0.09%	1.14%	0%	7.75%	0.46%
1997	0.09%	0.04%	---	---	---	0.04%	0.09%	0.04%	0.76%	0.11%	0.00%	---	---	---	0.51%	0.10%
1998	0.08%	0.14%	---	---	---	0.03%	---	---	---	0.15%	0.16%	---	---	---	0.26%	0.04%
1999	0.01%	0.23%	---	---	---	0.74%	2.66%	1.47%	1.19%	0.01%	0.31%	---	0.16%	0.09%	0.74%	0.53%
2000	0.13%	0.39%	---	---	---	0.49%	0.08%	0.49%	---	0.78%	---	---	---	---	---	0.21%
2001	---	0.01%	0.10%	0.64%	---	0.17%	---	0.06%	0.02%	0.09%	0.08%	0.08%	0.41%	0.28%	0.56%	0.14%
2002	0.69%	1.80%	0.05%	0.02%	6.61%	0.03%	0.12%	---	2.49%	3.24%	0.05%	---	---	---	0.98%	0.69%
2003	0.19%	1.32%	---	---	0.64%	0%	0.05%	---	3.11%	0.28%	0.66%	---	0.31%	---	0.47%	0.41%
2004	0.43%	0.55%	0.65%	---	---	0.07%	---	---	0.73%	0.05%	---	---	0.06%	---	0.66%	0.21%
2005	0.08%	---	---	---	---	0.07%	---	---	0.02%	0.11%	1.09%	---	---	0.04%	0.43%	0.07%
2006	3.99%	0.68%	0.09%	0.07%	---	0.03%	---	0.04%	0.59%	0.26%	0.24%	0.14%	0.05%	0.18%	0.64%	0.61%
2007	1.72%	3.68%	0.05%	---	---	0.01%	---	1.16%	0.64%	0.28%	---	---	---	---	0.16%	0.59%
2008	0.18%	0.49%	---	---	---	1.17%	6.07%	1.37%	0.37%	0.65%	1.16%	0.65%	0.23%	0.53%	0.31%	0.88%
2009	0.81%	---	---	---	0.01%	0.34%	---	---	3.61%	0.23%	---	---	0.26%	0.04%	1.63%	0.48%
2010	0.02%	---	---	0.07%	---	0%	---	0.07%	---	0.91%	0.33%	---	---	0.01%	0.05%	0.09%

Year	Los Padres- Angeles	Cleveland	Eldorado	Humboldt- Toiyabe	Inyo	Lassen	Los Padres	Plumas	San Bernardino	Sequoia	Sequoia Kings Canyon	Sierra	Stanislaus	Tahoe	Yosemite	TOTAL
2011	0.34%	0.35%	---	---	---	---	---	---	0%	1.04%	0.09%	0.01%	0.11%	---	0.30%	0.15%
2012	---	0.08%	---	---	---	1.22%	---	1.12%	0.14%	0.10%	---	---	0.03%	0.07%	0.28%	0.30%
2013	0.24%	0.39%	---	---	---	0.16%	---	---	0.15%	0.06%	---	0.89%	4.55%	0.57%	7.72%	0.72%
2014	---	---	2.28%	---	---	0.17%	---	---	0.08%	0.21%	0.19%	0.31%	0.12%	---	0.50%	0.25%
2015	---	0.24%	---	0.14%	---	---	0.15%	0.02%	1.41%	2.38%	0.86%	1.38%	0.61%	0.06%	0%	0.50%
2016	0.81%	0.04%	0.23%	---	---	0.03%	7.42%	0%	3.10%	0.91%	---	0.08%	---	---	0.19%	0.81%
2017	2.76%	0.14%	---	---	1.10%	---	0.15%	0.28%	0.54%	2.53%	---	0.43%	0.53%	0%	2.96%	0.73%
2018	0%	0.69%	---	0.03%	0.62%	2.01%	---	0.75%	0.23%	0.27%	0.23%	2.53%	1.66%	0.01%	1.14%	0.76%
2019	0.07%	---	0.15%	---	---	---	---	1.47%	0.11%	---	---	0.17%	---	---	---	0.19%
2020	0.45%	1.10%	0.10%	1.19%	6.28%	0.45%	2.60%	4.37%	4.57%	4.49%	2.30%	12.44%	---	0.03%	0.49%	2.62%
2021	---	---	5.58%	1.09%	---	6.86%	0.04%	6.72%	---	3.06%	6.48%	---	---	---	---	2.16%



DEPARTMENT OF THE INTERIOR

Fish and Wildlife Service

50 CFR Part 17

[Docket No. FWS-R8-ES-2022-0166; FF09E21000 FXES1111090FEDR 234]

RIN 1018–BG64

Endangered and Threatened Wildlife and Plants; California Spotted Owl; Endangered Status for the Coastal-Southern California Distinct Population Segment and Threatened Status with Section 4(d) Rule for the Sierra Nevada Distinct Population Segment

AGENCY: Fish and Wildlife Service, Interior.

ACTION: Proposed rule.

SUMMARY: We, the U.S. Fish and Wildlife Service (Service), propose to list two distinct population segments (DPSs) of the California spotted owl (*Strix occidentalis occidentalis*), a bird species from California and Nevada, under the Endangered Species Act of 1973, as amended (Act). This determination also serves as our 12-month finding on a petition to list the California spotted owl. After a review of the best available scientific and commercial information, we find that listing the Coastal-Southern California DPS as endangered is warranted, and that listing the Sierra Nevada DPS as threatened is warranted. Accordingly, we propose to list the Coastal-Southern California DPS as an endangered species under the Act and the Sierra Nevada DPS as a threatened species with a rule issued under section 4(d) of the Act (“4(d) rule”). If we finalize this rule as proposed, it will add these two DPSs to the List of Endangered and Threatened Wildlife and extend the Act’s protections to them.

DATES: We will accept comments received or postmarked on or before [INSERT DATE 60 DAYS AFTER DATE OF PUBLICATION IN THE FEDERAL REGISTER].

Comments submitted electronically using the Federal eRulemaking Portal (see **ADDRESSES**, below) must be received by 11:59 p.m. eastern time on the closing date. We must receive requests for a public hearing, in writing, at the address shown in **FOR FURTHER INFORMATION CONTACT** by [INSERT DATE 45 DAYS AFTER DATE OF PUBLICATION IN THE FEDERAL REGISTER].

ADDRESSES: *Written comments:* You may submit comments by one of the following methods:

(1) *Electronically:* Go to the Federal eRulemaking Portal:

<https://www.regulations.gov>. In the Search box, enter FWS-R8-ES-2022-0166, which is the docket number for this rulemaking. Then, click on the Search button. On the resulting page, in the panel on the left side of the screen, under the Document Type heading, check the Proposed Rule box to locate this document. You may submit a comment by clicking on “Comment.”

(2) *By hard copy:* Submit by U.S. mail to: Public Comments Processing, Attn: FWS-R8-ES-2022-0166, U.S. Fish and Wildlife Service, MS: PRB/3W, 5275 Leesburg Pike, Falls Church, VA 22041–3803.

We request that you send comments only by the methods described above. We will post all comments on <https://www.regulations.gov>. This generally means that we will post any personal information you provide us (see **Information Requested**, below, for more information).

Availability of supporting materials: Supporting materials, such as the species status assessment report, are available at <https://www.regulations.gov> under Docket No. FWS-R8-ES-2022-0166.

FOR FURTHER INFORMATION CONTACT: Michael Fris, Field Supervisor,
Sacramento Fish and Wildlife Office, 2800 Cottage Way, Sacramento, CA

95825; telephone 916–414–6700. Individuals in the United States who are deaf, deafblind, hard of hearing, or have a speech disability may dial 711 (TTY, TDD, or TeleBraille) to access telecommunications relay services. Individuals outside the United States should use the relay services offered within their country to make international calls to the point-of-contact in the United States.

SUPPLEMENTARY INFORMATION:

Executive Summary

Why we need to publish a rule. Under the Act, a species warrants listing if it meets the definition of an endangered species (in danger of extinction throughout all or a significant portion of its range) or a threatened species (likely to become endangered within the foreseeable future throughout all or a significant portion of its range). If we determine that a species warrants listing, we must list the species promptly and designate the species' critical habitat to the maximum extent prudent and determinable. We have determined that the Sierra Nevada DPS of the California spotted owl meets the definition of a threatened species, and the Coastal-Southern California DPS of the California spotted owl meets the definition of an endangered species; therefore, we are proposing to list them as such. Listing a species as an endangered or threatened species can be completed only by issuing a rule through the Administrative Procedure Act rulemaking process (5 U.S.C. 551 et seq.).

What this document does. We propose the listing of the Sierra Nevada DPS of the California spotted owl as a threatened species with a rule under section 4(d) of the Act and the Coastal-Southern California DPS of the California spotted owl as an endangered species under the Act.

The basis for our action. Under the Act, we may determine that a species is an endangered or threatened species because of any of five factors: (A) The present or threatened destruction, modification, or curtailment of its habitat or range; (B)

overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; or (E) other natural or manmade factors affecting its continued existence.

We have determined that both the Sierra Nevada population and the coastal-southern California population of the California spotted owl are discrete and significant under our DPS policy and are, therefore, listable entities under the Act. The Sierra Nevada DPS is found in the Sierra Nevada Mountain Ranges and foothills in California and western Nevada. The Coastal-Southern California DPS is found in the Coast, Transverse, and Peninsular Ranges of California. These two DPSs together represent the entirety of the California spotted owl's range.

The Sierra Nevada DPS of the California spotted owl is currently being impacted by high-severity fire, tree mortality, drought, and barred owls. This DPS still has resiliency throughout its range, and some areas remain in stable condition; however, we expect the magnitude of impacts from high-severity fire, tree mortality, drought, climate change, and other threats to increase into the future. Because the Sierra Nevada DPS is likely to become in danger of extinction within the foreseeable future, we propose to list it as threatened.

The Coastal-Southern California DPS has low resiliency, redundancy, and representation. The entirety of the range of this DPS is at extremely high risk of fire, and available habitat is fragmented. All areas of the Coastal-Southern California DPS are currently declining, and the DPS faces additional threats from tree mortality and drought. Because the Coastal-Southern California DPS is currently in danger of extinction, we propose to list it as endangered.

Information Requested

We intend that any final action resulting from this proposed rule will be based on the best scientific and commercial data available and be as accurate and as effective as

possible. Therefore, we request comments or information from other governmental agencies, Native American Tribes, the scientific community, industry, or any other interested parties concerning this proposed rule.

We particularly seek comments concerning:

(1) The species' biology, range, and population trends, including:

(a) Biological or ecological requirements of the species, including habitat requirements for feeding, breeding, and sheltering;

(b) Genetics and taxonomy;

(c) Historical and current range, including distribution patterns and the locations of any additional populations of this species;

(d) Historical and current population levels, and current and projected trends; and

(e) Past and ongoing conservation measures for the species, its habitat, or both.

(2) Factors that may affect the continued existence of the species, which may include habitat modification or destruction, overutilization, disease, predation, the inadequacy of existing regulatory mechanisms, or other natural or manmade factors.

(3) Biological, commercial trade, or other relevant data concerning any threats (or lack thereof) to this species and existing regulations that may be addressing those threats.

(4) Additional information concerning the historical and current status of this species.

(5) Information on regulations that may be necessary and advisable to provide for the conservation of the Sierra Nevada DPS of the California spotted owl and that we can consider in developing a 4(d) rule for the species. In particular, information concerning the extent to which we should include any of the section 9 prohibitions in the 4(d) rule or whether we should consider any additional exceptions from the prohibitions in the 4(d) rule.

(6) Whether we should include in our 4(d) rule for the Sierra Nevada DPS the provision at 50 CFR 17.7 for raptors in captivity.

(7) Which areas may be appropriate as critical habitat for the species and why areas should or should not be proposed for designation as critical habitat in the future, including whether there are threats to the species from human activity that would be expected to increase due to the designation and whether that increase in threat would outweigh the benefit of designation such that the designation of critical habitat may not be prudent.

(8) Specific information on:

(a) The amount and distribution of habitat for the Sierra Nevada DPS and the Coastal-Southern California DPS of the California spotted owl which should be considered for proposed critical habitat;

(b) What may constitute the physical or biological features essential to the conservation of the species within the geographical range currently occupied by the species;

(c) Where these features are currently found;

(d) Whether any of these features may require special management considerations or protection;

(e) What areas are currently occupied and contain features essential to the conservation of the species that should be included in the designation and why; and

(f) What unoccupied areas may be essential for the conservation of the species and why.

Please include sufficient information, such as scientific journal articles or other publications, to allow us to verify any scientific or commercial information you include.

Please note that submissions merely stating support for, or opposition to, the action under consideration without providing supporting information, although noted, do

not provide substantial information necessary to support a determination. Section 4(b)(1)(A) of the Act (16 U.S.C. 1533(b)(1)(A)) directs that determinations as to whether any species is an endangered or a threatened species must be made solely on the basis of the best scientific and commercial data available.

You may submit your comments and materials concerning this proposed rule by one of the methods listed in **ADDRESSES**. We request that you send comments only by the methods described in **ADDRESSES**.

If you submit information via <https://www.regulations.gov>, your entire submission—including any personal identifying information—will be posted on the website. If your submission is made via a hardcopy that includes personal identifying information, you may request at the top of your document that we withhold this information from public review. However, we cannot guarantee that we will be able to do so. We will post all hardcopy submissions on <https://www.regulations.gov>.

Comments and materials we receive, as well as supporting documentation we used in preparing this proposed rule, will be available for public inspection on <https://www.regulations.gov>.

Because we will consider all comments and information we receive during the comment period, our final determinations may differ from this proposal. Based on the new information we receive (and any comments on that new information), we may conclude that the Coastal-Southern California DPS is threatened instead of endangered, or that the Sierra Nevada DPS is endangered instead of threatened, or we may conclude that neither DPS warrants listing as either an endangered species or a threatened species. In addition, we may change the parameters of the prohibitions or the exceptions to those prohibitions in the 4(d) rule for the Sierra Nevada DPS if we conclude it is appropriate in light of comments and new information received. For example, we may expand the incidental-take prohibitions or the exceptions to those prohibitions in the 4(d) rule for the

Sierra Nevada DPS to include prohibiting additional activities if we conclude that those additional activities are not compatible with conservation of the DPS. Conversely, we may establish additional exceptions to the incidental-take prohibitions in the final rule if we conclude that the activities would facilitate or are compatible with the conservation and recovery of the DPS.

Public Hearing

Section 4(b)(5) of the Act (16 U.S.C. 1533(b)(5)) provides for a public hearing on this proposal, if requested. Requests must be received by the date specified in **DATES**. Such requests must be sent to the address shown in **FOR FURTHER INFORMATION CONTACT**. We will schedule a public hearing on this proposal, if requested, and announce the date, time, and place of the hearing, as well as how to obtain reasonable accommodations, in the *Federal Register* and local newspapers at least 15 days before the hearing. We may hold the public hearing in person or virtually via webinar. We will announce any public hearing on our website, in addition to the *Federal Register*. The use of virtual public hearings is consistent with our regulations at 50 CFR 424.16(c)(3).

List of Abbreviations and Acronyms

We use many abbreviations and acronyms in this proposed rule. For the convenience of the reader, we define some of them here:

ac = acres

BLM = Bureau of Land Management

CAL FIRE = California Department of Forestry and Fire Protection

CDWR = California Department of Water Resources

CI = confidence interval

cm = centimeters

dbh = diameter at breast height

DPS = distinct population segment

ft = feet

HCP = habitat conservation plan

ha = hectares

in = inches

km = kilometers

IPCC = Intergovernmental Panel on Climate Change

m = meters

mi = miles

MOU = memorandum of understanding

NPS = National Park Service

PAC = protected activity center

RCP = representative concentration pathway

SPI = Sierra Pacific Industries

SSA = species status assessment

USFS = U.S. Forest Service

Previous Federal Actions

For a detailed history of prior petitions, listing actions, and litigation, please see the 12-month finding published on May 24, 2006 (71 FR 29886). Subsequent to that finding, we were petitioned twice to list the California spotted owl as endangered or threatened and to designate its critical habitat under the Act (16 U.S.C. 1531 et seq.). The first petition was submitted in December 2014, by the Wild Nature Institute and John Muir Project of Earth Island Institute, and the second in August 2015, by Sierra Forest Legacy and Defenders of Wildlife. On September 18, 2015, we published a 90-day finding that the petitions presented substantial scientific or commercial information indicating that listing may be warranted for the California spotted owl (80 FR 56423). On

November 8, 2019, we published a 12-month finding that listing the California spotted owl was not warranted at that time (84 FR 60371).

In August 2020, Sierra Forest Legacy, Defenders of Wildlife, and the Center for Biological Diversity filed a complaint challenging our 12-month not-warranted finding. By stipulated settlement agreement approved by the court on November 30, 2021, we agreed to submit to the *Federal Register* a new 12-month finding for the California spotted owl on or before February 15, 2023 (*Sierra Forest Legacy, et al. v. U.S. Fish and Wildlife Service, et al.*, No. 5:20-cv-05800-BLF (N.D. Cal.)). This document serves as our 12-month finding and completes our obligations under that settlement agreement.

Peer Review

In 2022, a species status assessment (SSA) team prepared an SSA report for the California spotted owl. The SSA team was composed of Service biologists, in consultation with other species experts. The SSA report represents a compilation of the best scientific and commercial data available concerning the status of the species, including the impacts of past, present, and future factors (both negative and beneficial) affecting the species.

In accordance with our joint policy on peer review published in the *Federal Register* on July 1, 1994 (59 FR 34270), and our August 22, 2016, memorandum updating and clarifying the role of peer review of listing actions under the Act, we solicited independent scientific review of the information contained in the California spotted owl SSA report. The Service sent the SSA report to four independent peer reviewers and received one response. Results of this structured peer review process can be found at <https://www.regulations.gov>. In preparing this proposed rule, we incorporated the results of these reviews, as appropriate, into the SSA report, which is the foundation for this proposed rule.

Summary of Peer Reviewer Comments

We received comments from one peer reviewer on the draft SSA report. We reviewed all comments we received from the peer reviewer for substantive issues and new information regarding the information contained in the SSA report. The peer reviewer generally provided additional references, clarifications, and suggestions, including further definitions of some of the terms used. We updated the SSA report based on the peer reviewer's comments, including changing the approach to our scoring system for the current and future habitat analyses, clarifying specific points where appropriate, and adding additional details and suggested references where needed. Peer reviewer comments are addressed in the following summary and were incorporated into the SSA report as appropriate.

Comment 1: The peer reviewer stated that there was not enough discussion in the SSA report about how habitat factors have been observed to impact owls, particularly in regards to the existing studies analyzing demographic trends of California spotted owls. Further, the peer reviewer stated that the SSA report should discuss the methodology used in the demography studies.

Our response: We acknowledge that habitat factors and demographic factors are interrelated, and that understanding the relation between those two issues is crucial. We discuss how habitat factors influence demographic factors, and vice versa, in sections 3.1 and 3.2 of the SSA report (Service 2022, pp. 14–24). We have also incorporated all available information on how the two are related. Additionally, not all of the demographic studies discuss the relationship between vital rates or population trends and habitat factors, but we incorporated the information into the SSA report where available.

Regarding the methodology used in the demography studies, we added a paragraph to the SSA report that discusses different methodologies used in the different types of population studies available in the literature (Service 2022, p. 24). We will provide a list of all literature cited should any readers wish to review those studies in

more detail, and we will provide any studies not readily available on

<https://www.regulations.gov>.

Comment 2: The peer reviewer further questioned the assumption in the SSA report that high-quality habitat is equivalent to population stability, or vice versa.

Our response: While we recognize that data are limited, the best available scientific and commercial data, including all available information on habitat use and species needs for the California spotted owl, concluded that the relationship between high-quality habitat and population stability is sufficiently certain to rely upon for our analysis of species viability.

Comment 3: While recognizing that some protected activity center (PAC) information is out of date, the peer reviewer suggested adding the amount of PAC area to the analysis units in section 5.3 of the SSA report.

Our response: The detailed analysis unit descriptions describe the current condition of each unit. Because PAC information does not provide insight on the current condition of each analysis unit, it would not be appropriate to include in section 5.3 of the SSA report (a PAC is a designation made by the USFS to protect the best available 121 ha (300 ac) of habitat in as compact of a unit as possible around a nest tree). We do, however, incorporate information from PACs throughout the SSA report and this proposed rule to understand the impact, breadth, and distribution of threats across the landscape.

Comment 4: The peer reviewer questioned whether we should use the same criteria to analyze conditions in the Sierra Nevada and in coastal/southern California.

Our response: In order to present a standardized comparison across all analysis units, we used the same scoring criteria for the Sierra Nevada and coastal/southern California. However, we recognize that California spotted owls may use different-sized trees in the coastal-southern California population than in the Sierra Nevada population.

We presented a separate analysis acknowledging this, and we included the difference in tree sizes found in the two geographic areas (Service 2022, tables 9, 13, and 18).

I. Proposed Listing Determination

Background

A thorough review of the taxonomy, life history, and ecology of the California spotted owl (*Strix occidentalis occidentalis*) is presented in the SSA report (version 2.0; Service 2022, pp. 8–14).

California spotted owls are medium-sized brown owls measuring 46.6–48.3 cm (18.3–19.0 in) with a mottled appearance, round face, large pale brown facial disks, dark brown eyes, and a yellowish green bill (Verner et al. 1992, p. 55; Gutiérrez et al. 2020, “Appearance” section). Females are generally slightly larger than males (Verner et al. 1992, p. 55).

The American Ornithological Society (formerly the American Ornithologists’ Union (AOU)) currently recognizes three distinct subspecies of spotted owls: northern spotted owl (*Strix occidentalis caurina*), California spotted owl, and Mexican spotted owl (*Strix occidentalis lucida*) (AOU 1957). Given similarities between the subspecies of spotted owls, the SSA report and this proposed rule use available relevant literature for both the northern spotted owl and the Mexican spotted owl as necessary and appropriate and clearly identify when we refer to those entities. The term “spotted owl” is used when talking about *Strix occidentalis* as a whole. Additionally, under the Act, the term “species” includes any subspecies of fish or wildlife or plants. For the purposes of this proposed rule, we in general use “species” to refer to the California spotted owl rather than “subspecies.”

There is some overlap in range between northern spotted owls and the California spotted owl, and interbreeding between the two subspecies occasionally occurs (Haig et al. 2004, p. 690; Barrowclough et al. 2011, pp. 581, 583–586; Miller et al. 2017, pp.

6871, 6875–6877; Hanna et al. 2018, pp. 3947–3948, 3950–3951). California spotted owls have the lowest genetic diversity among the subspecies compared to northern and Mexican spotted owls, suggesting that the California spotted owl is of more recent origin than the other spotted owl subspecies or that populations of the California spotted owl are much smaller than the northern and Mexican spotted owl populations (Barrowclough et al. 1999, pp. 919, 927; Haig et al. 2004, p. 683). Within the California spotted owl, genetic differences between individuals found in the Sierra Nevada and individuals found in mountain ranges throughout southern California suggest limited interbreeding between these two areas (Barrowclough et al. 2005, pp. 1113–1114; Hanna et al. 2018, pp. 3947–3948, 3950). However, these genetic studies are limited by sample size and sampling locations. We are only aware of one study that includes California spotted owls from coastal California; this study shows gene flow between geographically adjacent spotted owl samples, with some evidence of asymmetrical gene flow between California spotted owls in Carmel, California (coastal California), and the Sierra Nevada (Barrowclough et al. 2005, p. 1114).

California spotted owls are distributed across habitat in California and Nevada including the Sierra Nevada, coastal California, and southern California. The California spotted owl has also been documented in the Sierra San Pedro Martir mountains in Baja California Norte, Mexico, with a few scattered records of the spotted owl in Baja California between 1887 and 1972 (Grinnell 1928, p. 242; Wilbur 1987, p. 170). However, many researchers now question whether the species ever actually occurred in Baja California (Erickson in litt. 2022; Unitt in litt. 2022). There are only a few accounts of the species, with none of those accounts mentioning breeding or evidence of breeding pairs. Therefore, we consider the California spotted owl to be only a rare visitor of Mexico, and do not consider Baja California as its own population.

California spotted owls are continuously distributed throughout the forests of the western side of the Sierra Nevada from Shasta County south to the Tehachapi Pass in Kern County (Gutiérrez et al. 2017, pp. 13–14). They are sparsely distributed on the eastern side of the Sierra Nevada into western Nevada (GBBO 2012, p. Spp-47-4). Outside of the Sierra Nevada, the species' range is not contiguous. Along the California coast and into southern California, the species is found in the Coast, Transverse, and Peninsular mountain ranges from Monterey County in the north to San Diego County in the south (Gutiérrez et al. 2020, "Distribution" section). However, there is a large break in the species' range around San Luis Obispo County, where the species is not known to occur. The Tehachapi Pass between the Sierra Nevada to the east and the Transverse Range to the west represents a gap between California spotted owls in the Sierra Nevada and California spotted owls in coastal and southern California (Verner et al. 1992, p. 4). California spotted owls are absent from the Santa Cruz Mountains (part of the Coast Range) in California, where suitable habitat appears to be present (Gutiérrez et al. 2017, p. 240).

California spotted owls are currently found throughout their known historical range, although there is evidence of a decrease in abundance in parts of the range including both the Sierra Nevada and southern California (Franklin et al. 2004, pp. 23–42; Tempel et al. 2014b, pp. 90–94; Conner et al. 2016, pp. 7–18; Hanna et al. 2018, pp. 3947–3949; Tempel et al. 2022, p. 18). The majority of California spotted owls are found in mid-elevation, mixed-conifer forest on the west slope of the Sierra Nevada (Gutiérrez et al. 2017, p. xviii).

California spotted owls are long-lived (approximately 16–23 years) with high adult survival and low reproductive output (Seamans and Gutiérrez 2007, p. 57; Gutiérrez et al. 2020, "Demography and Populations" section). Pairs exhibit high territory fidelity (Gutiérrez et al. 2020, "Sounds and Vocal Behavior" and "Behavior" sections).

Territories—the area actively defended by a breeding pair—can overlap with neighboring pairs and are smaller than home ranges (Gutiérrez et al. 2017, pp. xvi, 294). Estimates of territory size have varied from 203 ha (502 ac) to 813 ha (2,009 ac), with higher estimates in the northern Sierra Nevada and lower estimates in southern California (Bingham and Noon 1997, p. 136; Blakesley et al. 2005, p. 1556; Seamans and Gutiérrez 2007b, p. 568; Tempel et al. 2014b, p. 2091). Higher quality territories measured in adult survival, territory colonization, and territory extinction, tend to have a greater proportion of higher canopy cover (Tempel et al. 2014b, p. 2089; Gutiérrez et al. 2017, pp. 271–273). Home ranges, or areas used by a pair to meet requirements for survival and reproduction, are about 400–1,200 hectares (ha) (1,000–3,000 acres (ac)) in size (Gutiérrez et al. 2017, p. xviii). Home ranges are typically larger in the northern portion of the range (>1,000 ha (2,470 ac)) and smaller in the southern portion of the range (<1,000 ha (2,470 ac)) due to differences in selected prey species (Gutiérrez et al. 2017, p. xviii).

Breeding season begins in mid-February, and the juvenile dependency period can last through mid-September; nesting generally starts earlier at lower elevations (Gutiérrez et al. 2020, “Breeding” section). During the breeding season, California spotted owls tend to spend the majority of their time at activity centers of around 121 ha (299 ac) (Verner et al. 1992, p. 87; Berigan et al. 2012, p. 299). Activity centers are the areas where California spotted owls they nest, roost, and forage (Verner et al. 1992, p. 87; Gutiérrez et al. 2017, pp. 270–271). Spotted owls typically have only one nest per breeding season, and they rarely re-nest if the first nests fails (Gutiérrez et al. 2020, “Breeding” section). Females typically lay 1–3 eggs, with survival of offspring into adulthood highest when two young fledge in comparison to singletons and triplets (Peery and Gutiérrez 2013, p. 132; Gutiérrez et al. 2020, “Demography and Populations” section). Although difficult to estimate due to dispersal, juvenile survival in California spotted owls is low (Blakesley et al. 2001, p. 667; LaHaye et al. 2004, p. 1056).

Spotted owls always disperse from their natal areas in the year they hatch. Natal dispersal occurs during the fall, after juveniles have reached adult weight and parental care stops (Gutiérrez et al. 2020, “Breeding” section). Average juvenile dispersal in southern California is 9.7–11.3 km (6–7 mi), and ranges from 3.2–37.0 km (2–23 mi) (LaHaye et al. 2001, p. 691). Larger dispersal distances, up to 177 km (110 mi), have been documented in both northern and Mexican subspecies (Gutiérrez and Carey 1985, p. 60; Ganey et al. 1998, p. 206; Hollenbeck et al. 2018, p. 533). Adult California spotted owls typically do not shift territories or undergo breeding dispersal from an established territory (Blakesley et al. 2006, p. 76; Zimmerman et al. 2007, p. 963; Gutiérrez et al. 2011, p. 592); however, some breeding dispersal occurs in adults or pairs that have been unsuccessful in mating or if habitat is altered (Blakesley et al. 2006, p. 71).

Breeding only occurs once a pair is formed and settled into a territory (Gutiérrez et al. 2017, p. 15). Pairs can breed in consecutive years, but in certain conditions may postpone reproduction until temporarily poor environmental conditions improve (Stearns 1976, pp. 4, 15–26; Franklin et al. 2000, p. 539; Gutiérrez et al. 2017, p. xvi). The number of young fledged annually per territorial California spotted owl female in several areas within the Sierra Nevada ranged from 0.478–0.988 (Blakesley et al. 2010, pp. 1, 18).

In general, California spotted owls nest in areas of mature, multistoried forests with complex structure, larger trees, multi-layered high canopy cover, and large amounts of coarse woody debris, while areas with higher heterogeneity of forest types and the edges between them are important for foraging (Gutiérrez et al. 2017, p. xvii). In the Sierra Nevada, a majority of California spotted owls occur within mid-elevation ponderosa pine (*Pinus ponderosa*), mixed-conifer, white fir (*Abies concolor*), and mixed-evergreen forest types, with few occurring in the lower elevation oak woodlands of the western foothills (Gutiérrez et al. 2017, p. 109). In coastal and southern California,

California spotted owls are found in riparian/hardwood forests and woodlands, live oak/big cone fir forests, and redwood/California laurel forests (Gutiérrez et al. 2017, p. xxvi). In southern California, vegetation types differ relative to the Sierra Nevada, and what is considered a large tree in southern California may not be comparable to what is considered a large tree in the Sierra Nevada. However, California spotted owls in southern California still select for territories containing larger trees (LaHaye et al. 1997, pp. 42, 47) and predominantly closed canopy cover (Smith et al. 2002, pp. 137, 142, 144).

California spotted owls can use a variety of habitat types for nesting. At higher elevations, the species primarily uses conifers, and as elevations decrease, they increasingly use hardwoods (Gutiérrez et al. 2020, “Habitat” section). Important components of nesting habitat include high canopy cover, larger trees, and high habitat heterogeneity. For nest trees, California spotted owls use a subset of larger trees or snags, with the average nest tree measuring 124 cm (49 in) diameter at breast height (dbh) and 31 m (103 ft) tall in the Sierra Nevada (Gutiérrez et al. 2017, p. 50). In southern California, California spotted owls use cavity, broken-top, and platform nests with different characteristics (LaHaye et al. 1997, pp. 42, 47; Tanner 2022, pers. comm.). In southern California, California spotted owl use of platform or old raptor nests is more common; thus, owls with these types of nests were observed using smaller trees than used in other nest types (LaHaye et al. 1997, p. 45). Within their nesting territory, California spotted owls select for nest sites farther away from the forest edge (Phillips et al. 2010, p. 312). Overall, California spotted owl occupancy, colonization, adult survival, and reproductive success are all positively associated with an increasing amount of structurally complex habitat on the landscape (Franklin et al. 2000, p. 578; Blakesley et al. 2005, p. 1562; Tempel et al. 2014a, pp. 2103–2104).

California spotted owls can also use a variety of habitats to forage. California spotted owls primarily prey upon a variety of small to medium-sized mammals, including, but not limited to, flying squirrels, woodrats, and pocket gophers, as well as birds, lizards, and insects (Gutiérrez et al. 2017, p. 28). In the Sierra Nevada, above approximately 1,200 m (3,937 ft) in coniferous forests, California spotted owls most commonly consume Humboldt's flying squirrels (*Glaucomys oregonensis*) (Laymon 1988, pp. 130–154; Verner et al. 1992, pp. 4, 65–69; Munton et al. 2002, pp. 99, 101–104). Preferred habitat conditions of Humboldt's flying squirrels include cool, moist, mature forest with abundant standing and down snags where they can forage on mostly fungi and lichens (Cassola 2016, p. 3). In lower elevation oak woodlands and riparian-deciduous forests in the Sierra Nevada and southern California, California spotted owls select for woodrats (*Neotoma* spp.) (Verner et al. 1992, pp. 4, 65, 68–69; Smith et al. 1999, pp. 22, 24–28; Munton et al. 2002, pp. 99, 101–104). Due to this elevational gradient in prey distribution, California spotted owls select foraging sites characteristic of flying squirrel habitats at higher elevations and woodrat habitats at lower elevations (Kramer et al. 2021b, pp. 12–14). Some individuals have smaller home ranges where woodrats are the primary prey source, presumably because woodrats have a higher caloric gain per successful foraging event and are found in higher densities than northern flying squirrels (Zabel et al. 1995, pp. 433, 435–438). There is some evidence that California spotted owl diet may shift following wildfires. In national parks in the Sierra Nevada that have implemented longstanding fire management efforts (i.e., prescribed fire and managed wildfire), the California spotted owl diet contains a higher proportion of woodrats and pocket gophers relative to flying squirrels (Hobart et al. 2021, pp. 254, 256).

In regard to foraging habitat, important components include the presence of larger trees, high canopy cover, and coarse woody debris. California spotted owls tend to forage

in larger trees, likely due to the canopy cover provided by larger trees and the important resources such as shelter and food that larger trees provide for prey species (Laymon 1988, pp. 47, 71, 77, 100; Verner et al. 1992, pp. 9–10, 60, 88; Moen and Gutiérrez 1997, pp. 1281, 1284). However, California spotted owls use medium-size trees (defined by the authors as >25 cm dbh (9 in)) for foraging while avoiding areas dominated by small trees (<25 cm dbh (9 in)) (Kramer et al. 2021a, pp. 4, 6). Coarse woody debris is also an important habitat feature for California spotted owls because it provides food, shelter, and protection for prey species, especially woodrats (Waters and Zabel 1995, pp. 861–862; Pyare and Longland 2002, pp. 1016–1017; Innes et al. 2007, pp. 1523, 1526; Kelt et al. 2013, p. 1208). Heterogeneous forests, such as those found on private lands, may provide more habitat for California spotted owls than was previously understood (Atuo et al. 2019, p. 295), as some privately owned study areas have higher numbers of occupied sites than adjacent USFS study areas (Roberts et al. 2017, p. 113).

California spotted owl roosting habitat is very similar to nesting habitat. Specific components of roosting habitat include multi-layered high canopy cover and presence of large trees. It is believed that such forests provide young California spotted owls with protection from predators and from high temperatures. California spotted owls have a low heat tolerance in comparison to other bird species, beginning to show heat stress at 30–34 degrees Celsius (°C) (86–93 degrees Fahrenheit (°F)). The cooler microclimates that multi-layered high canopy cover provides are important for both juveniles and adults during warm summers (Weathers 1981, pp. 358–359; Barrows 1981, pp. 303–305; Weathers et al. 2001, pp. 678–679). Presence of large trees is also important for California spotted owl roosting, as individuals tend to roost in large trees, likely due to the canopy cover provided by large trees and the resources they provide for prey species (Laymon 1988, pp. 47, 71, 77, 100; Verner et al. 1992, pp. 9–10, 60, 88; Moen and Gutiérrez 1997, pp. 1281–1284).

Within the SSA report and this proposed rule, we define a population as a group of interbreeding California spotted owls that are more likely to breed among that group than outside of that group. We use information from genetic studies and habitat features to identify two California spotted owl populations: one in the Sierra Nevada, and another in coastal and southern California (hereafter referred to as the coastal-southern California population).

In the western Sierra Nevada, habitat is relatively continuous, without significant gaps in distribution (Gutiérrez et al. 2017, p. xviii); however, in the eastern Sierra Nevada, habitat is more discontinuous with disjunct patches (Dilts 2022, pp. 5–9). Despite this fragmentation, California spotted owls still have substantial gene flow within the Sierra Nevada. However, there is limited gene flow to coastal or southern California, and large-scale fragmentation of suitable habitat divides the Sierra Nevada from this other population (Barrowclough et al. 2005, pp. 1114–1116). We are not aware of specific information about individual California spotted owls moving between these two population areas.

In coastal and southern California, the California spotted owl population consists of subpopulations distributed among discrete mountain ranges, resulting in habitat “islands” surrounded by unsuitable habitat (Verner et al. 1992, p. 187). Areas between these habitat islands are typically lowland desert scrub and chaparral that is unsuitable for California spotted owls, or substantially modified by human-induced development and fragmentation (Verner et al. 1992, p. 187). Some of the subpopulations are separated by relatively narrow gaps, such as the gap between the San Gabriel and San Bernardino Mountains, while other gaps are more significant, such as the gap between the Northern and Southern Santa Lucia Mountains. California spotted owls in coastal and southern California are less well-studied than those in the Sierra Nevada, but there is a notable lack of documented California spotted owl movement between the coastal and southern

subpopulations, and we are not aware of any dispersal between them. This population is also described in the literature as being a presumed metapopulation (Verner et al. 1992, pp. 187–206; LaHaye et al. 1994, entire; Gutiérrez et al. 2017, p. 241) despite the documented lack of connectivity, even though dispersal among populations is a defining characteristic of a metapopulation (see Hanski and Gilpin 1991 for more on metapopulation theory). However, spatial structure of a metapopulation within and among subpopulations is critical for metapopulation functioning, and available evidence does not document successful dispersal between the San Bernardino, San Gabriel, and San Jacinto Mountains, which are adjacent mountain ranges, indicating that if mixing does occur it is very rare (LaHaye et al. 2001, entire; LaHaye et al. 2004, entire; Gutiérrez et al. 2017, pp. 242, 250). Further, not all subpopulations within the metapopulation have equal likelihood of "blinking out" or being rescued/recolonized by other subpopulations, which are important components of metapopulation theory (Gutiérrez et al. 2017, pp. 241–242, 250). Within the coastal-southern California population, the subpopulation inhabiting the San Bernardino and San Gabriel mountains is the largest subpopulation and is the subject of most ecological studies. The persistence of this subpopulation has been identified as important for persistence of the coastal-southern California population (Verner et al. 1992, pp. 197–206)

To conduct a more focused analysis of how different portions of each of the populations' ranges contribute to that population's overall resiliency, we further divided the Sierra Nevada and southern California populations into analysis units (see figure 1, below). We chose analysis units roughly based on public land management boundaries because of varying demographic data and management strategies across the range. Dividing the population up into analysis units based on land management boundaries allows a better assessment of the varying conditions across the range. We identified a total of 15 analysis units: Lassen, Plumas, Tahoe, Eldorado, Humboldt-Toiyabe,

Stanislaus, Yosemite, Sierra, Sequoia-Kings Canyon, Sequoia, Inyo, Las Padres, Las Padres-Angeles, San Bernardino, and Cleveland.



FIGURE 1—POPULATIONS AND ANALYSIS UNITS OF THE CALIFORNIA SPOTTED OWL (CSO).

Distinct Population Segment Evaluation

Under the Act, the term “species” includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature (16 U.S.C. 1532(16)). To guide the implementation of the DPS provisions of the Act, we and the National Marine Fisheries Service (National Oceanic and Atmospheric Administration—Fisheries), published the Policy Regarding the Recognition of Distinct Vertebrate Population Segments Under the Endangered Species Act (DPS Policy) in the *Federal Register* on February 7, 1996 (61 FR 4722). Under our DPS Policy, we use two elements to assess whether a population segment under consideration for listing may be recognized as a DPS: (1) The population segment’s discreteness from the remainder of the species to which it belongs, and (2) the significance of the population segment to the species to which it belongs. If we determine that a population segment being considered for listing is a DPS, then the population segment’s conservation status is evaluated based on the five listing factors established by the Act to determine if listing it as either endangered or threatened is warranted.

As discussed above in **Previous Federal Actions**, we were petitioned to list the California spotted owl subspecies throughout its range. In response to the petitions, we divided the species into two populations and our analysis covers the full range of the species. Under the Act, we have the authority to consider for listing any species, subspecies, or, for vertebrates, any distinct populations segment of these taxa if there is sufficient information to indicate that such action may be warranted. Therefore, we considered whether the two populations of the California spotted owl (the Sierra Nevada portion of the California spotted owl’s range, and the coastal and southern California portions of the California spotted owl’s range) meet the DPS criteria under the Act. These two populations comprise the entirety of the California spotted owl’s range (and thus the

entirety of the petitioned entity), and we have determined that it is appropriate to analyze them individually under our DPS policy.

Discreteness

Under our DPS Policy, a population segment of a vertebrate taxon may be considered discrete if it satisfies either of the following conditions: (1) It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation; or (2) it is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D) of the Act.

We conclude the two segments satisfy the “markedly separate” condition. The Sierra Nevada part of the range is separated from the coastal and southern California parts of the range by large-scale fragmentation of suitable habitat, with the Tehachapi Pass in Kern County identified as the dividing line between these areas (Verner et al. 1992, p. 4; Barrowclough et al. 2005, pp. 1114–1116). The distance between suitable habitat in the closest parts of the Sierra Nevada and the Transverse Range of southern California is only 40 km (25 mi). Although this distance is near the known average dispersal of juvenile California spotted owls, we are not aware of specific information about individual California spotted owls moving between the Sierra Nevada and California spotted owl habitat in coastal and southern California (Service 2022, p. 18).

As discussed above in **Background**, there are few genetic studies on the California spotted owl. However, existing analyses provide evidence that gene flow between the two parts of the range is limited and may have been restricted to historical asymmetrical gene flow from areas in the central California coast to the Sierra Nevada (Barrowclough et al. 2005, p. 1113), although the study acknowledges that more data are

needed to inform this conclusion. Our DPS policy notes that we do not consider it appropriate to require absolute reproductive isolation as a prerequisite to recognizing a distinct population segment. As the policy states, this would be an impracticably stringent standard, and one that would not be satisfied even by some recognized species that are known to sustain a low frequency of interbreeding with related species.

Therefore, because the two populations are markedly separated from each other, we have determined that both the Sierra Nevada and the coastal and southern California parts of the range both individually meet the condition for discreteness under our DPS Policy.

Significance

Under our DPS Policy, once we have determined that a population segment is discrete, we consider its biological and ecological significance to the larger taxon to which it belongs. This consideration may include, but is not limited to: (1) Evidence of the persistence of the discrete population segment in an ecological setting that is unusual or unique for the taxon, (2) evidence that loss of the population segment would result in a significant gap in the range of the taxon, (3) evidence that the population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historical range, or (4) evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

For the California spotted owl, we first considered evidence that loss of a population segment would result in a significant gap in the range of the taxon. As discussed above, the southwestern and northeastern parts of the range are separated by approximately 40 km (25 mi). The loss of the coastal and southern California parts of the range would result in the loss of the entire southwestern part of the species' range and decrease species redundancy and ecological and genetic representation, thus decreasing

the species' ability to withstand demographic and environmental stochasticity. The loss of the Sierra Nevada range would result in the loss of 70 percent of the species' range, also reducing the species' ability to withstand demographic and environmental stochasticity. Therefore, the loss of either part of the range would result in a significant gap in the range of the California spotted owl.

We then considered evidence whether either of the discrete population segments occur in an ecological setting that is unusual or unique for the taxon. In the Sierra Nevada, a majority of California spotted owls occur within mid-elevation mixed-conifer and mixed-evergreen forest types, with few occurring in the lower elevation oak woodlands of the western foothills (Gutiérrez et al. 2017, p. 109). As described above, in coastal and southern California, California spotted owls are found in riparian/hardwood forests and woodlands, live oak/big cone fir forests, and redwood/California laurel forests, more so than the mixed-conifer communities (Gutiérrez et al. 2017, p. xxvi). Use of these other communities is specific and unique to owls in these areas. What is considered a large tree in southern California may not be comparable to what is considered a large tree in the Sierra Nevada. California spotted owls use a subset of larger trees or snags as their nest trees, with the average nest tree measuring 124 cm (49 in) dbh and 31 m (103 ft) tall in the Sierra Nevada (Gutiérrez et al. 2017, p. 50). In southern California, use of platform or old raptor nests is more common; thus, owls with these types of nests were observed using trees as small as 33 cm (13 in) dbh (Tanner 2022, pers. comm.) with mean values of 75.0 cm (29.5 in) dbh (LaHaye et al. 1997, p. 45). Therefore, we conclude that, for the two populations of California spotted owls, each persists in a unique ecological setting for the species.

The evidence that a significant gap in the range of the taxon would result from the loss of either discrete population segment meets the significance criterion of the DPS Policy. Additionally, there is evidence that the coastal and southern California and the

Sierra Nevada parts of the range have persisted in a unique ecological setting for the species. Therefore, under the Service's DPS Policy, we find that the Sierra Nevada and the coastal and southern California parts of the California spotted owl's range are significant to the taxon as a whole.

Distinct Population Segment Conclusion

Our DPS Policy directs us to evaluate the significance of a discrete population in the context of its biological and ecological significance to the remainder of the species to which it belongs. Based on an analysis of the best available scientific and commercial data, we conclude that both parts of the California spotted owl's range are significant, because loss of either part would result in a significant gap in the range of the taxon, and because the population segments represent evidence that both parts of the range have persisted in a unique ecological setting for the species. Therefore, we conclude that both the Sierra Nevada and the coastal and southern California parts of the California spotted owl's range are both discrete and significant under our DPS Policy and are, therefore, uniquely listable entities under the Act.

Based on our DPS Policy (61 FR 4722; February 7, 1996), if a population segment of a vertebrate species is both discrete and significant relative to the taxon as a whole (i.e., it is a distinct population segment), its evaluation for endangered or threatened status will be based on the Act's definition of those terms and a review of the factors enumerated in section 4(a) of the Act. Having found that both parts of the California spotted owl's range meet the definition of a distinct population segment, we evaluate the status of both the Sierra Nevada DPS and the Coastal-Southern California DPS of the California spotted owl to determine whether either meets the definition of an endangered or threatened species under the Act.

Regulatory and Analytical Framework

Regulatory Framework

Section 4 of the Act (16 U.S.C. 1533) and the implementing regulations in title 50 of the Code of Federal Regulations set forth the procedures for determining whether a species is an endangered species or a threatened species, issuing protective regulations for threatened species, and designating critical habitat for endangered and threatened species. In 2019, jointly with the National Marine Fisheries Service, the Service issued a final rule that revised the regulations in 50 CFR part 424 regarding how we add, remove, and reclassify endangered and threatened species and the criteria for designating listed species' critical habitat (84 FR 45020; August 27, 2019). On the same day, the Service also issued final regulations that, for species listed as threatened species after September 26, 2019, eliminated the Service's general protective regulations automatically applying to threatened species the prohibitions that section 9 of the Act applies to endangered species (84 FR 44753; August 27, 2019).

The Act defines an "endangered species" as a species that is in danger of extinction throughout all or a significant portion of its range, and a "threatened species" as a species that is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range. The Act requires that we determine whether any species is an endangered species or a threatened species because of any of the following factors:

- (A) The present or threatened destruction, modification, or curtailment of its habitat or range;
- (B) Overutilization for commercial, recreational, scientific, or educational purposes;
- (C) Disease or predation;
- (D) The inadequacy of existing regulatory mechanisms; or

(E) Other natural or manmade factors affecting its continued existence.

These factors represent broad categories of natural or human-caused actions or conditions that could have an effect on a species' continued existence. In evaluating these actions and conditions, we look for those that may have a negative effect on individuals of the species, as well as other actions or conditions that may ameliorate any negative effects or may have positive effects.

We use the term “threat” to refer in general to actions or conditions that are known to or are reasonably likely to negatively affect individuals of a species. The term “threat” includes actions or conditions that have a direct impact on individuals (direct impacts), as well as those that affect individuals through alteration of their habitat or required resources (stressors). The term “threat” may encompass—either together or separately—the source of the action or condition or the action or condition itself.

However, the mere identification of any threat(s) does not necessarily mean that the species meets the statutory definition of an “endangered species” or a “threatened species.” In determining whether a species meets either definition, we must evaluate all identified threats by considering the species' expected response and the effects of the threats—in light of those actions and conditions that will ameliorate the threats—on an individual, population, and species level. We evaluate each threat and its expected effects on the species, then analyze the cumulative effect of all of the threats on the species as a whole. We also consider the cumulative effect of the threats in light of those actions and conditions that will have positive effects on the species, such as any existing regulatory mechanisms or conservation efforts. The Secretary determines whether the species meets the definition of an “endangered species” or a “threatened species” only after conducting this cumulative analysis and describing the expected effect on the species now and in the foreseeable future.

The Act does not define the term “foreseeable future,” which appears in the statutory definition of “threatened species.” Our implementing regulations at 50 CFR 424.11(d) set forth a framework for evaluating the foreseeable future on a case-by-case basis. The term “foreseeable future” extends only so far into the future as we can reasonably determine that both the future threats and the species’ responses to those threats are likely. In other words, the foreseeable future is the period of time in which we can make reliable predictions. “Reliable” does not mean “certain”; it means sufficient to provide a reasonable degree of confidence in the prediction. Thus, a prediction is reliable if it is reasonable to depend on it when making decisions.

It is not always possible or necessary to define the foreseeable future as a particular number of years. Analysis of the foreseeable future uses the best scientific and commercial data available and should consider the timeframes applicable to the relevant threats and to the species’ likely responses to those threats in view of its life-history characteristics. Data that are typically relevant to assessing the species’ biological response include species-specific factors such as lifespan, reproductive rates or productivity, certain behaviors, and other demographic factors.

Analytical Framework

The SSA report documents the results of our comprehensive biological review of the best scientific and commercial data regarding the status of the species, including an assessment of the potential threats to the species. The SSA report does not represent our decision on whether the species should be proposed for listing as an endangered or threatened species under the Act. However, it does provide the scientific basis that informs our regulatory decisions, which involve the further application of standards within the Act and its implementing regulations and policies.

To assess California spotted owl viability, we used the three conservation biology principles of resiliency, redundancy, and representation (Shaffer and Stein 2000, pp. 306–

310). Briefly, resiliency is the ability of the species to withstand environmental and demographic stochasticity (for example, wet or dry, warm or cold years), redundancy is the ability of the species to withstand catastrophic events (for example, droughts, large pollution events), and representation is the ability of the species to adapt to both near-term and long-term changes in its physical and biological environment (for example, climate conditions, pathogens). In general, species viability will increase with increases in resiliency, redundancy, and representation (Smith et al. 2018, p. 306). Using these principles, we identified the species' ecological requirements for survival and reproduction at the individual, population, and species levels, and described the beneficial and risk factors influencing the species' viability.

The SSA process can be categorized into three sequential stages. During the first stage, we evaluated the individual species' life-history needs. The next stage involved an assessment of the historical and current condition of the species' demographics and habitat characteristics, including an explanation of how the species arrived at its current condition. The final stage of the SSA involved making predictions about the species' responses to positive and negative environmental and anthropogenic influences. Throughout all of these stages, we used the best available information to characterize viability as the ability of a species to sustain populations in the wild over time. We use this information to inform our regulatory decision.

The following is a summary of the key results and conclusions from the SSA report (Service 2022, entire); the full SSA report can be found at Docket No. FWS-R8-ES-2022-0166 on <https://www.regulations.gov>.

Summary of Biological Status and Threats

In this discussion, we review the biological condition of the California spotted owl and its resources, and the threats that influence the species' current and future condition, in order to assess the species' overall viability and the risks to that viability.

We note that the California spotted owl SSA report discusses California spotted owls at the individual, population, and species level. The SSA does not make any analysis or conclusions with regard to policy decisions, such as DPS findings, and does not include mention of the two populations of the subspecies as DPSs. Instead, the SSA report provides the biological information that our decisionmakers can then use to inform those policy decisions. This proposed rule and its supporting record contain the policy decisions and rationale. Throughout this **Summary of Biological Status and Threats** discussion, we discuss the coastal-southern California population of California spotted owl, which we identify as the Coastal-Southern California DPS, and the Sierra Nevada population of California spotted owl, which we identify as the Sierra Nevada DPS.

California Spotted Owl Needs

Individual Needs

In this section, we assess the best available information to identify the specific habitat components needed to support individual fitness at all life stages for California spotted owls. Individual owls must have adequate nesting, foraging, and roosting habitat to be successful. For the purpose of the SSA report and this proposed rule, the components of nesting, foraging, and roosting habitat that we considered most significant include canopy cover, larger trees, and habitat heterogeneity. Habitat heterogeneity is important to California spotted owls as it provides protection from predators and extreme weather conditions, variable microclimates, and habitat for different prey species.

We acknowledge that these habitat components are not all-inclusive and there may be other components of nesting, foraging, and roosting habitat that are not being considered (such as prey). We also acknowledge that a history of fire suppression in the western United States, including throughout the range of both the Sierra Nevada DPS and the Coastal-Southern California DPS, has caused many ecological changes that are not fully understood (Mallek et al. 2013, p. 2). However, we chose to focus on habitat

components for which there are available spatial data across the range of the species.

Further, prey is indirectly considered in our analysis since the primary California spotted owl prey species also select for high canopy cover and coarse woody debris (Waters and Zabel 1995, p. 858), which are considered here as components of habitat heterogeneity.

Populations of California spotted owls require the same habitat components as individuals but at larger scales.

Multi-layered, or complex, high canopy cover is considered an important resource for spotted owls because it provides cool shaded microclimates, camouflage and cover for protection from predators and extreme weather conditions, and habitat for prey species (Forsman 1975, pp. 4, 90, 105; Barrows 1981, p. 302; Forsman et al. 1984, p. 5). High canopy cover from tall trees is associated with higher probability of successful prey capture by California spotted owls (Zulla et al. 2022, p. 8) and is an important predictor for California spotted owl nesting habitat (North et al. 2017, pp. 166, 172–175). Multi-layered high canopy cover around the nest tree and in territories is an important factor associated with California spotted owl reproductive success (Hunsaker et al. 2002, pp. 693–699; Blakesley et al. 2005, pp. 1554, 1558–1562). Areas with canopy cover greater than 70 percent are considered optimal for California spotted owl nest sites and occupancy sharply declines when canopy cover is less than 40 percent (Blakesley et al. 2005, p. 1559; Seamans 2005, pp. iii, 90, 100; Seamans and Gutiérrez 2007b, pp. 566, 568; Tempel et al. 2014a, pp. 2089, 2091, 2101; Tempel et al. 2016, pp. 747, 759). Even in southern California where the habitat is naturally more fragmented with less canopy cover available, California spotted owls still select for areas with higher canopy cover relative to what is available (Smith et al. 2002, pp. 142–143). Further, California spotted owls in Yosemite National Park had territory centers with average values of 40 percent canopy cover in burned forests (Schofield et al. 2020, pp. 4–5).

The presence of large trees, defined as trees that are greater than 61 cm (24 in) dbh (Seamans and Gutiérrez 2007b, pp. 566, 571–574; Tempel et al. 2014b, p. 2094; Jones et al. 2018, p. 344), is important for California spotted owl foraging, roosting, and nesting. California spotted owls tend to forage and roost in large trees, likely due to the canopy cover provided by large trees and the important resources such as shelter and food that large trees provide for prey species (Laymon 1988, pp. 47, 71, 77, 100; Verner et al. 1992, pp. 9–10, 60, 88; Moen and Gutiérrez 1997, pp. 1281, 1284). The presence of tall (>48 m (157 ft)) trees, and the canopy cover they provide, is the best predictor for California spotted owl occupancy, and areas with a high density of large trees are considered high-quality habitat (Blakesley et al. 2005, pp. 1554, 1558–1562; North et al. 2017, pp. 166, 171–176). California spotted owls use a subset of large trees or snags as their nest trees (LaHaye et al. 1997, pp. 42, 47; Blakesley et al. 2005, pp. 1554, 1558–1562; Gutiérrez et al. 2017, p. 50), and the nest tree itself is critical for California spotted owl reproductive success because it provides the space and structure needed for nests, along with protection from predators and inclement weather. California spotted owls do not build their own nests but rely on larger trees that provide multi-layered high canopy cover with open cavities (created as a result of fallen branches, woodpeckers, etc.), broken tops, platforms, and old raptor nests (Gutiérrez et al. 2020, “Habitat” and “Breeding” sections). The nest tree chosen within a territory is typically one of the oldest and largest live or dead trees within the nesting territory with many defects like cracks, disease scars, or decaying wood (Verner et al. 1992, pp. 6, 60, 71; North et al. 2000, p. 797).

The preferential use of mature forests with high canopy cover and large trees is well-known for California spotted owls (Gutiérrez et al. 2017, p. iii). However, there have been several recent studies showing the importance of other habitat types, habitat edges, and habitat heterogeneity (Atuo et al. 2019; Hobart et al. 2019; Kramer et al.

2021b; Zulla et al. 2022; Wilkinson et al., in prep.). California spotted owl occupancy, colonization, adult survival, and reproductive success are all positively associated with the proportion of structurally complex forests (Franklin et al. 2000, p. 539; Blakesley et al. 2005, p. 1562; Tempel et al. 2014b, p. 2089; Tempel et al. 2016, p. 747). The biological and physical components that create habitat heterogeneity and complex structure are areas of multi-layered high canopy cover, large trees, coarse woody debris, understory and mid-story vegetation, patches of burned habitat, riparian habitat, large diameter standing dead trees (snags), and some open areas within a California spotted owl's home range.

Coarse woody debris (fallen dead trees and the remains of large branches on the ground) is an important habitat feature for California spotted owls because it provides food, shelter, and protection for California spotted owl prey species, especially woodrats (Waters and Zabel 1995, pp. 861–862; Pyare and Longland 2002, pp. 1016–1017; Innes et al. 2007, pp. 1523, 1526; Kelt et al. 2013, p. 1208). Coarse woody debris in areas of multi-layered high canopy cover is conducive for fungal growth, a food source for many California spotted owl prey species (Verner et al. 1992, pp. 71–72; Pyare and Longland 2002, pp. 1016–1017). Rates of prey capture by California spotted owls are observed to be higher in taller multilayered forests, in areas with higher vegetation heterogeneity, and near forest-chapparral edges (Wilkinson et al. in prep., p. 2). There are a variety of habitats within a heterogeneous landscape that California spotted owls use and which may provide specific resources. The size of a California spotted owl's home range increases as the heterogeneity, or number of different vegetation patches, increase (Williams et al. 2011, p. 333); the hypothesis is that there may be an optimal point of habitat heterogeneity for California spotted owls beyond which territory quality declines (Williams et al. 2011, p. 333).

Population Needs

Populations of California spotted owls must have adequate amounts of nesting, foraging, and roosting habitat containing the habitat components described above in sufficient amounts and the appropriate configuration on the landscape to support a stable or increasing growth rate. They also need connectivity between territories and home ranges. Populations meeting these requirements are better able to withstand stochastic events. In many instances, however, data are insufficient or completely lacking regarding a population's size and growth rate. In the absence of such data, we examine other characteristics that may serve as surrogate indicators of general population health and, subsequently, resiliency. Essentially, an assessment of the availability of a species' identified needs (suitable habitat, food, breeding sites) may allow us to make assumptions about the potential resiliency of any given population. However, unless there is a documented positive correlation between the availability of species' needs and a population's known demographic condition, the uncertainty regarding such assumptions must be made clear.

In the SSA report, we describe the demographic factors that are considered important for California spotted owls, including natal dispersal, survival, fecundity, occupancy, and population growth. We describe the importance of each demographic factor to California spotted owl persistence and how the individual needs influence these factors.

There is little available information about dispersal and dispersal habitat between the defined California spotted owl populations and analysis units within the SSA report and this proposed rule. Dispersal habitat is described for northern spotted owl as 50 percent of the forest matrix outside of activity centers in stands with an average of 28 cm (11 in) dbh and 40 percent canopy closure (Thomas et al. 1990, p. 15). This contrasts with dispersal for Mexican spotted owls, which may move across large areas of unforested habitat to access suitable habitat on different mountain ranges (Gutiérrez et al.

1995, p. 5; Gutiérrez et al. 2017, p. 242). It is unknown how far California spotted owls will disperse across unsuitable habitat to find a new territory, but adult northern spotted owls have been found to occasionally move long distances if forced out of a territory (Forsman in litt. 2018, p. 22).

For dispersal to be successful, many of the individual needs must be present within the areas to which California spotted owls disperse. Canopy cover, large trees, and coarse woody debris all must be available in sufficient amounts and the appropriate configuration on the landscape (habitat heterogeneity) for juveniles or sub-adults to successfully settle into a territory to begin breeding.

Survival for California spotted owls is closely linked to population growth and is important for maintaining population resiliency (Seamans and Gutiérrez 2007a, p. 57; Blakesley et al. 2010, p. 27). Adult California spotted owls have high annual survival rates ranging from 0.796–0.814 in different study areas within analysis units in southern California (LaHaye et al. 2004, p. 1056; Franklin et al. 2004, p. 22), and 0.811–0.891 in study areas within analysis units in the Sierra Nevada (Blakesley et al. 2001, p. 671; Franklin et al. 2004, p. 22; Blakesley et al. 2010, p. 10; Tempel et al. 2014a, p. 92). In comparison, juvenile survival is difficult to estimate due to dispersal, and has been found to be low, ranging from 0.087–0.333 in study areas within analysis units in the Sierra Nevada (Blakesley et al. 2001, p. 671; Tempel et al. 2014a, p. 92), and 0.368 for southern California (LaHaye et al. 2004, p. 1056). For northern spotted owl, juveniles tend to have high mortality during the dispersal phase (Miller 1989, pp. 41–44; Forsman et al. 2002, p. 18).

All the individual needs discussed above influence survival. For example, survival is related to the amount of forest dominated by medium to large trees, high canopy cover, and habitat complexity (Blakesley et al. 2005, p. 1554; Tempel et al. 2014b, pp. 2089,

2098; McGinn et al. 2022, p. 9). In northern spotted owls, habitat heterogeneity is correlated with higher survival rates (Franklin et al. 2000, p. 539).

Fecundity is defined as the ability to produce offspring and is measured by the number of viable female offspring that an individual can produce over a specific time period. Annual reproductive output, measured by presence or absence of offspring in a nest, for female California spotted owls in a demographic study in the Sierra Nevada was found to range from 0.478–0.988 (Blakesley et al. 2010, p. 1). Reproduction throughout all the demographic studies has ranged from no reproduction within a study area to nearly all birds reproducing in a study area in a particular year (Franklin et al. 2004, pp. 32–33; Seamans and Gutiérrez 2007a, p. 65; Blakesley et al. 2010, p. 17; MacKenzie et al. 2012, p. 597; Tempel et al. 2014a, p. 91; Stoelting et al. 2015, p. 46). Fecundity, measured as female young produced per female annually, has been found to range from 0.284–0.409 in the Sierra Nevada and to be 0.362 in southern California (Franklin et al. 2004, pp. 11, 23).

Many of the individual needs discussed above influence fecundity. Reproductive output decreases as non-forest habitat increases within the area around the nest, and nest success increases as the presence of large remnant trees within the nest stand increases (Blakesley et al. 2005, p. 1554). Reproduction is positively correlated to the foliage volume above the nest tree (North et al. 2000, p. 797), although habitat heterogeneity is also important for reproduction (Franklin et al. 2000, p. 539; Tempel et al. 2014b, p. 2089; McGinn et al. 2022, p. 9) and foraging (Zulla et al. 2022, pp. 7–8). Annual variation in weather also plays a role in reproductive success (North et al. 2000, p. 797; Seamans and Gutiérrez 2007a, p. 57; MacKenzie et al. 2012, p. 597; Stoelting et al. 2015, p. 46). For example, California spotted owls experienced increased fecundity when a dry breeding season followed a previously wet year (LaHaye et al. 2004, pp. 1056, 1062). Although survival of breeding California spotted owls is an important factor that is

closely connected to population growth, reproductive output may be more influential to population growth because it varies more than adult survival (Blakesley et al. 2001, p. 667; Seamans and Gutiérrez 2007a, p. 57).

In the SSA report and this proposed rule, we define California spotted owl occupancy as the stable (not transient) presence of at least one adult within a territory. California spotted owls select and defend territories in which they spend most of their life. California spotted owl pairs will only reproduce once they have established an occupied territory. The measure of occupancy has been found to be strongly correlated with regional abundance of California spotted owls and can provide reliable inferences on population trends (Tempel and Gutiérrez 2013, pp. 1093–1093).

Many of the individual needs discussed above need to be present in order for California spotted owls to occupy a territory. Occupancy is generally higher and more consistent with an increasing proportion of the territory containing large trees and high canopy cover (Blakesley et al. 2005, p. 1554; Seamans and Gutiérrez 2007b, p. 572; Roberts et al. 2011, p. 610; Tempel et al. 2014b, p. 2089; Gutiérrez et al. 2017, p. vxii). As the proportion of forest types that are not used for nesting (smaller, similar-aged young trees) increases, occupancy tends to decrease (Blakesley et al. 2005, pp. 1554, 1560).

In the SSA report and this proposed rule, we define California spotted owl population growth as the change in the number of individuals within a particular study area, which correspond to our analysis units. Population growth is determined by the demographic factors of survival, fecundity, and occupancy, with fecundity likely the most influential because it is more variable (Blakesley et al. 2001, p. 667; Seamans and Gutiérrez 2007a, p. 57; Seamans and Gutiérrez 2007b, p. 566; Blakesley et al. 2010, p. 27; Tempel and Gutiérrez 2013, pp. 1093–1094; Gutiérrez et al. 2017, p. 99). Population growth is variable throughout study areas in the Sierra Nevada DPS where we have

available information, with documented declines ranging from -50 percent to -31 percent in some study areas and a population increase of 25 percent in another (Tempel et al. 2014a, pp. 86, 90–92; Conner et al. 2016, p. 15). The only available demographic data for the Coastal-Southern California DPS is from the San Bernardino National Forest. A population decline of -9 percent was observed from 1987–1998, with more recent occupancy analyses showing further declines in population size (LaHaye et al. 2004, pp. 1056, 1064; Tempel et al. 2022, p. 20, table 5). All individual needs described above need to be present for positive California spotted owl population growth.

Species Needs

At the species level, we assess the redundancy and representation of the entire California spotted owl's range to better understand the viability of the species. For the California spotted owl, we evaluate redundancy by considering the number of resilient populations distributed across the species' range. Having resilient populations distributed across the range increases the species' ability to withstand catastrophic events.

For this species, we evaluate representation by considering the distribution of populations across their various ecological settings and whether those populations are able to maintain adequate amounts of genetic diversity. Having a variety of ecological settings that the species can occupy and a breadth of genetic diversity increases the species' ability to withstand and adapt to long-term environmental changes.

Threats

Following are summary evaluations of eight threats analyzed in the SSA report for the California spotted owl: wildfire (Factor A), tree mortality (Factor A), drought (Factor A), climate change (Factor A), fuels reduction and forest management (Factor A), competition and hybridization with barred owls (*Strix varia*) (Factor E), rodenticides (Factor E), and development (Factor A). We also evaluate existing regulatory mechanisms (Factor D) and ongoing conservation measures.

In the SSA report, we also considered four additional threats: Overutilization due to recreational, educational, and scientific use (Factor B); disease (Factor C); predation (Factor C); and recreation (Factor E). We concluded that, as indicated by the best available scientific and commercial information, these threats are currently having little to no impact on the California spotted owl and thus the overall effect of these threats now and into the future is expected to be minimal. Therefore, we will not present summary analyses of those threats in this document, but we considered them in the current and future condition assessments in the SSA report, and we will consider them in our determination of the species' status. For full descriptions of all threats and how they impact the species, please see the SSA report (Service 2022, pp. 25–68).

For the purposes of this assessment, we consider the foreseeable future to be the amount of time on which we can reasonably determine a likely threat's anticipated trajectory and the anticipated response of the species to those threats. For this proposed rule, we consider the foreseeable future to be 40–50 years. This time period represents our best professional judgment of future conditions related to climate change for California, the California spotted owl's generation time, and the regeneration time of medium to large trees.

Wildfire

Fire is a natural part of California spotted owl habitat (Verner et al. 1992, pp. 247–248) and is necessary for maintaining heterogeneous forests and overall habitat heterogeneity. Wildfire and associated tree mortality can be beneficial or detrimental for the California spotted owl depending on scale and severity. Fires with predominantly low to moderate severity burn patterns, with small patches of high-severity fire scattered throughout the fire perimeter, can increase habitat heterogeneity, ultimately result in higher prey densities, increase amounts of forest edge for California spotted owl foraging, and provide for unburned refugia within the fire perimeter that have higher tree survival

and more vegetative cover during the immediate postfire years (Roberts et al. 2011, p. 610; Lee et al. 2012, p. 792; Bond et al. 2013, pp. 114, 122; Eyes et al. 2017, p. 384; Blomdahl et al. 2019, pp. 1046, 1048, 1049). There is also evidence to suggest that more pyrodiverse (spatial or temporal variability in fire effects; Jones and Tingley 2021, p. 1) landscapes support greater habitat heterogeneity, which may promote greater biodiversity (Steel et al. 2021, pp. 7–8; Stephens et al. 2021, p. 5). For example, in areas where woodrats are the primary prey species, a juxtaposition of mature forests and open canopy patches promotes higher prey diversity and abundance, and northern spotted owls preferentially select for these areas (Zabel et al. 1995, p. 433; Ward and Noon 1998, p. 79; Franklin et al. 2000, p. 539; Zabel et al. 2003, p. 1027).

Although burned areas can reduce the amount of canopy cover available, California spotted owls forage on the edge of and within areas that have been burned at a range of severities (Bond et al. 2009, p. 1116; Bond et al. 2016, p. 1290; Eyes et al. 2017, p. 375) although typically avoiding larger areas of high-severity fire (Jones et al. 2016a, p. 304; Eyes et al. 2017, p. 383). Thus, many researchers advocate for the use of ecologically beneficial fire to help sustain California spotted owl habitat and report that low to moderate severity fire minimizes the effects of future high-severity wildfire (Stephens et al. 2019, pp. 395–396; Stephens et al. 2020, entire; Stephens et al. 2021, p. 5; Taylor et al. 2022, p. 4).

In contrast, large-scale, high-severity fires have a detrimental effect on both the California spotted owl and its habitat. Large-scale high-severity fire (often referred to as a megafire) is generally defined as over 10,000 ha (24,711 ac) of area burned with 75–100 percent canopy mortality (Jones et al. 2016a, p. 300; Linley et al. 2022, pp. 6, 8). Megafires can degrade or destroy California spotted owl habitat, completely incinerating large trees and canopy cover (Eyes 2014, p. ii; Roberts et al. 2015, pp. 112–115; Jones et al. 2016a, pp. 300–305). Habitat suitability for northern spotted owls decreased postfire

and depended on fire severity (higher fire severity resulted in greater declines of habitat suitability) (Wan et al. 2020, p. 7); thus, megafires have a greater potential to alter the availability of suitable habitat.

The loss of habitat from large-scale, high-severity fires also results in direct impacts to California spotted owl individuals and populations. As megafires alter the number of large trees (including nest trees), multi-layered high canopy cover, habitat heterogeneity, and patch size, California spotted owl dispersal, fecundity, and occupancy are subsequently reduced. It has been observed that large patches of high-severity fire significantly reduce colonization (dispersal), occupancy, and habitat use across the California spotted owl's range (Eyes 2014, p. 42; Tempel et al. 2014b, p. 2089; Jones et al. 2016a, pp. 300, 303–305; Eyes et al. 2017, pp. 381, 384; Jones et al. 2019, p. 26; Jones et al. 2020, entire; Schofield et al. 2020, pp. 5–6; Jones et al. 2021a, p. 5; Tempel et al. 2022, p. 13) and for other subspecies (Rockweit et al. 2017, entire; Lesmeister et al. 2019, p. 13; Duchac et al. 2021, p. 12). Fires may cause direct mortality to eggs and juveniles during the nesting season, and fast-moving fires also have the potential to cause direct mortality to adult California spotted owl individuals (Jones et al. 2016a, p. 305). No data are available on how many California spotted owls are killed annually by direct impacts of large-scale, high-severity fire. Although most birds are able to move to escape direct mortality from fires, smoke from fires can impact birds by damaging their lungs (Verstappen and Dorrestein 2005, p. 139). While many species have existed with frequent fire over evolutionary time, megafires and extreme smoke events are novel influences that may act as an additional selective pressure on certain species (Nimmo et al. 2021, p. 5689). There is limited research on the effects of wildfire smoke on wildlife in general, but there is clear evidence that smoke can have both acute and chronic health impacts on a variety of taxa, which may ultimately affect demographic rates (Sanderfoot et al. 2021, p. 13).

As discussed above, high-severity fire has negative effects on individual California spotted owls and their habitat, ranging from reduced occupancy to direct mortality of individuals. However, several publications conclude that spotted owls will continue to use areas burned at high-severity and, therefore, there are no negative effects of high-severity fire for California spotted owls (Lee and Bond 2015, entire; Hanson et al. 2018, entire; Hanson et al. 2021, entire; Lee 2018, entire). We have reviewed these publications and acknowledge this disagreement in the literature. However, our review of all the best available science, including those sources that conclude no negative effects, has led us to agree with the vast majority of science, which concludes that overall spotted owls avoid large patches of high-severity fire and that high-severity fire is increasing throughout California and the western United States. For more analysis on the conflicting results of these studies and our analysis, please see the SSA report (Service 2022, pp. 27–28).

Current conditions in the California spotted owl's range may contribute to ongoing fire risk, and depending on the portion of the range and the land manager, fire management activities may vary. Decades of fire suppression have led to overall higher canopy cover from small and medium trees, higher dead biomass density, and more surface fuels in forests of the western United States (Verner et al. 1992, pp. 247–248; Agee and Skinner 2005, p. 83). The historical fire return interval for the Sierra Nevada was around 11–16 years, but fire suppression over the last 100 years has led to a change in fire behavior of larger, more severe fires in recent years (Safford and Stevens 2017, pp. v–vi). The multi-layered high canopy cover and biomass provide important habitat for California spotted owls but also tend to increase the vulnerability of forests to high-severity fire (Verner et al. 1992, pp. 251–258; Agee and Skinner 2005, p. 83) in present day fire-suppressed forests. The higher fuel loads, particularly large, dead wood (like snags and logs), tend to burn at higher severity as densities increase (Lydersen et al.

2019, p. 7). In a recent megafire, dead biomass directly contributed to the fire effects observed, as areas with high amounts of dead biomass pre-fire burned at high severity (Stephens et al. 2022, p. 8).

On top of the higher fuel loads, extended droughts and longer wildfire seasons have led to larger and more severe fires in the California spotted owl's range and throughout western North America (Miller and Safford 2012, p. 41; Mallek et al. 2013, p. 1; Nigro and Molinari 2019, p. 20; Parks and Abatzoglou 2020, p. 4; Safford et al. 2022, p. 12). In 2020 and 2021, more than 1 million ha (2.4 million ac) burned in California, resulting in more area burned over these 2 years than in the past 7 years of all California fires combined (Safford et al. 2022, p. 5). An increase in high-severity fire changes how fire interacts with important habitat features for California spotted owls. For example, fire often killed, but left standing, trees that would subsequently serve as locations for California spotted owl nests. However, large patches of high-severity fire burn hotter and can end up entirely consuming the features important to California spotted owls. Between the years of 2000 and 2014, 7 percent of suitable California spotted owl nesting habitat (a total of 85,046 ha (210,153 ac) out of 1,166,560 ha (2,882,633 ac)) was burned either partially at moderate severity (typically 25–50 percent tree basal area mortality) or entirely at high severity (typically >75 percent tree basal area mortality), causing ≥ 50 percent tree basal area mortality and reducing canopy cover to <25 percent (Stephens et al. 2016, pp. 1, 9).

The size and severity of a fire determines how much it will impact California spotted owls at the population level. If a high-severity fire occurs in a large enough area, it can eliminate entire territories or home ranges of California spotted owls, displacing individuals that may or may not establish a new territory (Jones et al. 2016a, pp. 300–305). Site occupancy by California spotted owls after wildfire appears to be a function of the amount of suitable habitat remaining after the fire (Gutiérrez et al. 2017, p. xxiii). If

habitat becomes unsuitable, it takes decades for large trees to reestablish on the landscape. Based on fire activity and anticipated trends over the next 75 years, the cumulative amount of nesting habitat burned at ≥ 50 percent tree basal area mortality will exceed the total existing habitat in the Sierra Nevada (Stephens et al. 2016, pp. 1, 12). In other words, the loss of suitable California spotted owl habitat would exceed the rate of new forest growing post-fire (Stephens et al. 2016, pp. 11–13). Thus, future habitat persistence for California spotted owls is concerning given that high-severity fire appears to be increasing across all lands (both public and private) occupied by California spotted owls and throughout the western United States (Parks and Abatzoglou 2020, pp. 4–5). When private lands are considered separately, the odds of high severity fire occurring on industrially managed forests and adjacent lands were 1.8 and 1.4 times higher, raising some concern over California spotted owl persistence on private lands (Levine et al. 2022, p. 4).

In the Sierra Nevada, the proportion of high severity fire throughout the California spotted owl's range has dramatically increased in recent years. The proportion of high-severity fire in California montane forests in 2020 was on average 43–76 percent higher than the combined average between 1984 and 2008, and was three to six times higher than the estimates of pre-Euroamerican settlement (Safford et al. 2022, p. 17). Between 1984–2019, 1,084,171 ha (2,679,044 ac; 55.7 percent) burned throughout the California spotted owl range in the Sierra Nevada with 317,605 ha (784,820 ac; 46.6 percent) burned at high severity (Keane in litt. 2022, p. 3). In contrast, between 2020 and 2021, 862,625 ha (2,131,593 ac; 44.3 percent) burned throughout the California spotted owl's range with almost 363,812 ha (899,000 ac; 53.4 percent) of that at high severity (Keane in litt. 2022, p. 3). This comparison illustrates how megafires in 2020 and 2021 burned more habitat at high severity in 2 years than fires over the past three and a half decades. In addition, between 1984 and 2021, 50 percent of California spotted owl PAC

acres have been impacted by wildfire, with 56 percent of that total burned in 2020 and 2021. Further, of the 56 percent that burned between 2020 and 2021, 65 percent burned at high severity (Keane in litt. 2022, p. 5). Because California spotted owls are displaced from areas where the entire PAC or majority of the PAC has burned at high severity, it is unlikely the species will continue to persist in these areas until the habitat can recover, which can take decades.

We conducted a fire severity analysis within the entire California spotted owl's range; details of the methodology used in this analysis are available in the SSA report (Service 2022, pp. 29–30). Of the California spotted owl's range, approximately 47 percent burned between 1984 and 2021, with 15 percent at high severity. Most of the area burned at high severity occurred in 2020 and 2021, with 2 percent and 4 percent, respectively (Service 2022, table 3). Additionally, based on an existing dataset from the California Department of Forestry and Fire Protection of the potential threat of future wildfire in California, the majority of the California spotted owl's range occurs within the very high wildfire threat category (Service 2022, figure 8). Much of the coastal-southern California population of the California spotted owl falls within the extreme fire risk. This dataset contains fire information through 2014, and so does not consider how the recent fires from 2014 to 2021 affect future fire threat. Overall, we expect that the pattern of both area burned and wildfire severity will continue or increase into the future due to the effects of climate change.

Some regulatory mechanisms and conservation measures can reduce the potential severity or scale of wildfires. Wildfire fuel reduction treatments, such as prescribed fire and mechanical thinning, can reduce the amount or degree of spotted owl habitat loss from a high-severity fire, and a balanced approach to fuel reduction treatments may ensure suitable California spotted owl habitat is maintained (Jones et al. 2016a, p. 305; Service 2017, pp. 24–25; Chiono et al. 2017, p. 1; Jones et al. 2021a, entire). The 2004

USFS Sierra Nevada Forest Plan Amendment has a goal of actively restoring fire-adapted ecosystems by reducing unnaturally dense conditions, and there are also measures in place in the framework to avoid disturbance within California spotted owl PACs to the greatest extent possible (USFS 2004, pp. 34–35). Fuel reduction treatments are actively taking place on USFS land, but special considerations, including the timing of treatments to avoid the breeding season and the methods that are used, are evaluated to avoid impacts to owls within PACs. In 2017 and in 2020, an MOU was signed by Sierra Pacific Industries, California Department of Forestry and Fire Protection, National Fish and Wildlife Foundation, and the USFS to coordinate on certain actions that may contribute to forest fuel reductions and California spotted owl conservation. The purpose of the MOU is to try to minimize the threat of large-scale, high-severity fire while still providing quality habitat for California spotted owls. However, large-scale, high-severity fire cannot be completely addressed by regulatory mechanisms. Fuel reduction treatments may not prevent catastrophic damage in an extreme fire event; however, when fire is a part of the fuel reduction treatment, future fire severity can be reduced and more fire treatments should be included to achieve fuels reduction goals, including areas surrounding spotted owl nests and riparian corridors (North et al. 2021, pp. 527, 529; Taylor et al. 2022, p. 4).

High-severity fire is likely to continue to be a threat into the future for California spotted owls. Although some individuals could be harmed or killed by large fires, the primary impact of this threat is habitat-based. These habitat changes also affect demographic parameters: following high severity fires, colonization declines and territory extinction increases, leading to overall declines in occupancy (Tempel et al. 2022, pp. 13–16). Overall, large-scale, high-severity fire is currently and will likely continue to be a threat throughout the range of the California spotted owl, including for both the Sierra Nevada and the coastal-southern California populations.

Tree Mortality

Widespread increases in tree mortality have been occurring in California due to drought, disease, and bark beetles above historical levels of mortality (van Mantgem et al. 2009, pp. 521–523; Asner et al. 2015, p. 249; McIntyre et al. 2015, p. 1458; Preisler et al. 2017, p. 166). When tree stand densities are too high compared to available resources (water, light, nutrients), trees become stressed due to competition for resources and thus are more vulnerable to mortality (USFS 2017, p. 9). Large trees are often especially prone to drought, disease, and beetle-related mortality (Smith et al. 2005, p. 266; Mueller et al. 2005, p. 1085; Allen et al. 2010, p. 668; McIntyre et al. 2015, p. 1458). Increased tree mortality may be contributing to loss of California spotted owl habitat (Gutiérrez et al. 2017, p. 137), but the magnitude of the impacts on California spotted owls is uncertain. Large-scale tree mortality reduces the availability of canopy cover and large trees, potentially resulting in California spotted owl population declines because of reduced habitat available for dispersal and occupancy. However, some tree mortality events can have some positive effects on California spotted owl habitat, as these events contribute to habitat heterogeneity and the availability of coarse woody debris for prey species.

Between 2010 and 2016, an estimated 102 million trees died across about 3,106,367 ha (7,676,000 ac) throughout California (Tree Mortality Task Force 2017, p. 2). By February 2019, total tree mortality in California increased to an estimated 147 million dead trees (Cal Fire and USFS 2019, p. 1). The latest estimate shows that between 2010 and 2021, the drought combined with subsequent beetle attacks resulted in approximately 173 million dead trees in California with approximately 3.3 percent of the surveyed forest area in 2021 showing signs of elevated mortality (USFS 2021, p. 5). The tree mortality events are particularly severe in the southern Sierra Nevada area. Most of the tree mortality observed is due to effects from the 2012–2016 drought, with less

mortality occurring from 2018–2021; however, another drought period started in 2020 (USFS 2021, p. 5).

In 2015, the Governor of California declared a state of emergency due to the unprecedented number of dead and dying trees in the State. In response, the California Tree Mortality Task Force, which is now the Forest Mortality Working Group within the California Wildfire and Forest Resilience Task Force, was created to coordinate emergency protective actions and monitor ongoing conditions. The group collects and manages the tree mortality data, provides recommendations to land managers, presents grants for research funding, and provides public outreach. The task force will likely continue to provide the services listed into the future due to the ongoing and large-scale nature of the tree mortality events in California.

Regulatory mechanisms and management actions could provide some protection from the effects of tree mortality. Efforts to restore historical forest conditions and reduce stand densities through fuels reduction treatments (mechanical thinning, prescribed fire, etc.) may indirectly contribute to reducing future tree mortality by reducing competition. Further, the goal should be to eliminate the excessive levels of tree mortality currently being observed in the landscape and not limit all tree mortality, as tree mortality is a natural part of the forest ecosystem and ultimately creates features important to California spotted owls (snags, tree cavities). Tree mortality is likely to continue throughout the range of the California spotted owl due to predicted increases in drought conditions that will likely continue to weaken trees and make them susceptible to bark beetles and disease (Millar and Stephenson 2015, pp. 823–826; Young et al. 2017, pp. 78, 85). Excessive tree mortality is likely to continue to be a threat into the future for the California spotted owl.

Drought

California has experienced extreme drought conditions in 2007–2009 and 2012–2016 (Williams et al. 2015, pp. 6823–6824; CDWR 2021, p. 4), and as of May 2022, a majority of the California spotted owl’s range is considered in severe to moderate drought (CDWR 2022, entire). Anthropogenic warming likely contributed to more recent drought anomalies and increases the overall likelihood of extreme droughts in California into the future (Williams et al. 2015, pp. 6819, 6826; CDWR 2022, entire).

Drought conditions can negatively impact the California spotted owl’s ecological needs. As described above, drought conditions contribute to tree mortality, which reduces canopy cover, likely leading to a decline in occupancy. Further, drought conditions likely reduce the availability of prey species (Franklin et al. 2000, p. 589; Glenn et al. 2010, p. 2549; Glenn et al. 2011, p. 174). Drought and hot temperatures in the previous summer are linked to lower reproductive success in California spotted owls (LaHaye et al. 2004, p. 1066) and lower survival and recruitment in northern spotted owls in the next breeding season (Glenn et al. 2011, pp. 159, 174). Inversely, increases in precipitation either before or after the nesting season are linked to increased survival and fecundity in all three subspecies of spotted owls (Seamans et al. 2002, p. 321; LaHaye et al. 2004, pp. 1056, 1064; Glenn et al. 2011, pp. 159, 174). Thus, drought likely negatively impacts the California spotted owl’s habitat components, and its demographic needs of dispersal, survival, fecundity, and occupancy. No regulatory mechanisms or conservation measures in place ameliorate the direct impacts of drought. It is likely that drought conditions will continue to be a threat into the future across the California spotted owl’s range and will likely worsen due to the effects of climate change.

Climate Change

Scientific measurements spanning several decades demonstrate that changes in climate are occurring and that the rate of change has been faster since the 1950s. There is strong scientific support for projections that warming will continue through the 21st

century, and that the magnitude and rate of change will be influenced substantially by the extent of greenhouse gas emissions (Meehl et al. 2007, pp. 760–764, 797–811; Ganguly et al. 2009, pp. 15555–15558; Prinn et al. 2011, pp. 527, 529; IPCC 2013, pp. 19–23).

Projected changes in climate and related impacts can vary substantially across and within different regions of the world (IPCC 2013, pp. 15–16). Therefore, we used downscaled projections from California’s Fourth Climate Change Assessment, including the following four regional assessments that cover the California spotted owl’s range: Sierra Nevada (Dettinger et al. 2018, entire), the Central Coast Region (Langridge 2018, entire), Los Angeles (Hall et al. 2018, entire), and San Diego (Kalansky et al. 2018, entire). Ten global climate models were used for all four regional assessments, and each model considered two different emissions scenarios, one in which greenhouse gas emissions continue to increase into the next century (RCP 8.5) and one in which greenhouse gas emissions stabilize by mid-century and then decline to levels seen in the 1990s by the end of the century (RCP 4.5) (Dettinger et al. 2018, pp. 15, 17; Hall et al. 2018, p. 9; Kalansky et al. 2018, p. 18; Langridge 2018, p. 12).

Under both emissions scenarios, projected annual average temperatures throughout the California spotted owl’s range are projected to increase. The largest increases under both emissions scenarios and timeframes are projected for the eastern portions of the Sierra Nevada (Dettinger et al. 2018, p. 17, figure 2.3). Projected changes will result in greater temperatures than historically experienced in the Sierra Nevada, and this degree of temperature change will likely result in a shift in the rain to snow transition by 1,500–3,000 feet (Dettinger et al. 2018, pp. 17, 20). Projected temperature increases are more pronounced in the inland portions of the Central Coast Region, with the ocean acting as a buffer for coastal areas (Langridge 2018, p. 14, figure 4). In addition, the average number of extremely hot days (defined as days that exceed the 98th percentile of observed, historical (1961–1990) daily maximum temperatures between April 1 and

October 31) are expected to increase throughout the Central Coast Region (Langridge 2018, pp. 14–15, table 4).

Regional assessments covering southern California include the Los Angeles and San Diego Regional Assessments (Hall et al. 2018, entire; Kalansky et al. 2018, entire). Projected annual average maximum temperatures throughout the Los Angeles Region increase under both emissions scenarios (Hall et al. 2018, p. 10, figure 2). For the San Diego Region, projected annual average maximum and minimum temperatures also increase under both emissions scenarios. Similar to the Central Coast Region, these changes will be more pronounced in the interior portions of the Los Angeles and San Diego Regions (Hall et al. 2018, p. 11, figure 3).

In addition to temperature projections, the regional assessments for California's Fourth Climate Change Assessment also considered future changes in precipitation, both the amount and the timing. Within the Sierra Nevada Region, changes in precipitation are projected to be relatively small and will vary depending on the area. In general, average annual precipitation in the southern portion of the Sierra Nevada Region is projected to stay similar or decrease by 5 percent, regardless of emission scenario. In other portions of the Sierra Nevada Region, particularly along the eastern side, the amount of precipitation is projected to increase by up to 10 percent. In addition to projections showing the northern portions of the range will receive more precipitation than southern portions, areas at higher elevations are also more likely to receive an increase in precipitation. Although the average change in precipitation is projected to be small, the models show there will be an increase in extreme conditions with more dry days overall interspersed with higher intensity precipitation events, when they do occur (Dettinger et al. 2018, p. 19). Further, in some areas more precipitation will fall as rain instead of snow, as the rain to snow transition is projected to shift by 457–914 m (1,500–3,000 ft) (Dettinger et al. 2018, pp. 17, 20).

Similar to the Sierra Nevada Region, interannual variability within the Central Coast Region is expected to increase with more dry days overall, but more precipitation when rain events do occur (Langridge 2018, p. 16). In southern California, the amount of precipitation in the Los Angeles and San Diego Regions is highly variable (Hall et al. 2018, p. 12, figure 5; Kalansky et al. 2018, p. 24). Similar to other regions, projections for the Los Angeles and San Diego Regions show an increase in extreme conditions such as high-intensity precipitation events, known as atmospheric rivers, and severe drought conditions (Hall et al. 2018, pp. 13–14, figure 6; Kalansky et al. 2018, pp. 24–25, figures 7 and 9).

Because the California spotted owl has a wide geographic range and the projected changes in climate vary across the range, the effects those changes will have on the species and its habitat will vary. Future climate projections of Sierra Nevada vegetation distribution indicate that low- and mid-elevation forests are vulnerable to conversion to unsuitable habitat for California spotted owls, such as shrublands and grasslands (Gutiérrez et al. 2017, p. 215). These changes in climate may also include potential shifts in forest communities upslope, which would have impacts on both the California spotted owl's habitat and prey habitat (Gutiérrez et al. 2017, pp. 132, 215, 288). This potential upslope shift in suitable habitat may mitigate some climate-induced habitat threats over ecological time, although it would require many decades for suitable large nest trees to develop in areas where they do not currently exist (Gutiérrez et al. 2017, p. 215). These differences in net habitat loss versus net habitat gained under future climate scenarios will likely depend not only on the rate of warming but also how individual plant and prey species respond (Seamans and Gutiérrez 2007a, p. 61).

Changing climatic conditions may have direct impacts on California spotted owl physiology, survival, reproduction, recruitment, or population growth. The thermal neutral zone (the range of temperatures tolerated by a warm-blooded animal) for

California spotted owls is 18.2–35.2 °C (64.8–95.4 °F) (Weathers et al. 2001, p. 682). Above this zone, California spotted owls experience heat stress (Weathers et al. 2001, p. 678). The relatively low thermal neutral zone may make California spotted owls more susceptible to increased temperatures or cause behavioral or habitat shifts to cooler microclimates on the landscape. Behaviorally, California spotted owls can select cooler microclimates for roosting, especially within warmer forest stands (McGinn et al. in review, p. 2). Changing climatic conditions may also have indirect impacts including changes in habitat and prey distribution, abundance, and quality. California spotted owls must be able to adjust to the changing climate through behavioral changes, spatial shifts, or adaptation in order to persist. Under projected warming conditions in the future, cooler microclimate refugia are likely to be critically important for the persistence of California spotted owl individuals and populations (McGinn et al. in review, p. 3). It is likely that climate change will reduce the quantity and quality of California spotted owl habitat, which would likely result in population impacts, including a decrease in dispersal, fecundity, and occupancy. Both the habitat components and demographic factors of California spotted owls will likely be impacted by climate change, but the full extent of impacts climate change may have on California spotted owls is poorly understood (Wan et al. 2018, p. 690).

Climate modeling specific to the central Sierra Nevada portion of the California spotted owl's range has shown that maintaining high canopy cover, especially at higher elevations, will be important for California spotted owls to persist into the future, as high canopy cover helps maintain future refugia for individuals to select for cooler microclimates (Jones et al. 2016b, entire). Under both a low climate change prediction scenario (RCP 2.6) and a high climate change scenario (RCP 8.5), California spotted owl occupancy decreases in comparison to baseline climate conditions (Jones et al. 2016b, p. 901). However, this model did not consider projected increases in frequency and size of

high-severity fires due to climate change, which would likely result in more significant declines in occupancy than predicted by the model (Jones et al. 2016b, p. 903). Earlier modeling of spotted owl response to projected climate changes show that different subspecies and populations of spotted owls are anticipated to respond differently across their ranges (Peery et al. 2011, p. 14).

The climate change projections described above suggest increasing interannual climate variability throughout the range of the California spotted owl. Interannual climate variability is defined as when annual weather patterns differ from historical average climate, including prolonged drought conditions, heavy rain conditions, and higher or lower than average temperatures. Interannual climate variability has been shown to have impacts on the survival and reproductive success of California spotted owls. Drought conditions and hot temperatures during the summer have been found to reduce fecundity in California spotted owls during the next breeding season (LaHaye et al. 2004, p. 1056). Increases in precipitation either before or after the nesting season are linked to increased survival and fecundity, whereas increased precipitation during the nesting season reduces reproductive success (North et al. 2000, p. 804; LaHaye et al. 2004, pp. 1056, 1064). It is hypothesized that northern spotted owls exhibit a bet-hedging reproduction strategy and that an absence of reproduction is linked to environmental conditions (Franklin et al. 2000, pp. 539, 576). California spotted owls likely have a similar bet-hedging reproductive strategy (Stoelting et al. 2015, p. 46; Gutiérrez et al. 2017, pp. 14–15). California spotted owls are sensitive to warm temperatures and, therefore, may be physiologically sensitive to weather patterns with increased temperatures (Weathers et al. 2001, p. 684). Temperature, either too hot or too cold, may affect spotted owls directly by increasing energy demands (Gutiérrez et al. 2017, p. 20). This increase may have direct impacts on the physiology of spotted owls or on breeding if mates must bring more food to the nest for the female to survive. Increased interannual climate variability due to

climate change will likely impact the California spotted owl throughout its range, which would result in lower fecundity.

Regulatory mechanisms and management actions that are or could potentially provide some protection from the effects of climate change include the Clean Air Act (42 U.S.C. 7401 et seq.) and the California Global Warming Solutions Act. Both address climate change by reducing greenhouse gas emissions within the United States and California, respectively. There are no regulatory mechanisms or management actions that fully address the effects of the climate change.

The effects of climate change will continue to impact California spotted owls into the future by exacerbating the negative influencing factors described above, especially extreme weather events such as prolonged drought and severe storms. The loss or reduction of suitable habitat throughout the California spotted owl's range will likely reduce the subspecies' reproduction, occupancy, survival, recruitment, and population growth.

Fuels Reduction and Forest Management

Forest management has long been a controversial topic regarding species that require old growth forest habitat, including the spotted owl (Gutiérrez 2020, p. 337). With the increasing frequency and extent of high-severity fire in California in recent decades, fire mitigation has become a key issue for spotted owl management and conservation. The goal of fuels management is to reduce the buildup of fuels in forests that contribute to these large-scale, high-severity fires, which can effectively mitigate subsequent fire behavior and their effects, even under extreme weather (Hessburg et al. 2021, p. 7; Prichard et al. 2021, p. 9). The long-term benefits of properly managed fuel treatments for reducing the risk of severe wildfire are likely to outweigh the short-term negative impacts to spotted owl habitat (Ager et al. 2007, pp. 54–55; Roloff et al. 2012, p. 7; Jones et al. 2021b, pp. 4–5). These trade-offs are complex and ultimately depend on

the extent that treatments have negative impacts to owl habitat and the magnitude of effects from subsequent wildfires (Jones et al. 2021b, p. 2). Fuels reductions and forest management practices vary throughout the California spotted owl's range. Below, we discuss clearcutting, mechanical thinning, salvage logging, and prescribed fire, and the positive and negative influences that these practices can have on the species.

Clearcutting, sometimes referred to as even-aged management, is defined as an even-age regeneration or harvest method that removes all trees in the stand, producing a fully exposed microclimate for the development of a new age class in one entry (Gutiérrez et al. 2017, p. 292). The natural range of variation for forest gaps in the Sierra Nevada has been found to range from 0.03–1.17 ha (0.07–2.89 ac) (Safford and Stevens 2017, p. 140), and within the SSA report and this proposed rule, clearcutting refers to complete removal greater than the natural range of variation.

Clearcutting is a mostly historical threat to California spotted owls, although it still occurs in some areas of the Sierra Nevada. By removing entire stands of trees, clearcutting reduces the amount of large trees, high canopy cover, and coarse woody debris available for California spotted owls. Commercial timber harvest no longer occurs within the California spotted owl's range on public lands in the Coastal-Southern California DPS (Gutiérrez et al. 2017, p. 254). Clearcutting also does not occur on USFS lands on the eastern side of the Sierra Nevada range (Boatner in litt. 2022). Clearcutting still occurs on private timber harvest lands but is limited to 8.1-ha (20-ac) parcels by California State forest practice rules (California Code of Regulations (CCR), title 14, article 3 (14 CCR 913 et seq.)). Additionally, there must be at least 91.44 m (300 ft) of forested area between clearcuts, and adjacent lands cannot be cut for at least 5 years (14 CCR 913 et seq.). Even with the reduction of clearcutting in recent history, it will take decades or centuries for large trees to grow back from the past removal practices; therefore, there are residual effects that may be impacting California spotted owl

populations and the habitat that is available (Jones et al. 2018, p. 1). California spotted owls may use clearcut habitat, likely for foraging activities, but these areas are used significantly less than high canopy cover and large tree areas (Atuo et al. 2019, pp. 295, 301–302).

Mechanical thinning is a forest management strategy to thin trees either in even or uneven-aged stands by removing trees in rows, strips, or by using fixed pacing intervals, usually implemented to meet forest management objectives. It can be done for commercial harvest of trees or to reduce fuel loads to decrease the likelihood of large-scale, high-severity fires (Gutiérrez et al. 2017, p. 292). Within the SSA report and this proposed rule, we use “mechanical thinning” to include both individual tree selection (new age classes are created in uneven-aged stands by removing individual trees of all size classes more or less uniformly throughout the stand to achieve desired stand structure) and group tree selection (treatment involves salvage harvest in a stand where small groups of trees are harvested because of tree mortality due to windstorm, wildfire, insects, disease, or other animals).

Mechanical thinning is actively used to manage forests occupied by California spotted owls and can have positive or negative impacts on the California spotted owl’s habitat and demographics depending on the specific methods used. The 2004 Sierra Nevada Forest Plan Amendment promotes reducing, using methods including mechanical thinning, unnaturally dense forest conditions on the landscape to reduce the risk of large-scale, high-severity fire (USFS 2004, pp. 34–35). Minimal area is treated mechanically, especially when compared to area burned by wildfire (566,560 ha (1,400,000 ac) burned between 2017–2020 versus 61,852 ha (152,842 ac) previously treated; North et al. 2021, p. 524). Treatments are located to avoid California spotted owl activity centers to the greatest extent possible (USFS 2004, pp. 34–35), which often leaves the PACs untreated and potentially vulnerable to stand-replacing fires (Stephens et al. 2019, p. 395). Further,

strategic thinning can promote forest resiliency, but removing some large, fire-intolerant tree species like fir and cedar may be necessary to promote future resilience of forested habitat (Stephens et al. 2020, entire; North et al. 2021, p. 530).

Resilience of California spotted owl habitat results from low stand densities, which reduces competition and allows trees to grow, so more intensive fuels treatments (mechanical thinning and prescribed fire) may be needed to achieve historically lower levels of tree densities (North et al. 2022, p. 6). When conducted outside California spotted owl activity centers, mechanical thinning will likely reduce the amount of damage the habitat may experience due to high-severity fire while also minimizing short-term habitat impacts (Stephens et al. 2014, p. 904; Tempel et al. 2015, p. 1; Chiono et al. 2017, p. 1). Strategic mechanical thinning to reduce fuel loads and reduce the risk of large-scale, high-severity fire, while also maintaining the necessary forest structure components of large trees, multi-layered high canopy cover, habitat heterogeneity, and coarse woody debris, will be important for California spotted owl management into the future (Jones et al. 2016a, p. 305; Tempel et al. 2016, p. 305; Jones et al. 2019, p. 22). Strategically placed landscape fuel treatments can decrease future fire severity while also increasing seedling densities (Tubbesing et al. 2019, p. 54). Many studies emphasize the importance of scaling-up fuel reduction treatments (mechanical thinning and prescribed fire) and suggest an increased benefit of treating within California spotted owl territories for long-term persistence, although positive effects would not be observed until mid-century and treatments should still strive to maintain large trees and high canopy cover forest (Jones et al. 2021b, p. 3; Safford et al. 2022, p. 17).

This fuels management technique has little to no impact on occupancy if carried out in a strategic way (for example, maintaining some patches of high canopy cover mixed with patches of moderate canopy cover to provide for the primary habitat of California spotted owls and incorporating limited operating periods that restrict activities

from occurring during the critical nesting period) (Tempel et al. 2016, p. 747). However, mechanical thinning can decrease California spotted owl occupancy and is negatively correlated with reproduction (Tempel et al. 2014a, p. 2089; Stephens et al. 2014, p. 903; Tempel et al. 2022, p. 19). Although one study detected some negative effects of fuels reduction treatments on California spotted owls in southern California, the authors suggested that occupancy declines were small compared to the potential negative effects of fire (Tempel et al. 2022, p. 22). Similarly, there is evidence of reduced foraging in fuel treatment areas that have a moderate to high proportion of forest gaps with little to no canopy cover (Gallagher et al. 2018, pp. 487, 494–499). Forest thinning has complex effects on both California spotted owls and their mammalian prey species. Thinning may have negative short-term effects on prey species by increasing the risk of predation by removing above-ground cover and reducing canopy connectivity, and thinning may remove suitable nesting substrates; however, there may be positive effects in the long term (over decades) by promoting growth of the midstory layer of trees that is favorable to certain mammalian prey species (Wilson and Forsman 2013, p. 79).

Salvage logging is a practice where damaged or dying trees are removed to recover their economic value and promote forest health (Gutiérrez et al. 2017, p. 293; Jones et al. 2020, p. 11). Salvage logging often occurs after natural disturbances such as wildfires, disease, and insect infestation (Lindenmayer et al. 2008, p. 4). Post-fire fuels treatment that includes the removal of smaller trees and surface and ladder fuels is not generally considered a threat to California spotted owls relative to the threat posed by megafires (Jones et al. 2021b, p. 7). Negative effects of salvage logging have been documented for wildlife, vegetation, and soils, but there is a paucity of literature on the subject, which may lead to inaccurate comparisons when studies occur across varied geographic regions; nevertheless, the negative effects may be mediated by altering equipment, timing of operations, and harvest prescriptions to leave more large snags

(Nemens et al. 2019, entire). California spotted owls inhabit areas of low-medium severity fire, patchy high-severity fire, and areas with dead trees; therefore, salvage logging likely reduces the amount of habitat available for California spotted owls (Gutiérrez et al. 2017, p. 276). Salvage logging can result in short-term decreased vegetation regrowth (Wagenbrenner et al. 2015, p. 176), which would likely impact prey species for California spotted owls. However, salvage logging does not appear to make much difference in long-term vegetation regrowth, so salvage logged areas have the potential to again become suitable habitat after the centuries it takes to establish large trees in the area (Peterson and Dodson 2016, p. 56). Salvage logging in certain instances may also be necessary to reduce future fire severity as high levels of dead biomass are associated with high-severity fire (Lydersen et al. 2019, p. 7; Stephens et al. 2022, p. 8); salvage logging may also be required for restoration personnel to safely access an impacted site for re-planting activities (Sawyer in litt. 2022).

The California spotted owl's response to salvage logging appears to be at least partly dependent on the characteristics of the fire after which it occurs, which can make it difficult to analyze these relationships (detailed in Jones et al. 2019). For example, salvage logging that occurs within a large, burned area is less likely to negatively impact spotted owls relative to salvage logging that occurs within a smaller burned area (Jones et al. 2020, p. 12). There is some evidence that northern spotted owl (Clark et al. 2012, p. 15) and California spotted owl occupancy decreases with salvage logging (Lee et al. 2013, p. 1327; Lee and Bond 2015, p. 228; Hanson and Chi 2021, p. 5), while other evidence suggests that salvage logging has no effect on California spotted owl persistence or colonization (Jones et al. 2021b, p. 5). Salvage logging can be a threat to California spotted owls when their habitat components of large trees, coarse woody debris, and habitat heterogeneity are removed from the landscape, resulting in a decrease in occupancy at the population level. The 2004 Sierra Nevada Forest Plan Amendment

prohibits salvage harvest in California spotted owl PACs unless a biological evaluation determines that the areas proposed for harvest have been rendered unsuitable for the purpose they were intended (i.e., California spotted owl habitat) by a catastrophic stand-replacing event (USFS 2004, pp. 52–53).

Prescribed fire or cultural burning as a tool for ecosystem management had been used for millennia by Native Americans; with the colonization of North America, Europeans introduced a culture of fire suppression onto the landscape (Marks-Block et al. 2021, p. 3). Wildfire suppression is still the dominant management practice over prescribed or controlled burning across much of western North America (Stephens et al. 2019, p. 391). Between 2017 and 2020, approximately 49,000 ha (120,000 ac) per year were treated with prescribed burning across Federal, State, and Tribal lands in California (Gabbert 2022, entire). The State of California recently released a report outlining a plan to increase the use of “beneficial fire” to 162,000 ha (400,000 ac) annually by 2025 (California Wildfire & Forest Resilience Task Force 2022, p. 3). Spotted owls can persist in low- and moderate-severity fire areas with similar probabilities to unburned landscapes (Roberts et al. 2011, p. 617), demonstrating their adaptation to a natural fire regime (Verner et al. 1992, pp. 247–248; Stephens et al. 2019, p. 394). However, studying the relationship between spotted owls and prescribed fire alone is difficult because there are usually confounding factors of past timber harvest or salvage logging (Clark et al. 2012, p. 15). Prescribed “ecologically beneficial” fire is an important tool for protecting nesting and roosting habitat from catastrophic fires and for maintaining diverse California spotted owl habitat throughout the landscape (Roberts et al. 2011, p. 617; Stephens et al. 2019, p. 394).

Fuels reductions and forest management practices within the California spotted owl’s range include clearcutting, mechanical thinning, salvage logging, and prescribed fire. Depending on the method used and how it is implemented, fuels reductions and

forest management practices can have both positive and negative influences on the species. The existing regulatory mechanisms and conservation measures do not completely ameliorate the negative impacts of fuels reductions and forest management practices to California spotted owls; however, land management direction, including the Sierra Nevada Forest Plan Amendment, includes protective standards and guidelines that must be adhered to while conducting management activities in California spotted owl habitat.

Fuels reduction in some form is necessary to ensure California spotted owl habitat persistence because long-term gains in habitat protection outweigh the short-term negative effects, especially when conservation measures are implemented appropriately (Jones et al. 2021a, p. 2; Jones et al. 2021b, entire; North et al. 2022, entire; Safford et al. 2022, entire). Differences in forest management may help explain why California spotted owl populations occurring in some mixed ownership landscapes have higher occupancy, density, and probability of reproduction compared to public land (Roberts et al. 2017, p. 113; Hobart et al. 2019, p. 198; SPI et al. 2022, pp. 9, 17). The need to increase the pace and scale of fuels reduction efforts is recognized across agencies, and, recently, the Department of the Interior announced funding through the Bipartisan Infrastructure Law (Infrastructure Investment and Jobs Act, Pub. L. 117–58, 135 Stat. 429) to increase fuels treatments across the United States (DOI 2022, entire). The USFS also identified preliminary projects to address fuel reduction projects through its wildfire crisis landscape investments, and two projects are expected in the near term within the California spotted owl's range that include mechanical thinning and prescribed fire (Tahoe National Forest and the Stanislaus National Forest; USFS 2022a, entire). Fuels reductions and forest management practices will likely continue to have varied effects on California spotted owls throughout the species' range.

Competition and Hybridization with Barred Owls

The barred owl is a closely related species to the spotted owl, native to eastern North America (Mazur and James 2000, “Introduction” section). Since the 1960s, the barred owl has been extending its range westward, first coming in contact with northern spotted owls and more recently moving into the California spotted owl’s range (Peterson and Robins 2003, p. 1162; Livezey 2009, p. 49; Keane et al. 2018, p. 5). Barred owls were first detected in northwestern California in 1982 (Evens and LeValley 1982, p. 890), the Sierra Nevada in 1991 (Dark et al. 1998, p. 53), and along the coast as far south as Marin County in California by 2002 (Jennings et al. 2011, p. 105).

Barred owls and spotted owls have similar habitat requirements, with old forests representing high-quality habitat for both, although barred owls use a broad mix of forest types (Wiens et al. 2014, pp. 14, 32). Because barred owls have more habitat flexibility than spotted owls, there is potential for barred owls to expand into spotted owl habitat through corridors of lower quality habitat. For example, recent barred owl sightings from Davis, California (eBird 2022, entire), suggest that barred owls could expand across the Central Valley into California spotted owl habitat from the west in addition to the more likely pathway through forests in the Sierra Nevada. Although the California spotted owl’s range has a gap between the Sierra Nevada DPS and the Coastal-Southern California DPS, barred owls may be able to colonize the coastal-southern California spotted owl’s range because of the barred owl’s ability to use other forest types. Detections of barred owls in coastal forests in the Santa Cruz Mountains in San Mateo County, California, an area without known occurrences of the California spotted owl, suggests a pathway towards connectivity to the coastal portion of the California spotted owl’s range.

Barred owls are aggressively outcompeting and displacing spotted owls on the landscape (Wiens et al. 2014, p. 1; Gutiérrez et al. 2017, p. xvi; Long and Wolfe 2019, entire). Barred owls are larger than spotted owls (Gutiérrez et al. 2007, pp. 185–186) and

behaviorally dominant (Van Lanen et al. 2011, pp. 2197–2198). Although diet overlaps between the two species, with both predominantly feeding on nocturnal mammals, barred owls are generalists that consume many more prey species in comparison to spotted owls (Wiens et al. 2014, pp. 24–25; Kryshak et al. 2022, pp. 12–13).

Competition between the two species results in negative effects to the survival, productivity, and recruitment of northern spotted owls (Dugger et al. 2016, pp. 69–91), and barred owls have been described as demographically superior to northern spotted owls because they have higher survival estimates and produced, on average, 4.4 times more young than northern spotted owls over a 3-year period (Wiens et al. 2014, p. 28). The presence of barred owls has caused lower detection rates and occupancy probabilities in northern spotted owls (Olson et al. 2005, p. 918; Crozier et al. 2006, p. 760; Kroll et al. 2010, p. 1264; Yackulic et al. 2012, p. 1953; Yackulic et al. 2014, p. 265). Although there is some evidence that lower detection rates may be in part due to northern spotted owls responding less frequently in the presence of barred owls (Crozier et al. 2006, p. 760), the negative effects of barred owls on spotted owls are clear.

Although there is no evidence of barred owls wounding or killing northern spotted owls (Wiens et al. 2014, p. 33), competition ultimately has population-level effects because of impacts to occupancy and reproduction. Additionally, barred owls can hybridize with spotted owls (Gutiérrez et al. 2017, p. 211). There are likely broader impacts on the ecosystem from the barred owl's range expansion, such as an imbalance in predator/prey relationships, causing even greater impacts to spotted owl interspecific competition (Holm et al. 2016, p. 615). Because of the wide and diverse diet of barred owls in comparison to spotted owls, barred owls will not be ecological replacements to the spotted owls that they displace, and this could have widespread ecological impacts (Kryshak et al. 2022, pp. 15–16).

Barred owl detections within the California spotted owl's range have continued to increase. From 1989 to 2013, 51 barred owls and 27 barred owl/spotted owl hybrids had been detected in the Sierra Nevada (Gutiérrez et al. 2017, p. xxv). By 2017, the number of barred and barred owl/spotted owl hybrid detections in the Sierra Nevada increased to approximately 145 (Keane et al. 2018, p. 7), with another 2.6-fold increase between 2017 and 2018 (Wood et al. 2020, p. 4). Even these seemingly low numbers of barred owls in the California spotted owl's range are of concern, given that in the northern spotted owl's range, replacement of northern spotted owls began at a slow rate in the early years of the expansion, followed by a rapid rate of replacement once the barred owl population reached a critical mass (Forsman in litt. 2018, p. 1). As shown, over the last 10 years in particular, barred owl detections throughout the California spotted owl's range have increased at a higher rate (Service 2022, figure 11).

Experimental barred owl removal studies were first initiated and are currently ongoing in the northern spotted owl's range (e.g., Diller et al. 2012, entire; Wiens et al. 2020, entire). In Washington and Oregon, removals successfully decreased site use by barred owls and increased northern spotted owl use within treatment areas (Wiens et al. 2021, entire). Further, successful barred owl removals can result in competitive release for spotted owls (Wiens et al. 2021, pp. 4–5) (competitive release describes a situation in which one of two similar species competing for the same resources is removed, allowing the remaining species to use more of the resources; this is generally considered beneficial for the remaining species). In another (smaller) example of barred owl removals within the northern spotted owl's range, after nine barred owls were removed from historical northern spotted owl sites, all sites were re-occupied by northern spotted owls within a year of removal: four by the original residents and five by new residents (Diller et al. 2012, p. 405). However, barred owls again replaced the northern spotted owls at three sites within 1–4 years of the northern spotted owls reoccupying those territories (Diller et

al. 2012, p. 405). Overall, evidence to date indicates some measure of success for northern spotted owls related to barred owl removal efforts in at least some cases. However, species experts caution that forest conditions, densities of barred owls, and numbers of spotted owls would all factor into whether or not similar results could be obtained in other areas (Wiens et al. 2020, p. 1).

Experimental barred owl removal studies have also recently been initiated in the California spotted owl's range, specifically in the Sierra Nevada (Hofstadter et al. 2022, entire). In 2017, a California spotted owl conservation assessment concluded that control measures for barred owls in the California spotted owl's range were likely to be more successful and cost efficient while densities of barred owls are still relatively low in the California spotted owl's range, and that if control measures were not taken, barred owls would most likely replace California spotted owls on the landscape in the future (though the timescale of this replacement was uncertain) (Gutiérrez et al. 2017, pp. xxxi, xxv; see also Wood et al. 2020, pp. 5–7). Within the California spotted owl's range, barred owl removal experiments were initiated in 2018, and have continued through 2022 (Hofstadter et al. 2022, entire). Between 2018 and 2020, researchers removed 76 owls (63 barred owls and 13 hybrids) from the Sierra Nevada, decreasing barred owl occupancy by a factor of 6.3 down to 0.03 (confidence interval: 0.01–0.04). Experimental removals were guided by passive acoustic monitoring, which was also used to measure the efficacy of removals. Partnerships were crucial to the regional-scale removal, with public-private partnerships allowing access to 92 percent of the California spotted owl's range in the Sierra Nevada, including almost all known barred owls in the area and minimizing refugia for barred owls. California spotted owls rapidly colonized territories where barred owls were removed: 15 out of 27 territories were recolonized by California spotted owls within 1 year of barred owl removals, with successful breeding documented in five of these territories (Hofstadter et al. 2022, pp. 4–5). Early and effective

experimental removals of barred owls within the California spotted owl's range in the Sierra Nevada has dampened the urgency of this threat, but the potential for continued and persistent expansion into the range remains. Funding is currently available to continue barred owl removal experiments in the California extent of the Sierra Nevada through 2024 (Peery in litt. 2022). However, continued barred owl monitoring and experimental removal would likely need to continue into the future (Hofstadter et al. 2022, p. 6). Management options are currently being evaluated for potential future implementation.

Regulatory mechanisms and management actions that are providing or could potentially provide some protection from the effects of barred owl expansion include management teams, management plans, and habitat conservation plans (HCPs) that coordinate, fund, and implement the experimental removals described above. However, barred owls are a significant threat to the persistence of California spotted owls, and we expect the magnitude of the threat to increase into the foreseeable future, particularly if management efforts are not continued.

Rodenticides

Exposure of nontarget wildlife to anticoagulant rodenticides threatens many species, including California spotted owls, likely because of ingestion of exposed prey animals, known as secondary exposure (Gabriel et al. 2018, p. 5; Franklin et al. 2018, p. 2). Secondary exposure to anticoagulant rodenticides in predators such as raptors can be lethal, with higher levels causing severe blood loss and internal hemorrhaging that can result in organ failure and death (Gomez et al. 2022, p. 147). Although this threat has potential impacts to individuals, the loss of just a few individuals may reduce survival and the population growth rate because the California spotted owl is a long-lived species with low reproductive rates. This threat would be particularly detrimental if a parent were exposed during the breeding season because hatchlings and juveniles rely on parental

care to survive, so the loss of just one parent would likely result in the loss of offspring as well.

Rates of mortality in free-living wild birds due to anticoagulant rodenticides are often unknown due to the difficulty of linking exposure to death and the lack of understanding of toxicity thresholds in different species (Gomez et al. 2022, pp. 147–148). Documentation of anticoagulant rodenticides in ovaries of female barred owl suggests the possibility for in-utero transfer to chicks (Hofstadter et al. 2021, pp. 7–8). Sub-lethal effects of anticoagulant rodenticides in other owl species include reduced clutch size, brood size, fledging success, slower clotting time, residual transfer to eggs, anemia, and impaired mobility; however, these impacts have not yet been documented in spotted owls (Rattner et al. 2012, p. 832; Salim et al. 2014, p. 113; Gabriel et al. 2018, p. 7; Gomez et al. 2022, p. 148).

Although there is little information specific to California spotted owls regarding the exposure rates and resulting impacts of rodenticides, available literature on other species suggests the potential for widespread exposure. Exposure of nontarget species to anticoagulant rodenticides is commonly associated with agricultural or urban settings, but exposure in forest settings in northern California is detrimental to northern spotted owls and barred owls (Gabriel et al. 2018, p. 5; Franklin et al. 2018, p. 2). Seven out of 10 northern spotted owl carcasses tested positive for anticoagulant rodenticides, and 40 percent of 84 barred owls tested in the northern spotted owl's range had been exposed (Gabriel et al. 2018, pp. 4–5). In another study using barred owls as a proxy for spotted owls, almost half of barred owls sampled (n=40) and one northern spotted owl sampled demonstrated exposure to anticoagulant rodenticides (Wiens et al. 2019, p. 4). High rates of exposure were also demonstrated in barred owls and barred owl/spotted owl hybrids in California, with females having higher rates of exposure than males (Hofstadter et al. 2021, pp. 6–7). Large amounts of rodenticides and other pesticides have been found on

USFS land in the southern Sierra Nevada (Thompson et al. 2013, pp. 95–99).

Approximately 85 percent of fisher (*Martes pennanti* -- a carnivorous predator with similar habitat requirements as California spotted owls) carcasses tested in the Sierra National Forest had been exposed to rodenticides (Gabriel et al. 2012, pp. 1–14; Thompson et al. 2013, pp. 91).

Anticoagulant rodenticide use has increased throughout California with increases in illegal marijuana cultivation, as anticoagulant rodenticides are used to control rodent damage to the plants (Franklin et al. 2018, p. 1). A comparison of marijuana cultivation site likelihood with northern spotted owl suitable habitat found almost 50 percent overlap between the two (Wengert et al. 2021, p. 10). Although the number of illegal marijuana growing operations within the California spotted owl's range is unknown, considering the number of illegal marijuana growing operations found throughout the State, there are likely thousands within the California spotted owl's range (Gabriel et al. 2012, pp. 12–13; Thompson et al. 2013, pp. 95–99; Gabriel et al. 2018, p. 6).

In 2014, the California Department of Pesticide Regulation restricted the purchase, possession, and use of anticoagulant rodenticides in the State to purchase and use by a certified pesticide applicator with a permit issued by the county agricultural commissioner in order to protect wildlife; however, anticoagulant rodenticides associated with illegal marijuana grows are more likely the source of contaminants. If illegal marijuana grows are found, State law enforcement will shut the operations down, but there is currently no standardized clean-up protocol and a limited amount of funding to ensure removal of all rodenticides. Recently there has been an increased effort to locate and shutdown illegal marijuana grows on public lands in California called Operation Forest Watch (Department of Justice 2018, entire). Overall, anticoagulant rodenticides are likely affecting owls across their range, and we expect this threat will continue into the foreseeable future.

Development

Anthropogenic land use (including both cultivation and development) in California is expected to increase 28 percent by 2100 with a projected 3 percent decrease in overall forest land cover (Sleeter et al. 2017, pp. 1068, 1075). Urbanization is projected to be a primary driver of land use and land cover change in California over this time frame (Sleeter et al. 2017, p. 1076). Urban development is a threat throughout the range of California spotted owls; however, the threat is more substantial in the coastal and southern California population (Sleeter et al. 2017, p. 1081, figures 6 and 7). A majority of California spotted owl habitat occurs on public lands (approximately 71 percent of total range); therefore, this threat is primarily limited to a small amount of private lands.

Southern California faces high development demands with specific threats of wind farms and large reservoirs impacting connectivity within the California spotted owl's range (Gutiérrez et al. 2017, pp. 253–254). Loss of riparian areas due to water diversion in southern California has created barriers to dispersal among small populations (Gutiérrez et al. 2017, pp. 253–254). The southern California area of the California spotted owl's range is fragmented, with low dispersal between populations, so more development could further exacerbate fragmentation (LaHaye et al. 2001, p. 692; Barrowclough et al. 2005, p. 1116; Gutiérrez et al. 2017, pp. 253–254)

In the Sierra Nevada, low- to mid-elevation development is considered a threat to the California spotted owl and its habitat (Verner et al. 1992, pp. 264–265). Low- and mid-elevation zones in the Sierra Nevada continue to experience human population growth, which may increase the demand for development. Fifty percent of known California spotted owl sites on the west slope of the Sierra Nevada are considered wildland-urban interface and may be vulnerable to further development (Gutiérrez et al. 2017, p. 207). The northern Sierra Nevada is expected to have a higher level of forest

harvest compared to other parts of the California spotted owl's range (Sleeter et al. 2017, p. 1081, figure 7). Overall, development is likely affecting owls across their range, and we expect this threat will continue into the foreseeable future.

Conservation Efforts and Regulatory Mechanisms

Mechanisms and actions related to the California spotted owl and its habitat include State and Federal laws and regulations, federal incidental take permits, and forest management on USFS lands. In this proposed rule, we describe the key actions related to the California spotted owl and its habitat. For a full description of all conservation efforts and regulatory mechanisms, please see the SSA report (Service 2022, pp. 57–66).

The USFS has been a part of ongoing conservation efforts for California spotted owls, including the 2004 Sierra Nevada Forest Plan Amendment, which includes USFS land in the Lassen, Plumas, Tahoe, Humboldt-Toiyabe, Eldorado, Stanislaus, Sierra, Inyo, and Sequoia California spotted owl analysis units, and the 2005 Southern California National Forest Land Management Plans, which includes the Los Padres, Angeles, San Bernardino, and Cleveland California spotted owl analysis units. In 2019, the Inyo National Forest completed its own land management plan, and revised forest plans for the Sierra and Sequoia National Forests are expected to be final in 2023 (Miller in litt. 2022). Once these plans are finalized, the Inyo, Sierra, Sequoia National Forests will follow their individual plans and no longer follow the 2004 Sierra Nevada Forest Plan Amendment. All of these are regulatory documents that provide conservation measures for California spotted owls on USFS lands (USFS 2004, entire; USFS 2005, entire; USFS 2019a, pp. 43–47; USFS 2022b, pp. 59–68; USFS 2022c, pp. 59–68). The main goals of these conservation efforts include protection and management of California spotted owl activity centers and home range core areas, increasing the frequency of large trees on the landscape, and increasing structural habitat diversity. The goals relate to increasing the condition of the species' ecological needs to increase resiliency and provide conservation

efforts related to the threats of large-scale, high-severity fire; clearcutting; mechanical thinning; and salvage logging.

The 2004 and 2005 USFS land management plans and the 2019 Inyo National Forest and 2022 draft versions of the Sierra and Sequoia National Forest plans maintain the designation of PACs for California spotted owls, which encompass the best available 121 ha (300 ac) of habitat in as compact of a unit as possible around a nest tree (USFS 2004, p. 37; USFS 2005, p. 109; USFS 2019a, p. 43; USFS 2022b, p. 61; USFS 2022c, pp. 61–62). There are special considerations for any land management activities or projects that may take place within a PAC. Depending on the plan, management standards and guidelines include conducting surveys during the planning process of vegetation treatments where appropriate (i.e., in areas of suitable habitat for California spotted owls), limiting activities to reducing surface and ladder fuels through prescribed fire, limiting mechanical treatments to only allow fuel reduction treatments in some wildland urban defense zones where prescribed fire is not feasible, identifying maximum size of canopy gaps created within California spotted owl territories, requiring a limited operating period for when vegetation treatments can occur, and limiting the impacts a vegetation treatment can have on a PAC per year (USFS 2004, pp. 50–51, 54, 60–61; USFS 2005, pp. 7, 82–83; USFS 2019a, pp. 43–47; USFS 2022b, pp. 63–68; USFS 2022c, pp. 63–68).

In addition to protections, the 2004 Sierra Nevada Forest Plan Amendment and the 2022 version of the Sierra and Sequoia National Forest Plans outline desired conditions for PACs and other large habitat blocks within the home range that include at least two tree canopy layers, dominant and co-dominant trees with average diameters of at least 61 cm (24 in) dbh, at least 60 percent to 70 percent canopy cover, some very large snags (greater than 114 cm (45 in) dbh), and snag and coarse woody debris levels that are higher than average (USFS 2004, pp. 37, 39–40; USFS 2022b, pp. 60–61; USFS 2022c,

pp. 60–61). As discussed below, in April 2019, the USFS finalized a new California spotted owl conservation strategy for the Sierra Nevada (USFS 2019b, entire). The intention of the strategy is to be used for adaptive management and to be incorporated into future forest plan updates, although it is not legally enforceable and does not commit agency action or inaction.

As described above in “Fuels Reduction and Forest Management,” there is disagreement about whether or not measures in these plans, such as mechanical thinning, are beneficial or detrimental to California spotted owls, and whether or not protections afforded to PACs are sufficient to ameliorate impacts to California spotted owls (John Muir Project of Earth Island Institute and The Wild Nature Institute 2014, pp. 70–71, 98, 108; Sierra Forest Legacy and Defenders of Wildlife 2015, pp. 39–40). However, a meta-analysis of California spotted owl occupancy and forest management practices indicated that mechanical thinning treatments that maintain canopy cover at 40 percent or greater would not substantially reduce California spotted owl occupancy, although canopy cover at 50 percent or above is more strongly correlated with California spotted owl occupancy (Tempel et al. 2016, pp. 761–762). Forest management practices from the 2004 Sierra Nevada Framework generally maintain at least 50 percent canopy cover as well as large trees within PACs, and in the 2005 Southern California plan, 40–50 percent canopy cover must be maintained. The 2019 Conservation Strategy also maintains a minimum of 50 percent canopy cover within PACs (USFS 2019b, p. 28). Overall, PACs are designated to preserve key habitat used by California spotted owls, and some researchers have concluded that PACs are a key conservation tool that should continue to be implemented (Berigan et al. 2012, pp. 300, 303). In contrast, other research has shown that PACs can be more susceptible to the effects of high-severity fire due to the relatively larger amounts of surface fuel (North et al. 2012, p. 395).

In April 2019, the USFS completed an updated California spotted owl conservation strategy for the Sierra Nevada national forests (USFS 2019a, entire). The updated strategy includes new scientific understanding since the 2004 Sierra Nevada Forest Plan Amendment and will be incorporated into national forest land management plans as they are updated in the coming years, in accordance with USFS regulations in title 36 of the Code of Federal Regulations (CFR) at part 219. Until the revised national forest land management plans can be completed, the Pacific Southwest Region of the USFS sent a letter of direction to the Sierra Nevada national forests on April 19, 2019, to provide guidance on implementing the new conservation strategy in the interim (USFS 2019b, entire). The new conservation strategy gives direction for increased pace and scale of ecological restoration to provide more resilient habitat for California spotted owls, while simultaneously continuing to protect the most important habitat attributes and areas for California spotted owls.

The three main goals for the 2019 conservation strategy include: (1) Maintain a well-distributed and stable California spotted owl population across the Sierra Nevada by minimizing impacts from non-habitat threats (such as barred owls and contaminants); (2) promote and maintain well-distributed California spotted owl habitat by developing key habitat elements and connectivity; and (3) promote California spotted owl persistence by enhancing habitat resilience to multiple disturbances, considering climate change. This increased habitat resilience will lead to improved conditions on the landscape and greater population resiliency. The new strategy provides adaptive management and metrics for success in order to ensure the conservation measures outlined in the plan are beneficial to California spotted owls.

In addition to the conservation strategy, the USFS is planning to implement a new monitoring plan using acoustic recording units to cover the Sierra Nevada portion of the California spotted owl's range. The goal is to use the information from the new

monitoring plan to allow the USFS to conduct a future California spotted owl occupancy modeling effort to provide information over a larger portion of the California spotted owl's range and allow greater potential for inference on broad-scale effects of restoration and disturbance (USFS 2019c, pp. 14–15). Elements of the strategy may entail some short-term, localized reduction in occupancy. These elements allow for more forest management flexibility in application of fuels reduction and other landscape treatment projects as compared to the 2004 Sierra Nevada Forest Plan Amendment both within PACs and on the landscape, as well as more flexibility in the retirement of PACs when they are no longer occupied. Additional flexibility in these landscape treatments provides access to additional tools to maintain and restore California spotted owl habitat (USFS 2019a, entire). We anticipate that the short-term impacts that may occur for the purpose of fuel reduction and forest health will be outweighed by the long-term benefit as more sustainable and dynamic habitat is developed through active management (USFS 2019a, p. 2).

On August 30, 2017, an MOU (hereafter referred to as the Fire MOU) was signed by SPI, CAL FIRE, National Fish and Wildlife Foundation, and the USFS, which will impact all lands from Lassen National Forest south through Stanislaus National Forest. The purpose of the Fire MOU is to document the agreement between the parties to coordinate on certain actions to reduce the risk of large-scale, high-severity wildfire through forest fuels reduction to benefit California spotted owl conservation. This MOU involves establishing a strategic conservation framework to help restore and protect areas where California spotted owls are threatened by habitat degradation due to uncharacteristically extensive and severe adverse fire effects. The Fire MOU is designed for signatories to engage in collaborative landscape-level fuels and fire risk reduction treatments to: (1) Minimize potential fire-related impacts to California spotted owl activity centers on Federal, State, and private lands; and (2) better coordinate

implementation of fuels reduction work on Federal, State, and private lands to maximize the effectiveness of this work. Sites for fuels treatment are selected to minimize risk to known occupied California spotted owl activity centers. Measures associated with the Fire MOU include fire management activities such as increased mechanical thinning that may benefit California spotted owls by decreasing risk of large-scale, high-severity fire. If mechanical thinning is planned with consideration of the California spotted owl's habitat needs, there may be some negative impacts, but these would be outweighed by reducing the risk of large-scale, high-severity fire in California spotted owl activity centers (Jones et al. 2016a, p. 305; Service 2017, pp. 24–25; Chiono et al. 2017, p. 1; Jones et al. 2021b, p. 6).

The USFS, SPI (a private corporation), and CAL FIRE manage forest lands in California that are frequently adjacent to each other and have ongoing programs to protect and enhance habitat for fish and wildlife. On these lands, forest fuels are managed to reduce fire risk and its potential impacts on wildlife species. Under State law, SPI has the authority to participate in fire suppression on its own lands, while CAL FIRE, contract counties, USFS, and other government agencies have primary fire suppression responsibility for all Federal, State, and private wildlands in California. The parties also have responsibilities and interests in the inventory of their respective lands for species recognized as endangered, threatened, proposed as endangered or threatened, candidate, and sensitive species by the Federal or State government. The parties also have responsibility and interest in the development of appropriate protection measures for these species. Due to these natural resource challenges, the Fire MOU parties believe it is important to establish a coordinated, multi-stakeholder agreement to help protect and enhance forest resources.

Though the Fire MOU was initially set to expire on December 2019, an amendment was signed in April 2019 to extend the terms of the MOU through December

2024. In March 2020, a new MOU that supersedes the 2017 MOU and 2019 amendment was signed by the same parties. An amendment to the 2020 Fire MOU was signed in September 2020 to add a number of new commercial forest landowners. The terms of the 2020 MOU are effective through December 2024. The Service is actively engaged with the signatory parties to discuss fuels reduction efforts and associated monitoring.

Barred owls have expanded into western North America over the past several decades, first through the Pacific Northwest and more recently into the Sierra Nevada. The Service and the USFS are funding researchers at the University of Wisconsin-Madison to carry out an ongoing barred owl removal study. The project grant was signed in August of 2018, and funding has been secured from the Service and potentially University of Wisconsin-Madison through 2025 (Peery in litt. 2022). The project addresses several key questions related to the range expansion of barred owls in the Sierra Nevada and will inform the development of a scientifically based barred owl management plan. Specifically, this project: (1) Assesses the current distribution and density of barred owls; (2) conducts experimental barred owl removals; (3) tests for reductions in barred owl site occupancy rates; (4) quantifies spatiotemporal patterns of barred owl recolonization; and (5) characterizes barred owl dispersal into and within the Sierra Nevada. This project takes place primarily in the northern and central Sierra Nevada, including Lassen National Forest, Lassen National Park, Plumas National Forest, Tahoe National Forest, Eldorado National Forest, Yosemite National Park, and Sequoia-Kings Canyon National Park.

Additionally, on July 22, 2022, the Service published in the *Federal Register* (87 FR 43886) a notice of intent to prepare an environmental impact statement, initiating a 30-day public scoping period seeking input on barred owl management in the northern spotted owl's and California spotted owl's ranges. Preventative barred owl management for California spotted owls will likely be considered in the environmental impact

statement. Northern spotted owls are the main focus right now, but barred owls have expanded into northern California into the California spotted owl's range and are expected to continue to expand without continued management.

Currently, two HCPs include the California spotted owl. Habitat conservation plans are planning documents required as part of an application for an incidental take permit; they can apply to both listed and non-listed species, including those that are candidates or have been proposed for listing. They describe the anticipated effects of the proposed taking; how those impacts will be minimized or mitigated to the maximum extent practicable; and how the HCP is to be funded.

Sierra Pacific Industries is the largest private forest land owner in California, with approximately 744,621 ha (1,840,000 ac) of timberland in northern California (SPI 2021, p. 1). Sierra Pacific Industries' habitat conservation plan for both the northern spotted owl and California spotted owl covers all areas on SPI-managed property where covered activities will occur within the range of the two spotted owl subspecies, which is more than 607,028 ha (1,500,000 ac) (SPI 2021, p. 2). Covered activities under the HCP include timber operations and other forest management activities. Major activities associated with the HCP include growing, harvesting, and transporting timber; timber stand regeneration and improvements; road and landing construction and maintenance; fuel break construction and maintenance; and monitoring and research (including for spotted owls) (Service 2020, p. 8). Implementation of the HCP is not expected to result in direct injury or mortality of California spotted owls due to the implementation of conservation measures that will be implemented throughout the 50-year permit term. These measures will support California spotted owl species needs and address threats currently affecting the species, including reducing the risk of catastrophic fire and eradication of illegal marijuana plantations (Service 2020, pp. 10–13).

In 2015, SPI began studying barred owls via removal experiments. In 2018, the study was revised to include the following objectives: (1) assess the genetic differentiation of barred owl populations across northern and central California, (2) analyze allele frequency changes on the front of the range expansion, (3) estimate the amount of spotted owl-barred owl interbreeding (admixture) in each population, and (4) identify what barred owls are preying on in California. These efforts are ongoing, and SPI has committed to continue these efforts during the term of the permit, as feasible. Ongoing research and monitoring efforts for California spotted owls on SPI land have indicated that some California spotted owl populations in mixed-ownership landscapes have higher occupancy, density, and probability of reproduction compared to California spotted owl populations on public land (Roberts et al. 2017, p. 113; Hobart et al. 2019, p. 198; SPI et al. 2022, pp. 9, 17).

The Western Riverside County Multiple Species Habitat Conservation Plan (MSHCP) is one of the largest habitat conservation plans in the United States, covering 202,343 ha (500,000 ac). The California spotted owl is currently listed as a “species not adequately conserved” under the MSHCP until an MOU is executed with the USFS that addresses management of California spotted owls on USFS lands. The MSHCP plan area includes 21,901 ha (54,119 ac) of modeled habitat for California spotted owls. If the MOU with the USFS is signed, the loss of 5,223 ha (12,905 ac) (24 percent) of this modeled habitat is anticipated over the 75-year permit term. With the low density of California spotted owls in the plan area, loss of these 5,223 ha (12,905 ac) is not anticipated to result in direct mortality of adult birds. However, loss of foraging and nesting habitats to development will cause California spotted owls in impacted areas to disperse in search of other habitats. Thus, loss of breeding and foraging habitat may impact overall population numbers of California spotted owls within the plan area over the long term by reducing the number of areas suitable for use as foraging and nesting

sites (Service 2004, p. 449). In order to offset these impacts, the MSHCP will conserve and manage 535 ha (1,321 ac) (2 percent) of modeled habitat for California spotted owls within additional reserve lands. In total, 16,679 ha (41,214 ac) (76 percent) of the modeled habitat for California spotted owls will be included in the MSHCP conservation area. If the MOU with the USFS is signed, additional monitoring and management would occur in habitat for California spotted owls within USFS lands included in the MSHCP conservation area.

Combined Impacts of Threats

The threats discussed above not only act independently, but also interact with each other. It is important to assess the relationship between threats because there may be new or exacerbated impacts that are not considered when a threat is assessed alone. There are a vast number of ways threats may be interacting with each other, but the SSA report and this proposed rule only focus on what is currently most relevant to the viability of the species.

For example, climate change intensifies the threats of large-scale, high-severity fire; drought; and tree mortality, and it increases interannual climate variability (Kadir et al. 2013, pp. 132, 137; Stephens et al. 2018, p. 77). Development in wildland-urban interfaces also increases the likelihood of large-scale, high-severity fire (Mann et al. 2016, pp. 14–18). An increase of large-scale, high-severity fires with changing climate conditions can lead to accelerated, fire-facilitated conversion of forest edge to non-forested habitat (Parks et al. 2019, pp. 1, 7). The impacts to the California spotted owl would likely range from direct physiological impacts to indirect habitat and prey impacts. The loss of trees due to high-severity fire, drought, and tree mortality would likely lead to increased salvage logging on the landscape, further reducing California spotted owl habitat. Additionally, the expansion of barred owls outcompeting California spotted owls in combination with timber harvest outside of PACs further worsens the outlook for

habitat availability. Spotted owls living near the wildland-urban interface may be at a higher risk for exposure to anticoagulant rodenticides, as is the case for barred owls and hybrids (Hofstadter et al. 2021, p. 8).

Barred owls are moving south into the California spotted owl's range, so the northern portion of the Sierra Nevada DPS will likely experience a greater magnitude of this threat, and earlier in time. Tree mortality is more concentrated in the Sierra Nevada DPS than other parts of the landscape and may experience more significant impacts from this threat. The threat of wildfire is of higher magnitude in the Coastal-Southern California DPS. Considering the temporal, spatial, and interactive components of all the threats together is important for understanding the viability of California spotted owls throughout their range now and into the future.

Current Condition

For our current condition analysis in the SSA report and this proposed rule, we considered the status of the two populations of California spotted owls: the Sierra Nevada population and the coastal-southern California population. As described above in **Background**, to analyze these populations in more detail, we further divided them into analysis units; however, we recognize that these units do not function independently, and in areas where the species' distribution is continuous, like the Sierra Nevada population, impacts to one unit may result in impacts to an adjacent unit. We assessed the condition of all California spotted owls' ecological needs where information was available for each analysis unit, including the demographic factors of survival, fecundity, occupancy, and population growth, and habitat components of large trees and canopy cover. In addition, because high-severity fire has significant effects on the condition of habitat within an analysis unit, we also incorporated results from our fire analysis. For each population, we present an overview of the available information on ecological conditions and threats across the entire population, our analysis of the demographic factors and habitat

components within each analysis unit to determine current condition, and a summary assessing population resiliency. In this proposed rule, for each DPS, we then assess California spotted owl redundancy and representation under the current condition analysis.

For detailed information on how we determined all demographic and habitat scores, total scores for each population and analysis unit, and uncertainties considered in the analysis, please see the SSA report (Service 2022, pp. 70–77).

Sierra Nevada DPS Current Resiliency

Resiliency is the ability of a species to withstand stochastic events, the normal year-to-year variations in both environmental conditions and demographic conditions (Redford et al. 2011, p. 40). Determined by the size and growth rate of the populations comprising the species, resiliency can be evaluated to gauge the ability of a species to weather the natural range of favorable and unfavorable conditions.

Until recently, California spotted owls and suitable habitat were relatively well-distributed in the Sierra Nevada with few barriers to dispersal (Gutiérrez et al. 2017, p. 94): as of 2017, an estimated 1.98 million ha (4.9 million ac) of suitable habitat for California spotted owls were available in the Sierra Nevada, primarily on Federal lands (Gutiérrez et al. 2017, pp. xx, 123). Of that land, 75 percent is managed by the USFS, 7 percent is managed by the NPS, and 18 percent is either privately owned or managed by other government agencies (Gutiérrez et al. 2017, p. xx). However, recent large, catastrophic fires have reduced available habitat and have likely created new barriers for California spotted owl dispersal in this DPS. Other barriers to dispersal include urban and suburban development, large reservoirs, physiographic features such as non-forested or unsuitable habitat or vegetation communities, or lack of riparian areas to act as corridors through unsuitable extents (Gutiérrez et al. 2017, pp. 94–95, 253–254).

From our habitat analyses, we found that the Sierra Nevada has higher canopy cover and tree size values than southern California (Service 2022, tables 5, 9, and 13). When comparing the northern to the southern Sierra Nevada, the north contains higher canopy cover, which aligns with historical forest structure data that tend to show more dense forests in the northern Sierra Nevada (Van Wagtendonk et al. 2006, p. 250), with the exception being on the east side of the Sierra Nevada (Humboldt-Toiyabe and Inyo analysis units), which contains more open and disjunct habitat than the west side. Higher canopy cover combined with higher precipitation levels tend to result in lower tree mortality in the northern Sierra Nevada, which may have helped reduce the potential for megafires in the northern Sierra Nevada in past years, but climate change impacts of reduced snowpack and increased temperatures show that increased fire risk is also occurring in the northern Sierra Nevada. We also found that the two units mostly composed of National Parks (Yosemite and Sequoia-Kings Canyon) contain the largest tree size percentages. Overall, the overlap values between canopy cover and large trees were low across all analysis units (Service 2022, table 9).

The threats that are currently impacting the Sierra Nevada population include large-scale, high-severity fire; tree mortality; drought; climate change; various impacts from fuels reductions and forest management; competition with barred owls; and rodenticides. These threats are not equivalent across all analysis units within the Sierra Nevada population (Service 2022, pp. 77–87). For example, competition with barred owls is more pronounced in the northern part of this population than in the southern portion, and the threat from rodenticides is more pronounced at the wildlife-urban interface. However, some threats, like fire, are considered a threat across the population, and there is a general increasing trend in the annual acreage and relative proportion of high-severity fires in the Sierra Nevada (Keane in litt. 2022, p. 3). In 2020–2021, the percent of habitat that burned at high severity within California spotted owl PACs in the

Sierra Nevada was almost twice as that from 1993–2019; in 1993–2019, 44 percent of habitat burned, with 35 percent of that at high severity, compared to 65 percent of fire being high severity in 2020–2021 (Keane in litt. 2022, p. 5).

We conducted a separate fire analysis for the entire California spotted owl's range, which includes PACs as well as additional acreage outside PACs (Service 2022, pp. 29–30, appendix I). Our fire analysis shows similar results, with approximately 42 percent of the California spotted owl's range in the Sierra Nevada burned between 1984 and 2021, with 7 percent and 12 percent of that total from acreages burned in 2020 and 2021, respectively. Of the 42 percent of California spotted owl's range burned within the Sierra Nevada, approximately 13 percent was burned at high severity (Service 2022, appendix I). In our supplemental analysis that analyzes habitat and fire metrics along an ecological boundary between the northern and southern Sierra Nevada, we found that both portions of the Sierra Nevada burned at similar amounts between 1984 and 2021 (Service 2022, appendix I). However, the majority of burned acreage in the northern Sierra Nevada occurred in 2021 (18 percent burned with 9 percent at high severity compared to 5 percent or less in all other years and 2 percent or less at high severity from 1984 to 2021). In the southern Sierra Nevada, 11 percent burned in 2020 with 2 percent at high severity in 2020 and 2021, compared to 5 percent or less total burned and 1 percent or less at high severity from 1984 to 2021 (Service 2022, appendix I). These results suggest higher levels of disturbance to the species and increased recovery time for habitat conditions to improve post-fire because such a large acreage burned over a relatively concentrated period of time.

In addition to common threats acting on all analysis units within this population, there are also common management actions taking place within the Sierra Nevada population. For example, the USFS designates PACs around known California spotted owl nest trees, so analysis units containing national forests (e.g., all Sierra Nevada

population analysis units except for Yosemite and Sequoia-Kings Canyon) include these protections. Further, barred owl removal experiments in the northern Sierra Nevada have so far been successful in avoiding the catastrophic impacts that could have occurred in the absence of any management.

The current condition of analysis units throughout the Sierra Nevada population varies, with three analysis units currently considered stable, five declining, and three strongly declining (Service 2022, table 12). All three of the units ranked as strongly declining are on the upper boundary of our scoring system for the SSA report. Based on these results, the overall condition of the Sierra Nevada population is declining and, therefore, has low resiliency. However, though resiliency has declined from historical conditions and connectivity has decreased, the Sierra Nevada population is still distributed throughout its historical range, and ongoing conservation measures and regulatory mechanisms are decreasing the magnitude of threats. Therefore, the Sierra Nevada population maintains the ability to withstand stochastic events.

Sierra Nevada DPS Current Redundancy

To assess current redundancy of the Sierra Nevada DPS, we consider the ability of a species to withstand catastrophic events, i.e., natural or anthropogenic stochastic events that would result in the loss of a substantial component of the overall species population. However, redundancy is not simply a measure of the total number of individuals or populations of a species, but instead must also be evaluated in the context of an assessment of reasonably plausible catastrophic events. For example, when we consider the redundancy of an entity comprised of a single population that is very large and widely distributed, it could have a high ability to withstand a catastrophic event that would only affect a small percentage of the overall population. Therefore, our characterization of the Sierra Nevada DPS's redundancy takes into consideration both an assessment of the size and distribution of its population, and an evaluation of the kinds

and likelihood of reasonably plausible catastrophic events to which the species could be exposed.

Of the two populations throughout the species' range, the Sierra Nevada population that makes up the Sierra Nevada DPS covers the most area and is the largest population. Catastrophic events that could impact California spotted owls include very large, high-severity wildfire; extreme drought; extreme weather events; and prolonged and persistent competition and displacement due to barred owl expansion. Overall, current California spotted owl redundancy has declined from historical condition, which risks making the species more vulnerable to extirpations from catastrophic events. However, the Sierra Nevada DPS is large, contiguous, and still distributed throughout its historical range, meaning it is more able to recover from events such large, catastrophic wildfires.

Sierra Nevada DPS Current Representation

In this proposed rule, to assess current representation, which is the California spotted owl's current ability to adapt to change, we considered the ecological setting and genetic diversity in the Sierra Nevada DPS. In the Sierra Nevada population, a majority of California spotted owls occur within mid-elevation ponderosa pine, mixed-conifer, white fir, and mixed-evergreen forest types, with few California spotted owls occurring in the lower elevation oak woodlands of the western foothills (Gutiérrez et al. 2017, p. xix). Further, California spotted owls in the northern portion of the Sierra Nevadas tend to have larger home range sizes than California spotted owls in the southern portion of the mountain range (Gutiérrez et al. 2017, p. xviii). Within the Sierra Nevada, the northern portion of the range experiences more precipitation and lower mean temperatures than the southern portion of the range (Climate Engine 2017, unpaginated). The diversity in habitat and climate between and within the areas for which we have data suggests that the species has some flexibility to adapt to changing environmental conditions.

Of the three spotted owl subspecies (northern, California, and Mexican), California spotted owls have the lowest genetic diversity when measured by unique haplotypes (Barrowclough et al. 1999, pp. 919, 927; Haig et al. 2004, p. 683). This suggests that California spotted owls have lower genetic representation in general than either of the other two subspecies. However, whether the observed level of genetic diversity indicates low representation is unclear. Because the California spotted owl has persisted throughout much of its historical range for an extended period of time, the relatively low genetic diversity may be an historical artifact rather than an indication of concern for representation. Within the California spotted owl subspecies, genetic differences are found between California spotted owls found in the Sierra Nevada and those found in coastal-southern California; this provides some degree of genetic representation at the subspecies level, although not enough for each population to be considered a separate subspecies (Barrowclough et al. 1999, p. 927; Gutiérrez et al. 2017, p. 101; Hanna et al. 2018, pp. 3946–3947, 3949). Whole-genome data indicate that there is greater genetic difference between California spotted owls (in the northern and southern extent of the subspecies' range) than there is between northern spotted owls and California spotted owls in the northern portion of the range; this is consistent with isolation-by-distance (geographic differences increase with geographic scale) (Hanna et al. 2018, pp. 3946–3947). The genetic differences observed between populations, as well as the habitat and climate differences, may represent a moderate degree of adaptation and thus moderate representation at the subspecies level.

Though the Sierra Nevada DPS has lower representation than the subspecies as a whole, the California spotted owl continues to inhabit different ecological settings throughout the Sierra Nevada. The overall condition of the DPS has declined, which has likely resulted in reduced genetic diversity. Therefore, current California spotted owl

representation in the Sierra Nevada DPS has declined from historical condition, suggesting that the ability for the taxon to adapt to change is decreased.

Coastal-Southern California DPS Current Resiliency

Habitat within the Coastal-Southern DPS is considered to be naturally fragmented, with little dispersal occurring between subpopulations due to discontinuous mountain ranges (Gutiérrez et al. 2017, pp. 93–95). This natural fragmentation has been further fragmented by development/habitat loss in the greater southern California area. Specific information about habitat and demographic conditions, when available, is incorporated below for each of our southern California analysis units. The available evidence does not document successful dispersal between the San Bernardino, San Gabriel, and San Jacinto Mountains, which are adjacent mountain ranges, indicating that if dispersal does occur within this population, it is very rare (LaHaye et al. 2001, entire; LaHaye et al. 2004, entire; Gutiérrez et al. 2017, pp. 242, 250).

As previously discussed, within this population, occupancy data are only available for the San Bernardino Mountains. The San Bernardino Mountains have historically contained the largest number of California spotted owls, suggesting that information extrapolated from this area would lead to a too optimistic view for the overall population (Gutiérrez et al. 2017, p. 242). Data from one recent study showed higher occupancy in the San Bernardino Mountains than the San Jacinto and San Gabriel Mountains, and the authors suggest that other parts of southern California may also have experienced greater declines than this area (Tempel et al. 2022, pp. 20–21).

As mentioned for the Sierra Nevada population, our habitat analyses found that habitat values for large trees and canopy cover were lower in southern California than in the Sierra Nevada (Service 2022, tables 5, 9, and 13). Overlap between canopy cover and large trees was also low (Service 2022, table 13). In southern California, high canopy cover is positively associated with California spotted owl reproductive output, but large

trees appeared to be more important than high canopy cover (Tempel et al. 2022, p. 22) and are also important for occupancy. Our analysis found large tree values for southern California are low, which may indicate lower habitat quality in this analysis unit. For this population, we conducted an additional analysis identifying the percentage of small trees within the overall population that could potentially support platform or stick nests (Service 2022, table 14). We found that 14 percent of the coastal-southern California analysis units contain these small trees compared to an overall value of 1 percent for large trees only trees larger than 61 cm dbh are considered. When looking at the combined total of small trees and large trees, 16 percent of southern California contains potential trees that could support the California spotted owl's ecological needs (Service 2022, table 14).

The threats that are likely currently impacting this population include large-scale, high-severity fire; tree mortality; drought; climate change; various impacts from fuels reductions and forest management; and rodenticides. Competition with barred owls is not yet considered a current threat within this population. Impacts from these threats may not be equally distributed across the population and are not equivalent to the ways that these threats impact the Sierra Nevada population. For example, what might be considered a stochastic event (in this case, an event that removes one or a few individuals from the population) in the Sierra Nevada population could instead be considered catastrophic if it were to occur in the coastal-southern California population because of the lower number of California spotted owls within this population. Our fire analysis shows that 60 percent of the California spotted owl's range in southern California burned between 1984 and 2021, 17 percent at high severity, with 6 percent of the total area burned in 2020 and 1 percent at high severity that year. There were no fires in 2021 within the range of this population. Typically, 4 percent or less of habitat within this population burned per year, with 1 percent or less burning at high severity, although some years burned at higher

percentages (2003 at 6 percent with 3 percent high severity, and 2007 at 8 percent with 4 percent high severity; Service 2022, appendix I). In addition to common threats acting on all analysis units within this population, there are also common management actions taking place throughout the analysis units comprising the coastal-southern California population. For example, analysis units containing national forests include PACs around known California spotted owl nest trees.

The current condition of analysis units within the Coastal-Southern California DPS is that two analysis units are strongly declining and two units are declining (Service 2022, table 17). Based on these results and our scoring of habitat conditions and available demographic information (Service 2022, table 18), the overall condition of the Coastal-Southern California DPS is strongly declining and, therefore, has very low resiliency.

Coastal-Southern California DPS Current Redundancy

As with the Sierra Nevada DPS, our characterization of redundancy for the Coastal-Southern California DPS takes into consideration both an assessment of the size and distribution of its population, and an evaluation of the kinds and likelihood of reasonably plausible catastrophic events to which the species could be exposed.

As with the Sierra Nevada DPS, catastrophic events that could impact the Coastal-Southern California DPS include very large, high-severity wildfire; extreme drought; extreme weather events; and prolonged and persistent competition and displacement due to barred owl expansion. The population that makes up the Coastal-Southern California DPS is highly fragmented with gaps between occupied areas. In areas where demographic data are available (the San Bernardino analysis unit), declines have accelerated over the last 30 years, and as stated above, information extrapolated from a study area that historically contained the largest number of California spotted owls could lead to an overly optimistic view for other areas of the coastal-southern California population (Gutiérrez et al. 2017, p. 242). Overall, current California spotted owl

redundancy in this DPS has declined from historical condition, making the species more vulnerable to extirpations and potentially extinction from catastrophic events.

Coastal-Southern California DPS Current Representation

To assess current representation, which is the California spotted owl's current ability to adapt to change, we considered the ecological setting and genetic diversity among the two California spotted owl populations. In coastal and southern California, California spotted owls are found in riparian/hardwood forests and woodlands, live oak/big cone fir forests, and redwood/California laurel forests (Gutiérrez et al. 2017, p. xxvi). California spotted owls use stick nests more frequently in southern California compared to in the Sierra Nevada. Further, California spotted owls in the northern portion of the range tend to have larger home range sizes than California spotted owls in the southern portion of the range (Gutiérrez et al. 2017, p. xviii). The climate of the Coastal-Southern California DPS is more arid than that of the Sierra Nevada (Climate Engine 2017, unpaginated).

In regard to genetic diversity, in the Coastal-Southern California DPS, the population has become highly fragmented, which likely has resulted in reduced genetic diversity. The increased fragmentation has reduced the amount of available habitat in throughout the coastal-southern California population. Therefore, current California spotted owl representation in the coastal-southern California population has declined from historical condition, suggesting that the ability for the DPS to adapt to change is decreased.

Future Condition

For our future condition analysis, we forecast the response of the Sierra Nevada DPS of the California spotted owl to two plausible future scenarios. These two scenarios represent the extremes of a range of future changes in environmental conditions and success of implemented conservation efforts. The future scenarios project the influences

to viability discussed above in *Current Condition* into the future and consider the impacts those influences would potentially have on California spotted owl viability. We apply the concepts of resiliency, redundancy, and representation to the future scenarios to describe the future viability of California spotted owls in the Sierra Nevada DPS.

For this analysis, we describe two future scenarios and assess future resiliency for the Sierra Nevada DPS. Scenario 1 assesses future viability with an increase in the trend and magnitude of threats with implemented management efforts having mixed success. Scenario 2 assesses the viability of the species if the trend and magnitude of threats were to continue at the current trajectory into the future with implemented management efforts being fully successful. A full comparison of the assumptions made for each scenario is available in the SSA report (Service 2022, table 19). Using two scenarios representing the extremes of plausible future projections for the species allows us to consider the full range of future possibilities for predicting the future viability of the Sierra Nevada DPS and incorporates any uncertainty regarding the impact of future environmental conditions and the success of implemented conservation efforts. For the SSA report and this proposed rule, we assessed future conditions at approximately 40–50 years. For a detailed description of our methods and assumptions for each future scenario, as well as more details on how the impacts of threats would differ under each scenario, please see the SSA report (Service 2022, pp. 97–100).

In the SSA report, we also applied our two future scenarios to the population of California spotted owls that makes up the Coastal-Southern California DPS. Because we determined that the current condition of the Coastal-Southern California DPS is consistent with an endangered species (see *Status of the Coastal-Southern California DPS of the California Spotted Owl Throughout All of Its Range*, below), we are not presenting the results of the future scenarios in this proposed rule. Please refer to the SSA report (Service 2022, pp. 100–125) for the full analysis of future scenarios.

Scenario 1

Scenario 1 considers viability of the Sierra Nevada DPS if some of the significant threats were to increase in magnitude into the future and future management efforts have mixed success in addressing those threats. Under this scenario, climate change models under RCP 8.5 project temperature increases of 4.5–6 °F, depending on the portion of the range. Increases in temperatures will likely increase extreme weather events, including heat waves and drought conditions (Kadir et al. 2013, pp. 38, 48). With increased drought conditions, tree mortality and large-scale, high-severity fire are likely to increase in frequency and size, especially if fuel loads in forests are not decreased (Westerling and Bryant 2008, pp. S244–S248; Abatzoglou and Williams 2016, pp. 11770, 11773; Young et al. 2017, p. 78). Extreme weather events or significant changes in interannual climate variability may have negative impacts on the California spotted owl's survival and reproduction. Although there are some protections in place for California spotted owls on public lands, timber harvest values can vary year to year. Therefore, it is possible that increases in timber harvest targets may reduce California spotted owl habitat that is available now or that may be available in the future for California spotted owls to establish new territories and disperse beyond the PACs.

Without continued ongoing experimental removals, barred owls will likely continue to expand their range into California spotted owl habitat, eventually reaching a point of exponential increase and significantly displacing and outcompeting California spotted owls on the landscape (Keane et al. 2018, pp. 8, 47). The timeline for barred owl expansion and replacement of California spotted owls on the landscape is unknown; however, because they were able to expand so quickly within the northern spotted owl's range, under future scenario 1 we assume barred owls would move beyond the Sierra Nevada and continue to expand into southern California. This expansion could be due to current experimental removal efforts becoming less successful over time (i.e., decreased

experimental removal efforts) or the barred owl being able to cross what was thought to be unsuitable habitat, like the Central Valley. Under scenario 1, it is also possible that rodenticide use could continue to increase in California due to the legalization of marijuana in 2016. There will likely continue to be an increase in demand for marijuana, which may increase illegal grow sites using anticoagulant rodenticides in California if the costs of buying land and acquiring/maintaining permits to legalize a grow operation are too high (Soboroff and Koss 2017, entire; Yakowicz 2018, entire; Harrison 2018, entire). In regards to disease and parasites, there is evidence that changing climate conditions could increase pathogen development and occurrence (Harvell et al. 2002, p. 2158), creating a slight chance that disease and parasites may become a more significant issue in the future. Finally, development may continue to encroach upon California spotted owl habitat as the California human population continues to grow (California Economic Forecast 2016, pp. xii–xiii, 233–236).

Under scenario 1, almost all analysis units degrade in condition, with four analysis units considered declining, four strongly declining, and three that will likely be extirpated (Service 2022, tables 20 and 22). Two of the units that will likely be extirpated under scenario 1 are currently small, peripheral units. Based on these results, under scenario 1 the future overall condition of the Sierra Nevada population will be strongly declining (average overall future condition score of 0.82). Therefore, the Sierra Nevada population has very low resiliency under future scenario 1.

Scenario 2

Scenario 2 considers a future where the threats continue at the current trajectory and ongoing management efforts are successful at addressing those threats. Under this scenario, climate change models under RCP 4.5 project temperature increases of 3.5–5 °F, depending on the portion of the range. Under future scenario 2, drought conditions, tree mortality events, and high-severity fire will likely continue at the current trajectory.

Currently, there are research actions in place to experimentally limit barred owl expansion within study areas, which have so far been successful and which we project will continue to be successful in limiting the barred owl's expansion under this scenario. Protections would continue to stay in place for California spotted owls on public lands, and timber harvest would remain at reduced levels on public lands. Rodenticide use would either remain the same or decrease due to continued law enforcement activity shutting down illegal marijuana grows. Under scenario 2, the current rate of human population growth will continue, leading to steadily increasing development, specifically in areas that are not on public land.

As in future scenario 1, under future scenario 2, large-scale, high-severity fire will likely impact a majority of the California spotted owl's ecological needs, with negative impacts to prey, large trees, habitat heterogeneity, and available nest trees, and there may be some increase in California spotted owl mortality. With a reduction in some of the key habitat components due to large-scale, high-severity fires, fecundity, occupancy, and population growth will likely decline under future scenario 2.

Under scenario 2, most analysis units degrade in condition, but some maintain their current condition. Overall, under scenario 2, we project the Sierra Nevada population will have four analysis units declining, five strongly declining, and two that will likely be extirpated (Service 2022, table 24). Based on these results, under scenario 2, the future condition of the Sierra Nevada population will be strongly declining, but to a lesser degree than under scenario 1. Therefore, the Sierra Nevada DPS has very low resiliency under future scenario 2.

Future Redundancy

Under future scenario 1, we anticipate the population that makes up the Sierra Nevada DPS would be less resilient compared to current condition. The California spotted owl will likely maintain a wide distribution throughout the Sierra Nevada;

however, the conditions of all analysis units within the Sierra Nevada population are declining, with over half the analysis units projected to be strongly declining or extirpated. Therefore, under scenario 1, redundancy would decline compared to the current condition, as the species would be less likely to be able to withstand catastrophic events with only one population with very low resiliency.

Under future scenario 2, the Sierra Nevada DPS would be less resilient compared to the current condition. The California spotted owl will likely maintain a majority of its current distribution throughout the Sierra Nevada. Overall, the DPS would be less likely to be able to withstand catastrophic events, with its population losing resiliency and a majority of analysis units declining or strongly declining with the potential to be extirpated under scenario 2. For species redundancy, the outcome of scenario 1 and scenario 2 are very similar after 40–50 years. There are differences in how quickly the population would decrease in condition, the likelihood of the impacts, and how many analysis units within a population may actually become extirpated. It is more likely that redundancy would be reduced, potentially from a catastrophic event, under scenario 1.

Future Representation

Predictions for future scenario 1 are that many of the habitat components identified for California spotted owls will likely have a limited ability to withstand predicted changes and are likely to further decline in condition in the future. This would indirectly cause a decrease in representation for the Sierra Nevada DPS if the current degree of diversity in habitat and climate declines. Further, with continued declines in occupancy, fecundity, and survival, population growth will decline and will likely further reduce genetic diversity. Under scenario 1, representation would decline compared to current condition as the species would have less flexibility to adapt to changing environmental conditions.

Under Scenario 2, most analysis units degrade in condition, but some maintain their current condition. Overall, under scenario 2 we project the Sierra Nevada population will have seven analysis units declining and four strongly declining (Service 2022, table 24). Based on these results, under scenario 2 the future condition of the Sierra Nevada population will be strongly declining (average overall future condition score of 1.9), but to a lesser degree than under scenario 1. An overall future condition score of 1.9 is at the very upper limit of our scoring boundary for a strongly declining population condition (Service 2022, tables 4 and 7). Therefore, the Sierra Nevada population has very low resiliency under future scenario 2, but it is closer to the boundary of low resiliency.

Table 1. Analysis Unit Current and Future Condition Comparisons (changes from current condition in bold).

Analysis Unit	Current Condition	Future Condition Scenario 1	Future Condition Scenario 2
Sierra Nevada Population			
Lassen	Declining	Strongly declining	Strongly declining
Plumas	Declining	Strongly declining	Declining
Tahoe	Stable	Declining	Declining
Eldorado	Declining	Strongly declining	Declining
Humboldt-Toiyabe	Strongly declining	Extirpated	Strongly Declining
Stanislaus	Declining	Declining	Declining
Yosemite	Stable	Declining	Declining
Sierra	Declining	Declining	Strongly declining
Sequoia-Kings Canyon	Stable	Strongly declining	Declining
Sequoia	Strongly declining	Extirpated	Strongly declining
Inyo	Strongly declining	Extirpated	Strongly declining

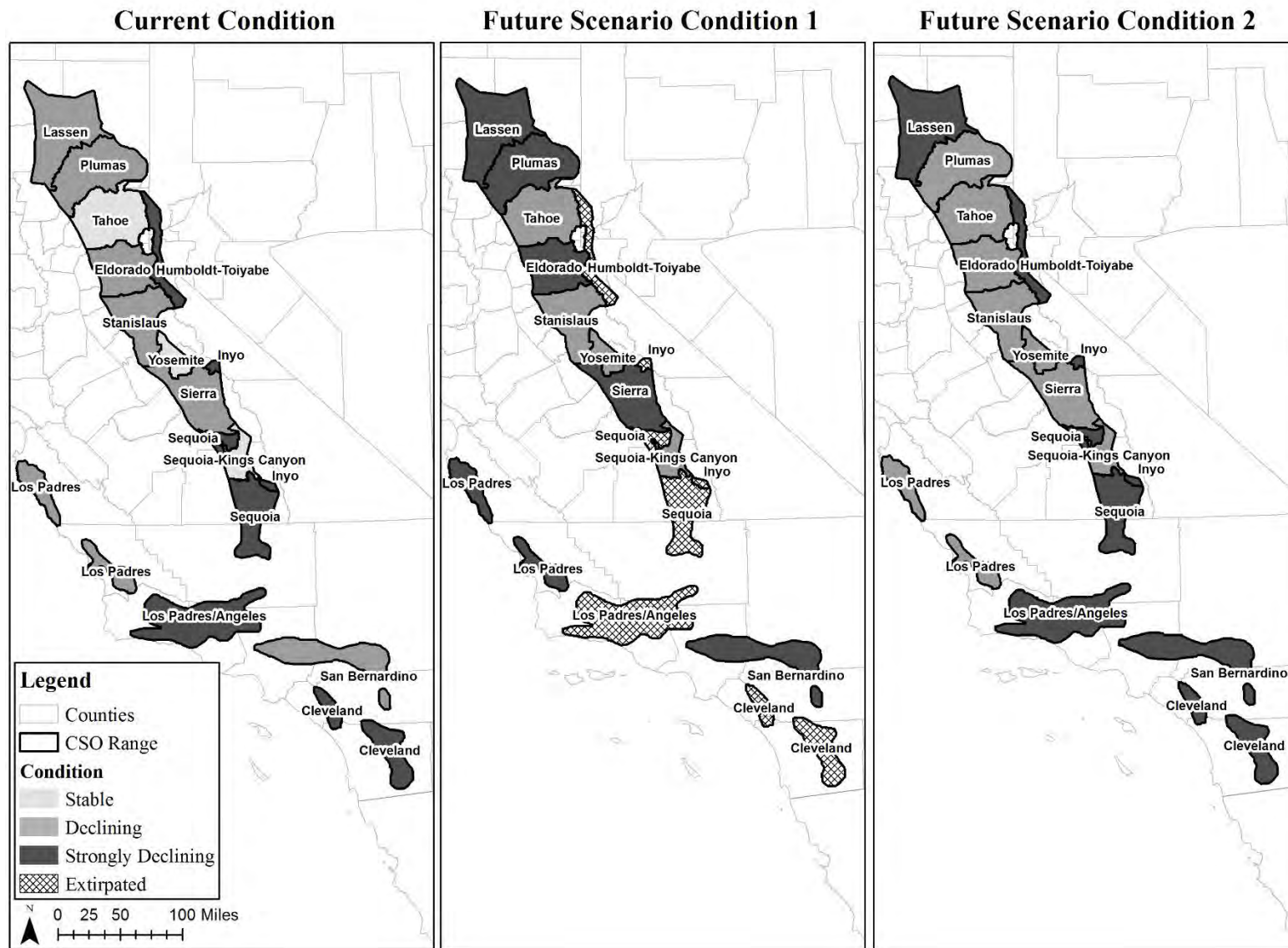


FIGURE 2—CONDITION OF CALIFORNIA SPOTTED OWL (CSO) ANALYSIS UNITS UNDER CURRENT AND FUTURE SCENARIOS.

Determination of California Spotted Owl's Status

Section 4 of the Act (16 U.S.C. 1533) and its implementing regulations (50 CFR part 424) set forth the procedures for determining whether a species meets the definition of an endangered species or a threatened species. The Act defines an “endangered species” as a species in danger of extinction throughout all or a significant portion of its range, and a “threatened species” as a species likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range. The Act requires that we determine whether a species meets the definition of an endangered species or a threatened species because of any of the following factors: (A) The present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; or (E) other natural or manmade factors affecting its continued existence.

Status of the Sierra Nevada DPS of the California Spotted Owl Throughout All of Its Range

We have carefully assessed the best scientific and commercial information available regarding the past, present, and future threats to the Sierra Nevada DPS of the California spotted owl and its habitat. In this proposed rule, we present summary evaluations of eight threats analyzed in the SSA report for the California spotted owl: wildfire (Factor A), tree mortality (Factor A), drought (Factor A), climate change (Factor A), fuels reduction and forest management (Factor A), competition and hybridization with barred owls (Factor E), rodenticides (Factor E), and development (Factor A), as well as the combined effects of those threats. We also evaluated existing regulatory mechanisms (Factor D) and ongoing conservation measures.

In the SSA, we also considered four additional threats: Overutilization due to recreational, educational, and scientific use (Factor B); disease (Factor C); predation

(Factor C); and recreation (Factor E). We concluded that, as indicated by the best available scientific and commercial information, these threats are currently having little to no impact on the California spotted owl, and thus their overall effect now and into the future is expected to be minimal. However, we consider them in this determination, because although these minor threats may have low impacts on their own, combined with impacts of other threats, they could further reduce the number of California spotted owls. For full descriptions of all threats and how they impact the species, please see the SSA report (Service 2022, pp. 25–68).

The California spotted owl needs an adequate amount of nesting, foraging, and roosting habitat to be successful, and requires the components of canopy cover, larger trees, and habitat heterogeneity. Over the last several decades, impacts from wildfire (Factor A), tree mortality (Factor A), and some forest management practices (Factor A), particularly the historical effects of clearcutting, have reduced the amount of forest with these habitat needs. Historical fire suppression has also contributed to the current increase in high-severity fire across the range of the Sierra Nevada DPS of the California spotted owl.

High-severity wildfire is one of the most significant threats currently affecting the California spotted owl and its habitat, including the Sierra Nevada DPS. The Sierra Nevada DPS occurs within a very high wildfire threat category. Approximately 47 percent of the California spotted owl's range burned between 1984 and 2021, with 15 percent burned at high severity. Most of the area burned at high severity occurred in 2020 and 2021. In the Sierra Nevada DPS specifically, over 1,000,000 ha (2,500,000 ac) burned between 1984–2019, with 317,605 ha (784,820 ac) burned at high severity (Keane in litt. 2022, p. 3). Areas burned at high fire severity can take decades to recover. Based on fire activity data from 2000 through 2014, the cumulative amount of fire burned at high severity within the next 75 years could exceed total existing habitat in the Sierra

Nevada, such that the loss of suitable habitat may exceed the rate of new habitat growing post-fire (Stephens et al. 2016, pp. 1, 11–13). Although important actions are being taken by the USFS and its partners, particularly through the recent Fire MOUs to reduce the scope and magnitude of wildfires, this magnitude of the threat of wildfire is expected to continue into the foreseeable future.

Under the current condition, 3 of the 11 Sierra Nevada analysis units are in stable condition, 5 analysis units are declining, and 3 analysis units are strongly declining. Based on recent demographic information and our habitat analysis, we found the current resiliency of the Sierra Nevada population is very low. Overall, the subspecies' current redundancy has decreased from historical condition. Although the species is currently distributed throughout its historical range within the Sierra Nevada, the condition of most analysis units is currently declining, reducing the species' ability to withstand catastrophic events. However, the subspecies maintains suitable habitat condition and retains habitat needs, particularly throughout the Sierra Nevada. Additionally, conservation efforts and regulatory mechanisms are decreasing the magnitude of effects from threats, including experimental removals of barred owls.

Effects from the threats described above are anticipated to increase into the foreseeable future, particularly drought and climate change (Factor A). Climate models project increased temperatures and more frequent drought in the Sierra Nevada DPS, with temperature increases projected to increase between 4–6 °F in the next 40 years. Climate projections also forecast snow moving to higher elevations, as well as more extreme precipitation and drought events. Overall increases in drought will increase tree mortality and the risk of high-severity fire. Invasions by barred owls (Factor E) are projected to continue into the foreseeable future and may outpace experimental removal efforts. In both our future scenarios, analysis units within the range of the Sierra Nevada DPS will be either strongly declining or extirpated due to the combined effects of all threats.

Overall, redundancy and representation would decline as conditions degrade throughout the range and population resiliency declines, reducing the species' ability to withstand catastrophic events and adapt to changing environmental conditions.

After evaluating threats to the species and assessing the cumulative effect of the threats under the Act's section 4(a)(1) factors, we find that the Sierra Nevada DPS is facing threats associated with high-severity fire, tree mortality, drought and climate change, rodenticides, and barred owls. Although it is declining in some parts of the DPS, the Sierra Nevada DPS currently retains resiliency, redundancy, and representation. Thus, it is not in danger of extinction now throughout all of its range. However, the threats of wildfire, climate change, and barred owls are anticipated to increase into the foreseeable future, and even in the more optimistic of the plausible future scenarios, habitat is still projected to severely decline, and we project that many parts of the range may become extirpated. Thus, after assessing the best available information, we conclude that the Sierra Nevada DPS is not currently in danger of extinction but is likely to become in danger of extinction within the foreseeable future throughout all of its range.

Status of the Sierra Nevada DPS of the California Spotted Owl Throughout a Significant Portion of Its Range

We evaluated the range of the Sierra Nevada DPS of the California spotted owl to determine if the DPS is in danger of extinction now in any portion of its range. The range can theoretically be divided into portions in an infinite number of ways. We focused our analysis on portions of the range that may meet the definition of an endangered species. For the Sierra Nevada DPS, we considered whether the threats or their effects on the DPS are greater in any biologically meaningful portion of the range than in other portions such that the DPS is in danger of extinction now in that portion.

The statutory difference between an endangered species and a threatened species is the timeframe in which the species becomes in danger of extinction; an endangered

species is in danger of extinction now while a threatened species is not in danger of extinction now but is likely to become so in the foreseeable future. Thus, we reviewed the best scientific and commercial data available regarding the time horizon for the threats that are driving the Sierra Nevada DPS of the California spotted owl to warrant listing as a threatened species throughout all of its range. We then considered whether these threats or their effects are occurring (or may imminently occur) in any portion of the range with sufficient magnitude such that the DPS is in danger of extinction now in that portion of its range. We examined the following threats: wildfire (Factor A); tree mortality (Factor A); drought (Factor A); climate change (Factor A); fuels reduction and forest management (Factor A); competition and hybridization with barred owls (Factor E); rodenticides (Factor E); development (Factor A); overutilization due to recreational, educational, and scientific use (Factor B); disease (Factor C); predation (Factor C); and recreation (Factor E), as well as the combined effects of those threats. We also evaluated existing regulatory mechanisms (Factor D) and ongoing conservation measures.

We found a potential difference in biological condition of the DPS in the Humboldt-Toiyabe, Inyo, and Sequoia analysis units (see figure 2, above), where our habitat analysis indicated that they are strongly declining in the current condition.

Our habitat analysis found that the Humboldt-Toiyabe unit has low amounts of suitable habitat for the California spotted owl, and 16 percent of the unit has recently burned. The Inyo unit is a small peripheral area with no recent detections, and habitat is considered degraded. The Sequoia unit has lower values for large trees and canopy cover than many other parts of the Sierra Nevada DPS, and wildfires have burned 60 percent of the unit between 1984 and 2021. We have no evidence that the magnitude of threats is higher in this portion of the range. However, the status of these units is degraded compared to the remainder of the DPS, and they may be in danger of extinction.

We next considered whether or not these three analysis units are significant to the Sierra Nevada DPS. We asked whether this portion of the range (i.e., the Humboldt-Toiyabe, Inyo, and Sequoia analysis unit portions of the Sierra Nevada DPS's range) is significant. The Service's most recent definition of "significant" within agency policy guidance has been invalidated by court order (see *Desert Survivors v. U.S. Department of the Interior*, 321 F. Supp. 3d 1011, 1070-74 (N.D. Cal. 2018)). In undertaking this analysis for the Sierra Nevada DPS, we considered whether these three units may be significant. Therefore, in light of the court decision, for the purposes of this analysis when considering whether this portion is significant, we considered whether the portion may (1) occur in a unique habitat or ecoregion for the species; (2) contain high-quality or high-value habitat relative to the remaining portions of the range, for the species' continued viability in light of the existing threats; (3) contain habitat that is essential to a specific life-history function for the species and that is not found in the other portions (for example, the principal breeding ground for the species); or (4) contain a large geographic portion of the suitable habitat relative to the remaining portions of the range for the species.

Overall, the three units make up approximately 14 percent of habitat in the DPS. There are limited owl detections in these areas, particularly in the Inyo and Humboldt-Toiyabe analysis units; thus, these areas are not contributing significantly to the resiliency of the Sierra Nevada population. The habitat in all three units is degraded. They also do not contain any unique or unusual habitat for the taxon, nor do they contain any habitat essential to any life-history functions that is not found in any other portions. Therefore, these portions do not meet the identified prongs for significance, as outlined above.

We also analyzed the five analysis units in the DPS that are currently in declining condition. In our definition of current condition, this means that these analysis units are

less likely to persist for the next 40–50 years, but are not in danger of extinction now. Limited population data are available for these analysis units. For the Lassen, Sierra, Eldorado, and portions of the Plumas unit, the most recent demography studies found that California spotted owls are declining under both occupancy and mark-recapture models (Tempel and Gutiérrez 2013, pp. 1091–1093; Tempel et al. 2014b, pp. 86, 90–92, Conner et al. 2016, p. 15). Reproductive output has varied in Lassen, Plumas, and Sierra analysis units, and has been declining in the Eldorado unit (Franklin et al. 2004, p. 24; Blakesley et al. 2010, pp. 17–19), Apparent adult survival remained high in all units with demographic data (Blakesley et al. 2010, pp. 12–19; Conner et al. 2016, p. 11). Within the Lassen, Plumas, and Sierra units, new owls (sub-adults and territorial adults) continued to be marked each year over the course of the demography studies (Conner et al. 2016, pp. 3, 7, table 1), indicating recruitment of owls into those areas through local reproduction or dispersal from other areas. Additionally, these units still maintain suitable habitat and species needs such as forest heterogeneity, tall trees, and canopy cover. These five analysis units overall retain contiguous suitable habitat, allowing for dispersal between areas. Because of this, these analysis units can recover from stochastic and catastrophic events, allowing this portion of the population as a whole to withstand threats and allowing potential dispersal or recolonization from surrounding analysis units. Thus, we conclude that these areas are not currently in danger of extinction.

Therefore, we determine that the Sierra Nevada DPS is likely to become in danger of extinction within the foreseeable future throughout all of its range. This does not conflict with the courts' holdings in *Desert Survivors v. U.S. Department of the Interior*, 321 F. Supp. 3d 1011, 1070-74 (N.D. Cal. 2018) and *Center for Biological Diversity v. Jewell*, 248 F. Supp. 3d 946, 959 (D. Ariz. 2017) because, in reaching this conclusion, we did not apply the aspects of the Final Policy on Interpretation of the Phrase “Significant Portion of Its Range” in the Endangered Species Act’s Definitions of “Endangered

Species” and “Threatened Species” (Final Policy; 79 FR 37578, July 1, 2014), including the definition of “significant,” that those court decisions held to be invalid.

Status of the Sierra Nevada DPS of the California Spotted Owl

Our review of the best available scientific and commercial information indicates that the Sierra Nevada DPS meets the Act’s definition of a threatened species. Therefore, we propose to list the Sierra Nevada DPS of the California spotted owl as a threatened species in accordance with sections 3(20) and 4(a)(1) of the Act.

Status of the Coastal-Southern California DPS of the California Spotted Owl Throughout All of Its Range

We have carefully assessed the best scientific and commercial information available regarding the past, present, and future threats to the Coastal-Southern California DPS of the California spotted owl and its habitat. In this proposed rule, we present summary evaluations of eight threats analyzed in the SSA report for the California spotted owl: wildfire (Factor A), tree mortality (Factor A), drought (Factor A), climate change (Factor A), fuels reduction and forest management (Factor A), competition and hybridization with barred owls (Factor E), rodenticides (Factor E), and development (Factor A), as well as the combined effects of those threats. We also evaluated existing regulatory mechanisms (Factor D) and ongoing conservation measures.

In the SSA, we also considered four additional threats: Overutilization due to recreational, educational, and scientific use (Factor B); disease (Factor C); predation (Factor C); and recreation (Factor E). We concluded that, as indicated by the best available scientific and commercial information, these threats are currently having little to no impact on the California spotted owl, and thus their overall effect now and into the future is expected to be minimal. As with the Sierra Nevada DPS, we now consider them in this determination, because although these minor threats may have low impacts on their own, combined with impacts of other threats, they could further reduce the number

of California spotted owls. For full descriptions of all threats and how they impact the species, please see the SSA report (Service 2022, pp. 25–68).

In the Coastal-Southern California DPS, impacts from wildfire are at very high magnitude, with all of the DPS considered to be at extreme fire risk. Our fire analysis shows that 60 percent of the range of the Coastal-Southern California DPS burned between 1984 and 2021, including 17 percent at high severity. These high-severity fires in particular are removing the California spotted owl's needs of canopy cover, large trees, and habitat heterogeneity. Given that habitat in the Coastal-Southern California DPS is already fragmented and that there is limited evidence of movement between habitat patches, any habitat burned at high severity is less likely to be able to recover from high-severity fires.

Development has further degraded naturally fragmented habitat in the Coastal-Southern California DPS, and owls in this DPS are affected by ongoing drought conditions and tree mortality. In southern California, there are high development demands with wind farms and large reservoirs impacting connectivity within the California spotted owl's range, and riparian areas used by California spotted owls are being lost to water diversion. These threats are continuing to reduce the California spotted owl's needs of high canopy cover and large trees, both of which are already at low condition. Barred owls are currently only having a limited impact on this DPS.

Limited population data are available for this part of the range, but in the San Bernardino Mountains, occupancy of territories has declined by half (Tempel et al. 2022, pp. 16, 18). Additionally, we were not able to find information about California spotted owls dispersing between mountain ranges in coastal or southern California. The number of owls in this part of the range is low. Therefore, what might be considered a stochastic event in the Sierra Nevada DPS leading to the removal of one or a few individuals from the population could have a much higher impact if it were to occur in the coastal-southern

California DPS. Additionally, due to the highly developed nature of the areas between suitable patches of habitat in coastal and particularly southern California, there is no record of owls dispersing between occupied areas. All four analysis units in this DPS are currently declining.

After evaluating threats to the species and assessing the cumulative effect of the threats under the Act's section 4(a)(1) factors, we find that threats associated with wildfire, drought, and tree mortality, as well as the current impacts of climate change, have degraded habitat in the Coastal-Southern California DPS of the California spotted owl, such that most of this part of the range could become extirpated. These threats are impacting the DPS now; thus, this DPS does not meet the Act's definition of a threatened species. Due to the extreme risk of wildfire, degraded habitat conditions, no dispersal between subpopulations, and very low population resiliency and redundancy, we find that the Coastal-Southern California DPS meets the Act's definition of an endangered species. Thus, after assessing the best available information, we determine that Coastal-Southern California DPS of the California spotted owl is in danger of extinction throughout all of its range.

Status of the Coastal-Southern California DPS of the California Spotted Owl Throughout a Significant Portion of Its Range

Under the Act and our implementing regulations, a species may warrant listing if it is in danger of extinction or likely to become so in the foreseeable future throughout all or a significant portion of its range. We have determined that the Coastal-Southern California DPS is in danger of extinction throughout all of its range and accordingly did not undertake an analysis of any significant portion of its range. Because the Coastal-Southern California DPS warrants listing as endangered throughout all of its range, our determination does not conflict with the decision in *Center for Biological Diversity v. Everson*, 435 F. Supp. 3d 69 (D.D.C. 2020) (*Everson*), which vacated the provision of the

Final Policy (79 FR 37578, July 1, 2014) providing that if the Services determine that a species is threatened throughout all of its range, the Services will not analyze whether the species is endangered in a significant portion of its range.

Status of the Coastal-Southern California DPS of the California Spotted Owl

Our review of the best available scientific and commercial information indicates that the Coastal-Southern DPS of the California spotted owl meets the Act's definition of an endangered species. Therefore, we propose to list the Coastal-Southern California DPS as an endangered species in accordance with sections 3(6) and 4(a)(1) of the Act.

Available Conservation Measures

Conservation measures provided to species listed as endangered or threatened species under the Act include recognition as a listed species, planning and implementation of recovery actions, requirements for Federal protection, and prohibitions against certain practices. Recognition through listing results in public awareness, and conservation by Federal, State, Tribal, and local agencies, private organizations, and individuals. The Act encourages cooperation with the States and other countries and calls for recovery actions to be carried out for listed species. The protection required by Federal agencies, including the Service, and the prohibitions against certain activities are discussed, in part, below.

The primary purpose of the Act is the conservation of endangered and threatened species and the ecosystems upon which they depend. The ultimate goal of such conservation efforts is the recovery of these listed species, so that they no longer need the protective measures of the Act. Section 4(f) of the Act calls for the Service to develop and implement recovery plans for the conservation of endangered and threatened species. The goal of this process is to restore listed species to a point where they are secure, self-sustaining, and functioning components of their ecosystems.

The recovery planning process begins with development of a recovery outline made available to the public soon after a final listing determination. The recovery outline guides the immediate implementation of urgent recovery actions while a recovery plan is being developed. Recovery teams (composed of species experts, Federal and State agencies, nongovernmental organizations, and stakeholders) may be established to develop and implement recovery plans. The recovery planning process involves the identification of actions that are necessary to halt and reverse the species' decline by addressing the threats to its survival and recovery. The recovery plan identifies recovery criteria for review of when a species may be ready for reclassification from endangered to threatened ("downlisting") or removal from protected status ("delisting"), and methods for monitoring recovery progress. Recovery plans also establish a framework for agencies to coordinate their recovery efforts and provide estimates of the cost of implementing recovery tasks. Revisions of the plan may be done to address continuing or new threats to the species, as new substantive information becomes available. The recovery outline, draft recovery plan, final recovery plan, and any revisions will be available on our website as they are completed (<https://www.fws.gov/program/endangered-species>), or from our Sacramento Fish and Wildlife Office (see **FOR FURTHER INFORMATION CONTACT**).

Implementation of recovery actions generally requires the participation of a broad range of partners, including other Federal agencies, States, Tribes, nongovernmental organizations, businesses, and private landowners. Examples of recovery actions include habitat restoration (e.g., restoration of native vegetation), research, captive propagation and reintroduction, and outreach and education. The recovery of many listed species cannot be accomplished solely on Federal lands because their range may occur primarily or solely on non-Federal lands. To achieve recovery of these species requires cooperative conservation efforts on private, State, and Tribal lands.

If these DPSs are listed, funding for recovery actions will be available from a variety of sources, including Federal budgets, State programs, and cost-share grants for non-Federal landowners, the academic community, and nongovernmental organizations. In addition, pursuant to section 6 of the Act, the States of California and Nevada would be eligible for Federal funds to implement management actions that promote the protection or recovery of the California spotted owl. Information on our grant programs that are available to aid species recovery can be found at:

<https://www.fws.gov/service/financial-assistance>.

Although the Sierra Nevada DPS and the Coastal-Southern California DPS of the California spotted owl are only proposed for listing under the Act at this time, please let us know if you are interested in participating in recovery efforts for these DPSs. Additionally, we invite you to submit any new information on the California spotted owl whenever it becomes available and any information you may have for recovery planning purposes (see **FOR FURTHER INFORMATION CONTACT**).

Section 7(a) of the Act requires Federal agencies to evaluate their actions with respect to any species that is proposed or listed as an endangered or threatened species and with respect to its critical habitat, if any is designated. Regulations implementing this interagency cooperation provision of the Act are codified at 50 CFR part 402. Section 7(a)(4) of the Act requires Federal agencies to confer with the Service on any action that is likely to jeopardize the continued existence of a species proposed for listing or result in destruction or adverse modification of proposed critical habitat. If a species is listed subsequently, section 7(a)(2) of the Act requires Federal agencies to ensure that activities they authorize, fund, or carry out are not likely to jeopardize the continued existence of the species or destroy or adversely modify its critical habitat. If a Federal action may affect a listed species or its critical habitat, the responsible Federal agency (action agency) must enter into consultation with the Service.

Examples of actions that may be subject to the section 7 processes are land management or other landscape-altering activities on Federal lands administered by the USFS, BLM, DOD, NPS, and the Service, as well as actions on State, Tribal, local, or private lands that require a Federal permit (such as a permit from the U.S. Army Corps of Engineers under section 404 of the Clean Water Act (33 U.S.C. 1251 et seq.) or a permit from the Service under section 10 of the Act) or that involve some other Federal action (such as funding from the Federal Highway Administration, Federal Aviation Administration, or the Federal Emergency Management Agency). Federal actions not affecting listed species or critical habitat—and actions on State, Tribal, local, or private lands that are not federally funded, authorized, or carried out by a Federal agency—do not require section 7 consultation. Examples of Federal agency actions that may require consultation for the California spotted owl could include forest and fuels management, land management planning, habitat restoration, recreation management, and road maintenance. Given the difference in triggers for conferencing and consultation, Federal agencies should coordinate with the local Service Field Office (see **FOR FURTHER INFORMATION CONTACT**, above) with any specific questions.

The Act and its implementing regulations set forth a series of general prohibitions and exceptions that apply to endangered wildlife. The prohibitions of section 9(a)(1) of the Act, codified at 50 CFR 17.21, make it illegal for any person subject to the jurisdiction of the United States to take (which includes harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect; or to attempt any of these) endangered wildlife within the United States or on the high seas. In addition, it is unlawful to import; export; deliver, receive, carry, transport, or ship in interstate or foreign commerce in the course of commercial activity; or sell or offer for sale in interstate or foreign commerce any species listed as an endangered species. It is also illegal to possess, sell, deliver, carry, transport, or ship any such wildlife that has been taken illegally. Certain exceptions apply

to employees of the Service, the National Marine Fisheries Service, other Federal land management agencies, and State conservation agencies.

We may issue permits to carry out otherwise prohibited activities involving endangered wildlife under certain circumstances. Regulations governing permits are codified at 50 CFR 17.22. With regard to endangered wildlife, a permit may be issued for the following purposes: for scientific purposes, to enhance the propagation or survival of the species, and for incidental take in connection with otherwise lawful activities. The statute also contains certain exemptions from the prohibitions, which are found in sections 9 and 10 of the Act.

It is our policy, as published in the *Federal Register* on July 1, 1994 (59 FR 34272), to identify to the maximum extent practicable at the time a species is listed those activities that would or would not constitute a violation of section 9 of the Act. The intent of this policy is to increase public awareness of the effect of a proposed listing on proposed and ongoing activities within the range of the species proposed for listing. For the Sierra Nevada DPS of the California spotted owl, which we are proposing to list as threatened, the discussion below under **II. Proposed Rule Issued Under Section 4(d) of the Act** regarding protective regulations under section 4(d) of the Act complies with our policy.

We now discuss specific activities related to the Coastal-Southern California DPS, which we are proposing to list as endangered. Based on the best available information, the following actions are unlikely to result in a violation of section 9 of the Act, if these activities are carried out in accordance with existing regulations and permit requirements; this list is not comprehensive:

(1) Any actions that may affect the Coastal-Southern California DPS of the California spotted owl that are authorized, funded, or carried out by a Federal agency,

when the action is conducted in accordance with the consultation requirements for listed species pursuant to section 7 of the Act;

(2) Any action taken for scientific research carried out under a recovery permit issued by us pursuant to section 10(a)(1)(A) of the Act;

(3) Land actions or management carried out under a habitat conservation plan approved by us pursuant to section 10(a)(1)(B) of the Act; and

(4) Recreation activities that comply with local rules and that do not result in take of listed species, including hiking and backpacking.

Based on the best available information, the following activities may potentially result in a violation of section 9 of the Act if they are not authorized in accordance with applicable law; this list is not comprehensive:

(1) Unauthorized modification of the forest landscape within the range of the Coastal-Southern California DPS; and

(2) Unauthorized use of first- and second-generation anticoagulant rodenticides within the range of the Coastal-Southern California DPS.

Questions regarding whether specific activities would constitute a violation of section 9 of the Act in regards to the Coastal-Southern California DPS of the California spotted owl should be directed to the Sacramento Fish and Wildlife Office (see **FOR FURTHER INFORMATION CONTACT**).

II. Proposed Rule Issued Under Section 4(d) of the Act

Background

Section 4(d) of the Act contains two sentences. The first sentence states that the Secretary shall issue such regulations as she deems necessary and advisable to provide for the conservation of species listed as threatened species. The U.S. Supreme Court has noted that statutory language similar to the language in section 4(d) of the Act

authorizing the Secretary to take action that she “deems necessary and advisable” affords a large degree of deference to the agency (see *Webster v. Doe*, 486 U.S. 592, 600 (1988)). Conservation is defined in the Act to mean the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to the Act are no longer necessary. Additionally, the second sentence of section 4(d) of the Act states that the Secretary may by regulation prohibit with respect to any threatened species any act prohibited under section 9(a)(1), in the case of fish or wildlife, or section 9(a)(2), in the case of plants. Thus, the combination of the two sentences of section 4(d) provides the Secretary with wide latitude of discretion to select and promulgate appropriate regulations tailored to the specific conservation needs of the threatened species. The second sentence grants particularly broad discretion to the Service when adopting one or more of the prohibitions under section 9.

The courts have recognized the extent of the Secretary’s discretion under this standard to develop rules that are appropriate for the conservation of a species. For example, courts have upheld, as a valid exercise of agency authority, rules developed under section 4(d) that included limited prohibitions against takings (see *Alsea Valley Alliance v. Lautenbacher*, 2007 WL 2344927 (D. Or. 2007); *Washington Environmental Council v. National Marine Fisheries Service*, 2002 WL 511479 (W.D. Wash. 2002)). Courts have also upheld 4(d) rules that do not address all of the threats a species faces (see *State of Louisiana v. Verity*, 853 F.2d 322 (5th Cir. 1988)). As noted in the legislative history when the Act was initially enacted, “once an animal is on the threatened list, the Secretary has an almost infinite number of options available to [her] with regard to the permitted activities for those species. [She] may, for example, permit taking, but not importation of such species, or [she] may choose to forbid both taking and

importation but allow the transportation of such species” (H.R. Rep. No. 412, 93rd Cong., 1st Sess. 1973).

The provisions of this proposed 4(d) rule would promote conservation of the Sierra Nevada DPS of the California spotted owl by encouraging management of its habitat in ways that facilitate conservation for the species. The provisions of this proposed rule are one of many tools that we would use to promote the conservation of the Sierra Nevada DPS of the California spotted owl. This proposed 4(d) rule would apply only if and when we make final the listing of the Sierra Nevada DPS of the California spotted owl as a threatened species.

As mentioned above in **Available Conservation Measures**, section 7(a)(2) of the Act requires Federal agencies, including the Service, to ensure that any action they fund, authorize, or carry out is not likely to jeopardize the continued existence of any endangered species or threatened species or result in the destruction or adverse modification of designated critical habitat of such species. In addition, section 7(a)(4) of the Act requires Federal agencies to confer with the Service on any agency action that is likely to jeopardize the continued existence of any species proposed to be listed under the Act or result in the destruction or adverse modification of proposed critical habitat.

If a Federal action may affect a listed species or its critical habitat, the responsible Federal agency (action agency) must enter into consultation with us. Examples of Federal actions that are subject to the section 7 consultation process are actions on State, Tribal, local, or private lands that require a Federal permit (such as a permit from the U.S. Army Corps of Engineers under section 404 of the Clean Water Act (33 U.S.C. 1251 et seq.) or a permit from the Service under section 10 of the Act) or that involve some other Federal action (such as funding from the Federal Highway Administration, Federal Aviation Administration, or the Federal Emergency Management Agency). Federal actions not affecting listed species or critical habitat—and actions on State, Tribal, local, or private

lands that are not federally funded, authorized, or carried out by a Federal agency—do not require section 7 consultation.

These requirements are the same for a threatened species with a species-specific 4(d) rule. For example, a Federal agency's determination that an action is "not likely to adversely affect" a threatened species will require the Service's written concurrence. Similarly, a Federal agency's determination that an action is "likely to adversely affect" a threatened species will require formal consultation and the formulation of a biological opinion.

Provisions of the Proposed 4(d) Rule

Exercising the Secretary's authority under section 4(d) of the Act, we have developed a proposed rule that is designed to address the conservation needs of the Sierra Nevada DPS of the California spotted owl. As discussed previously in **Summary of Biological Status and Threats**, we have concluded that the Sierra Nevada DPS of the California spotted owl is likely to become in danger of extinction within the foreseeable future primarily due to wildfire, tree mortality, drought, climate change, rodenticides, and barred owls. Section 4(d) requires the Secretary to issue such regulations as she deems necessary and advisable to provide for the conservation of each threatened species and authorizes the Secretary to include among those protective regulations any of the prohibitions that section 9(a)(1) of the Act prescribes for endangered species. We find that, if finalized, the protections, prohibitions, and exceptions in this proposed rule as a whole satisfy the requirement in section 4(d) of the Act to issue regulations deemed necessary and advisable to provide for the conservation of the Sierra Nevada DPS of the California spotted owl.

The protective regulations we are proposing for the Sierra Nevada DPS of the California spotted owl incorporate prohibitions from the Act's section 9(a)(1) to address the threats to the DPS. Section 9(a)(1) prohibits the following activities for endangered

wildlife: importing or exporting; take; possession and other acts with unlawfully taken specimens; delivering, receiving, carrying, transporting, or shipping in interstate or foreign commerce in the course of commercial activity; or selling or offering for sale in interstate or foreign commerce. This protective regulation includes all of these prohibitions because the Sierra Nevada DPS of the California spotted owl is at risk of extinction in the foreseeable future and putting these prohibitions in place will help to prevent further declines, preserve the DPS's remaining populations, slow its rate of decline, and decrease synergistic, negative effects from other ongoing or future threats.

In particular, this proposed 4(d) rule would provide for the conservation of the Sierra Nevada DPS of the California spotted owl by prohibiting the following activities, unless they fall within specific exceptions or are otherwise authorized or permitted: importing or exporting; take; possession and other acts with unlawfully taken specimens; delivering, receiving, carrying, transporting, or shipping in interstate or foreign commerce in the course of commercial activity; or selling or offering for sale in interstate or foreign commerce.

Under the Act, "take" means to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct. Some of these provisions have been further defined in regulations at 50 CFR 17.3. Take can result knowingly or otherwise, by direct and indirect impacts, intentionally or incidentally. Regulating take would help preserve the DPS's remaining populations, slow their rate of decline, and decrease synergistic, negative effects from other ongoing or future threats.

Therefore, we propose to prohibit take of the Sierra Nevada DPS of the California spotted owl, except for take resulting from those actions and activities specifically excepted by the 4(d) rule.

Exceptions to the prohibition on take would include all of the general exceptions to the prohibition against take of endangered wildlife, as set forth in 50 CFR 17.21 and certain other specific activities that we propose for exception, as described below.

The proposed 4(d) rule would also provide for the conservation of the species by allowing exceptions that incentivize conservation actions or that, while they may have some minimal level of take of the Sierra Nevada DPS of the California spotted owl, are not expected to rise to the level that would have a negative impact (that is, would have only de minimis impacts) on the conservation of the DPS. The proposed exceptions to these prohibitions include the following provisions (described below) that are expected to have negligible impacts to the Sierra Nevada DPS of the California spotted owl and its habitat:

(1) Forest or fuels management to reduce the risk or severity of wildfire (such as prescribed fire) where fuels management activities are essential to reduce the risk of catastrophic wildfire, and when such activities will be carried out in accordance with an established and recognized fuels or forest management plan that includes measures to minimize impacts to the California spotted owl and its habitat and results in conservation benefits to California spotted owls.

(2) Habitat management and restoration efforts that are specifically designed to provide for the conservation of the California spotted owl's habitat needs and include measures that minimize impacts to the California spotted owl and its habitat. These activities must be carried out in accordance with finalized State or Federal agency conservation plans or strategies for the California spotted owl.

(3) Management or cleanup activities that remove toxicants and other chemicals from trespass cannabis cultivation sites in California spotted owl habitat. Cleanup of these sites may involve activities that may cause localized, short-term disturbance to

California spotted owls, as well as require limited removal of some habitat structures valuable to California spotted owls (e.g., hazard trees that may be a suitable nest site).

We may, under certain circumstances, issue permits to carry out one or more otherwise-prohibited activities, including those described above. The regulations at 50 CFR 17.32 that govern permits for threatened wildlife state that the Director may issue a permit authorizing any activity otherwise prohibited with regard to threatened species. These include permits issued for the following purposes: for scientific purposes, to enhance propagation or survival, for economic hardship, for zoological exhibition, for educational purposes, for incidental taking, or for special purposes consistent with the purposes of the Act (50 CFR 17.32). The statute also contains certain exemptions from the prohibitions, which are found in sections 9 and 10 of the Act.

We recognize the special and unique relationship with our State natural resource agency partners in contributing to conservation of listed species. State agencies often possess scientific data and valuable expertise on the status and distribution of endangered, threatened, and candidate species of wildlife and plants. State agencies, because of their authorities and their close working relationships with local governments and landowners, are in a unique position to assist us in implementing all aspects of the Act. In this regard, section 6 of the Act provides that we must cooperate to the maximum extent practicable with the States in carrying out programs authorized by the Act. Therefore, any qualified employee or agent of a State conservation agency that is a party to a cooperative agreement with us in accordance with section 6(c) of the Act, who is designated by his or her agency for such purposes, would be able to conduct activities designed to conserve the Sierra Nevada DPS of the California spotted owl that may result in otherwise prohibited take without additional authorization.

Nothing in this proposed 4(d) rule would change in any way the recovery planning provisions of section 4(f) of the Act, the consultation requirements under

section 7 of the Act, or our ability to enter into partnerships for the management and protection of the Sierra Nevada DPS of the California spotted owl. However, interagency cooperation may be further streamlined through planned programmatic consultations for the DPS between us and other Federal agencies, where appropriate. We ask the public, particularly State agencies and other interested stakeholders that may be affected by the proposed 4(d) rule, to provide comments and suggestions regarding additional guidance and methods that we could provide or use, respectively, to streamline the implementation of this proposed 4(d) rule (see **Information Requested**, above).

III. Critical Habitat

Background

Critical habitat is defined in section 3 of the Act as:

(1) The specific areas within the geographical area occupied by the species, at the time it is listed in accordance with the Act, on which are found those physical or biological features

(a) Essential to the conservation of the species, and

(b) Which may require special management considerations or protection; and

(2) Specific areas outside the geographical area occupied by the species at the time it is listed, upon a determination that such areas are essential for the conservation of the species.

Our regulations at 50 CFR 424.02 define the geographical area occupied by the species as an area that may generally be delineated around species' occurrences, as determined by the Secretary (i.e., range). Such areas may include those areas used throughout all or part of the species' life cycle, even if not used on a regular basis (e.g., migratory corridors, seasonal habitats, and habitats used periodically, but not solely by vagrant individuals).

Conservation, as defined under section 3 of the Act, means to use and the use of all methods and procedures that are necessary to bring an endangered or threatened species to the point at which the measures provided pursuant to the Act are no longer necessary. Such methods and procedures include, but are not limited to, all activities associated with scientific resources management such as research, census, law enforcement, habitat acquisition and maintenance, propagation, live trapping, and transplantation, and, in the extraordinary case where population pressures within a given ecosystem cannot be otherwise relieved, may include regulated taking.

Critical habitat receives protection under section 7 of the Act through the requirement that Federal agencies ensure, in consultation with the Service, that any action they authorize, fund, or carry out is not likely to result in the destruction or adverse modification of critical habitat. The designation of critical habitat does not affect land ownership or establish a refuge, wilderness, reserve, preserve, or other conservation area. Such designation also does not allow the government or public to access private lands. Such designation does not require implementation of restoration, recovery, or enhancement measures by non-Federal landowners. Where a landowner requests Federal agency funding or authorization for an action that may affect a listed species or critical habitat, the Federal agency would be required to consult with the Service under section 7(a)(2) of the Act. However, even if the Service were to conclude that the proposed activity would likely result in destruction or adverse modification of the critical habitat, the Federal action agency and the landowner are not required to abandon the proposed activity, or to restore or recover the species; instead, they must implement “reasonable and prudent alternatives” to avoid destruction or adverse modification of critical habitat.

Under the first prong of the Act’s definition of critical habitat, areas within the geographical area occupied by the species at the time it was listed are included in a critical habitat designation if they contain physical or biological features (1) which are

essential to the conservation of the species and (2) which may require special management considerations or protection. For these areas, critical habitat designations identify, to the extent known using the best scientific data available, those physical or biological features that are essential to the conservation of the species (such as space, food, cover, and protected habitat).

Under the second prong of the Act's definition of critical habitat, we can designate critical habitat in areas outside the geographical area occupied by the species at the time it is listed, upon a determination that such areas are essential for the conservation of the species.

Section 4 of the Act requires that we designate critical habitat on the basis of the best scientific data available. Further, our Policy on Information Standards Under the Endangered Species Act (published in the *Federal Register* on July 1, 1994 (59 FR 34271)), the Information Quality Act (section 515 of the Treasury and General Government Appropriations Act for Fiscal Year 2001 (Pub. L. 106-554; H.R. 5658)), and our associated Information Quality Guidelines provide criteria, establish procedures, and provide guidance to ensure that our decisions are based on the best scientific data available. They require our biologists, to the extent consistent with the Act and with the use of the best scientific data available, to use primary and original sources of information as the basis for recommendations to designate critical habitat.

When we are determining which areas should be designated as critical habitat, our primary source of information is generally the information from the SSA report and information developed during the listing process for the species. Additional information sources may include any generalized conservation strategy, criteria, or outline that may have been developed for the species; the recovery plan for the species; articles in peer-reviewed journals; conservation plans developed by States and counties; scientific status

surveys and studies; biological assessments; other unpublished materials; or experts' opinions or personal knowledge.

Habitat is dynamic, and species may move from one area to another over time. We recognize that critical habitat designated at a particular point in time may not include all of the habitat areas that we may later determine are necessary for the recovery of the species. For these reasons, a critical habitat designation does not signal that habitat outside the designated area is unimportant or may not be needed for recovery of the species. Areas that are important to the conservation of the species, both inside and outside the critical habitat designation, will continue to be subject to: (1) Conservation actions implemented under section 7(a)(1) of the Act; (2) regulatory protections afforded by the requirement in section 7(a)(2) of the Act for Federal agencies to ensure their actions are not likely to jeopardize the continued existence of any endangered or threatened species; and (3) the prohibitions found in section 9 of the Act and the 4(d) rule. Federally funded or permitted projects affecting listed species outside their designated critical habitat areas may still result in jeopardy findings in some cases. These protections and conservation tools will continue to contribute to recovery of the species. Similarly, critical habitat designations made on the basis of the best available information at the time of designation will not control the direction and substance of future recovery plans, HCPs, or other species conservation planning efforts if new information available at the time of those planning efforts calls for a different outcome.

Prudency Determination

Section 4(a)(3) of the Act, as amended, and implementing regulations (50 CFR 424.12) require that, to the maximum extent prudent and determinable, the Secretary shall designate critical habitat at the time the species is determined to be an endangered or threatened species. Our regulations (50 CFR 424.12(a)(1)) state that the Secretary

may, but is not required to, determine that a designation would not be prudent in the following circumstances:

(i) The species is threatened by taking or other human activity and identification of critical habitat can be expected to increase the degree of such threat to the species;

(ii) The present or threatened destruction, modification, or curtailment of a species' habitat or range is not a threat to the species, or threats to the species' habitat stem solely from causes that cannot be addressed through management actions resulting from consultations under section 7(a)(2) of the Act;

(iii) Areas within the jurisdiction of the United States provide no more than negligible conservation value, if any, for a species occurring primarily outside the jurisdiction of the United States;

(iv) No areas meet the definition of critical habitat; or

(v) The Secretary otherwise determines that designation of critical habitat would not be prudent based on the best scientific data available.

As discussed earlier in this document, there is currently no imminent threat of collection or vandalism identified under Factor B for this species, and identification and mapping of critical habitat is not expected to initiate any such threat. In our SSA report and proposed listing determination for the California spotted owl, we determined that the present or threatened destruction, modification, or curtailment of habitat or range is a threat to both the Sierra Nevada DPS and the Coastal-Southern California DPS of the California spotted owl, and that those threats in some way can be addressed by section 7(a)(2) consultation measures. The two DPSs occur wholly in the jurisdiction of the United States, and we are able to identify areas that meet the definition of critical habitat. Therefore, because none of the circumstances enumerated in our regulations at 50 CFR 424.12(a)(1) have been met and because the Secretary has not identified other circumstances for which this designation of critical habitat would be not prudent, we have

determined that the designation of critical habitat is prudent for both the Sierra Nevada DPS and the Coastal-Southern California DPS of the California spotted owl.

Critical Habitat Determinability

Having determined that designation is prudent, under section 4(a)(3) of the Act we must find whether critical habitat for the California spotted owl is determinable. Our regulations at 50 CFR 424.12(a)(2) state that critical habitat is not determinable when one or both of the following situations exist:

(i) Data sufficient to perform required analyses are lacking, or

(ii) The biological needs of the species are not sufficiently well known to identify any area that meets the definition of “critical habitat.”

When critical habitat is not determinable, the Act allows the Service an additional year to publish a critical habitat designation (16 U.S.C. 1533(b)(6)(C)(ii)).

We reviewed the available information pertaining to the biological needs of the species and habitat characteristics where this species is located and data that would be needed to perform other required analyses. A careful assessment of the economic impacts that may occur due to a critical habitat designation is not yet complete, and we are in the process of working with the States and other partners in acquiring the complex information needed to perform that assessment. Because the information sufficient to perform a required analysis of the impacts of the designation is lacking, we conclude that the designation of critical habitat for both the Sierra Nevada DPS and the Coastal-Southern California DPS of the California spotted owl is not determinable at this time. The Act allows the Service an additional year to publish a critical habitat designation that is not determinable at the time of listing (16 U.S.C. 1533(b)(6)(C)(ii)).

Required Determinations

Clarity of the Rule

We are required by Executive Orders 12866 and 12988 and by the Presidential Memorandum of June 1, 1998, to write all rules in plain language. This means that each rule we publish must:

- (1) Be logically organized;
- (2) Use the active voice to address readers directly;
- (3) Use clear language rather than jargon;
- (4) Be divided into short sections and sentences; and
- (5) Use lists and tables wherever possible.

If you feel that we have not met these requirements, send us comments by one of the methods listed in **ADDRESSES**. To better help us revise the rule, your comments should be as specific as possible. For example, you should tell us the numbers of the sections or paragraphs that are unclearly written, which sections or sentences are too long, the sections where you feel lists or tables would be useful, etc.

National Environmental Policy Act (42 U.S.C. 4321 et seq.)

Regulations adopted pursuant to section 4(a) of the Act are exempt from the National Environmental Policy Act (NEPA; 42 U.S.C. 4321 et seq.) and do not require an environmental analysis under NEPA. We published a notice outlining our reasons for this determination in the *Federal Register* on October 25, 1983 (48 FR 49244). This includes listing, delisting, and reclassification rules, as well as critical habitat designations and species-specific protective regulations promulgated concurrently with a decision to list or reclassify a species as threatened. The courts have upheld this position (e.g., *Douglas County v. Babbitt*, 48 F.3d 1495 (9th Cir. 1995) (critical habitat); *Center for Biological Diversity v. U.S. Fish and Wildlife Service*, 2005 WL 2000928 (N.D. Cal. Aug. 19, 2005) (concurrent 4(d) rule)).

Government-to-Government Relationship with Tribes

In accordance with the President's memorandum of April 29, 1994 (Government-to-Government Relations with Native American Tribal Governments; 59 FR 22951), E.O. 13175 (Consultation and Coordination with Indian Tribal Governments), and the Department of the Interior's manual at 512 DM 2, we readily acknowledge our responsibility to communicate meaningfully with federally recognized Federal Tribes on a government-to-government basis. In accordance with Secretarial Order 3206 of June 5, 1997 (American Indian Tribal Rights, Federal-Tribal Trust Responsibilities, and the Endangered Species Act), we readily acknowledge our responsibilities to work directly with Tribes in developing programs for healthy ecosystems, to acknowledge that Tribal lands are not subject to the same controls as Federal public lands, to remain sensitive to Indian culture, and to make information available to Tribes. We sent letters to all affected Tribes when we began developing our 12-month finding for the California spotted owl. We will continue to work with Tribal entities during the development of a final determination on this proposal to list the Sierra Nevada DPS and the Coastal-Southern California DPS of the California spotted owl, as well as the proposed 4(d) rule for the Sierra Nevada DPS.

References Cited

A complete list of references cited in this proposed rule is available on the internet at <https://www.regulations.gov> and upon request from the Sacramento Fish and Wildlife Office (see **FOR FURTHER INFORMATION CONTACT**).

Authors

The primary authors of this proposed rule are the staff members of the Fish and Wildlife Service's Species Assessment Team and the Sacramento Fish and Wildlife Office.

List of Subjects in 50 CFR Part 17

Endangered and threatened species, Exports, Imports, Plants, Reporting and recordkeeping requirements, Transportation, Wildlife.

Proposed Regulation Promulgation

Accordingly, we propose to amend part 17, subchapter B of chapter I, title 50 of the Code of Federal Regulations, as set forth below:

PART 17—ENDANGERED AND THREATENED WILDLIFE AND PLANTS

1. The authority citation for part 17 continues to read as follows:

AUTHORITY: 16 U.S.C. 1361–1407; 1531–1544; and 4201–4245, unless otherwise noted.

2. In § 17.11, amend paragraph (h) by adding entries for “Owl, California spotted [Coastal-Southern California DPS]” and “Owl, California spotted [Sierra Nevada DPS]” to the List of Endangered and Threatened Wildlife in alphabetical order under BIRDS to read as follows:

§ 17.11 Endangered and threatened wildlife.

* * * * *

(h) * * *

Common name	Scientific name	Where listed	Status	Listing citations and applicable rules
* * * *	* * *	BIRDS		
* * * *	* * *			
Owl, California spotted [Coastal-Southern California DPS]	<i>Strix occidentalis occidentalis</i>	California (All California spotted owls in the vicinity of the Coast, Transverse, and Peninsular mountain ranges from Monterey County in the north to San Diego County in the south, and south of the Tehachapi Pass within Kern County)	E	[<i>Federal Register</i> citation when published as a final rule].

Owl, California spotted [Sierra Nevada DPS]	<i>Strix occidentalis occidentalis</i>	California and Nevada (All California spotted owls in the vicinity of the Sierra Nevada mountain range and the Sierra Nevada foothills from Shasta and Lassen Counties in the north, but north of the Tehachapi Pass, Kern County to the south, and east to Carson City, Douglas, and Washoe Counties in Nevada).	T	[<i>Federal Register</i> citation when published as a final rule]; 50 CFR 17.41(n). ^{4d}
* * * *	* * *			

3. Amend § 17.41 by adding a paragraph (n) to read as follows:

§ 17.41 Special rules—birds.

* * * *

(n) California spotted owl (*Strix occidentalis occidentalis*), Sierra Nevada DPS.

(1) *Prohibitions.* The following prohibitions that apply to endangered wildlife also apply to the Sierra Nevada distinct population segment (DPS) of the California spotted owl. Except as provided under paragraph (n)(2) of this section and §§ 17.4, 17.5, and 17.7, it is unlawful for any person subject to the jurisdiction of the United States to commit, to attempt to commit, to solicit another to commit, or cause to be committed, any of the following acts in regard to this DPS:

(i) Import or export, as set forth at § 17.21(b) for endangered wildlife.

(ii) Take, as set forth at § 17.21(c)(1) for endangered wildlife.

(iii) Possession and other acts with unlawfully taken specimens, as set forth at § 17.21(d)(1) for endangered wildlife.

(iv) Interstate or foreign commerce in the course of a commercial activity, as set forth at § 17.21(e) for endangered wildlife.

(v) Sale or offer for sale, as set forth at § 17.21(f) for endangered wildlife.

(2) *Exceptions from prohibitions.* In regard to this DPS, you may:

(i) Conduct activities as authorized by a permit under §17.32.

(ii) Take, as set forth at § 17.21(c)(2) through (4) for endangered wildlife, and (c)(6) and (7) for endangered migratory birds.

(iii) Take, as set forth at § 17.31(b).

(iv) Possess and engage in other acts with unlawfully taken wildlife, in accordance with the provisions set forth at § 17.21(d)(2) for Federal and state law enforcement officers regarding endangered wildlife, and in (d)(3) and (4) for certain persons as described therein with respect to sick, injured and/or orphaned endangered migratory birds.

(v) Take incidental to an otherwise lawful activity caused by:

(A) Forest or fuels management to reduce the risk or severity of wildfire (such as prescribed fire) where fuels management activities are essential to reduce the risk of catastrophic wildfire, and when such activities will be carried out in accordance with an established and recognized fuels or forest management plan that includes measures to minimize impacts to the California spotted owl and its habitat and results in conservation benefits to California spotted owls.

(B) Habitat management and restoration efforts that are specifically designed to provide for the conservation of the California spotted owl's habitat needs and include measures that minimize impacts to the California spotted owl and its habitat. These activities must be carried out in accordance with finalized State or Federal agency conservation plans or strategies for the California spotted owl.

(C) Management or cleanup activities that remove toxicants and other chemicals from trespass cannabis cultivation sites in California spotted owl habitat. Cleanup of these sites may involve activities that may cause localized, short-term disturbance to California spotted owls, as well as require limited removal of some habitat structures valuable to California spotted owls (e.g., hazard trees that may be a suitable nest site).

Wendi Weber,
Acting Director,
U.S. Fish and Wildlife Service.

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United States
Department of
Agriculture

Forest Service

Pacific Southwest
Research Station

General Technical
Report PSW-GTR-133



The California Spotted Owl:

A Technical Assessment of Its Current Status



Verner, Jared; McKelvey, Kevin S.; Noon, Barry R.; Gutiérrez, R. J.; Gould, Gordon I., Jr.; Beck, Thomas W., Technical Coordinators. 1992. **The California spotted owl: a technical assessment of its current status**. Gen. Tech. Rep. PSW-GTR-133. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 285 p.

This report is based on the Final Report submitted on May 8, 1992 by the Technical Assessment Team to the Interagency Steering Committee for the California Spotted Owl Assessment. The 13 chapters cover the assessment of the current status of the California spotted owl, its biology and habitat use, and forests where the subspecies occurs in the Sierra Nevada and southern California. The report suggests the direction of future inventories and research, identifies projected trends in habitat, and offers guidelines and recommendations for management of the California spotted owl.

Retrieval Terms: *Strix occidentalis occidentalis*, habitat attributes, old-growth, resource management, Sierra Nevada, southern California

Technical Coordinators:

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July 1992

The California Spotted Owl:

A Technical Assessment of Its Current Status

Technical Coordinators:

Jared Verner Kevin S. McKelvey Barry R. Noon R. J. Gutiérrez Gordon I. Gould, Jr.
Thomas W. Beck

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Preface

Maintaining viability of northern spotted owl populations in Washington, Oregon, and California, in the face of the many activities that take place in their habitats, especially logging, has challenged public land managers for nearly two decades. Policies and guidelines established by the USDA Forest Service during the late 1970s and early 1980s were challenged repeatedly, and from opposing camps. The timber industry is concerned that management of the owl's preferred habitat unnecessarily restricts commodity production, while environmental interests contend that Forest Service plans for the owl fall short of assuring long-term viability of the bird. Although the controversy has been more hotly debated over the northern spotted owl, the California spotted owl has recently taken part of the spotlight.

The Report and Its Origin

During most of the 1980s, the Forest Service implemented a conservation strategy based on retention of Spotted Owl Habitat Areas (SOHAs) capable of supporting one to three pairs of owls, separated from each other by distances ranging from 6 to 12 miles, edge-to-edge. A recent, comprehensive assessment of management for the northern spotted owl identified serious weaknesses in the SOHA strategy, however, and gave rise to a markedly different approach for conserving the owl.¹ Because the SOHA strategy is currently used to manage for the California subspecies, in June 1991 the Forest Service and various agencies of the State of California initiated a technical assessment of the current status of the California spotted owl, under auspices of an Interagency Steering Committee for the California Spotted Owl Assessment (the "Steering Committee").

The Steering Committee formed two investigative, advisory teams—the Technical Assessment Team and the Policy-Implementation Team. This report contains findings of the Technical Assessment Team, as transmitted to the Steering Committee on 8 May 1992. The Team's findings will be further evaluated by the Policy-Implementation Team, which will suggest policies and guidelines for implementing recommendations of the Technical Assessment Team. Final recommendations will then be made by the Steering Committee.

In developing this technical assessment, we have drawn information from many sources—the owl's biology, including its geographic distribution, habitat associations, life history, demography, and ecological relations; historical aspects of land management and disturbance in the Sierra Nevada and southern California; fuels management; principles of conservation biology; and risk analysis. This was consistent with our assignment,

as set forth in the charter that established the Technical Assessment Team. The charter also directed the Team to "follow accepted scientific standards and practices." Accordingly, to the extent possible, we have used the hypothetico-deductive process to guide our assessment of available information. We sought to falsify specific null hypotheses by using empirical data, computer models, widely accepted concepts and theories, and professional judgment (common sense!), rejecting hypotheses that failed these tests. This does not mean that surviving hypotheses are necessarily correct, only that they were not falsified by present information. This is the way of science. It inevitably leaves us with areas of uncertainty. How we deal with that uncertainty in the end depends, of course, on society's objectives.

The next step in following accepted scientific standards and practices was to submit a nearly final draft of our report for peer review by five other scientists not selected by the Team. This was accomplished by requesting that the Presidents of five learned societies—The American Ornithologists' Union, The Ecological Society of America, The Society of American Foresters, The Society for Conservation Biology, and The Wildlife Society—personally select one reviewer each, at their discretion. We then sent the draft document to each of these reviewers, whose critical comments and suggestions were taken into account in the revisions leading to this final report.

Although the report focuses on the California spotted owl, much more is at issue here. The owl is designated as an "indicator species" for old-growth ecosystems even though, as detailed in some of the chapters beyond, it is not restricted to just those habitats. But owl pairs use inordinately large areas in the course of their daily, seasonal, and annual activities, making the species an effective "umbrella" for a host of other species that satisfy their life requisites in the same habitats. Certainly commodity production must figure prominently when we weigh the pros and cons of maintaining viable populations of spotted owls. But prudence demands that the assessment be exhaustive and extend beyond the bottom line for the next year, or even the next decade. For the forest ecosystems we consider, our appraisal must look many decades, even centuries, into the future to be certain that decisions we make today are sustainable into the future—that they do not compromise future benefits from these ecosystems. A truly balanced assessment, therefore, "...must consider water quality, fisheries, recreation, soils, stream flows, scenic values, biological diversity, and other species of wildlife. All aspects of such a decision should be weighed in the balance. The issues are not limited to questions of owls and timber supply, as important as those are. The matter is not that simple—it never has been."¹

¹Thomas, Jack Ward; Forsman, Eric E.; Lint, Joseph B.; Meslow, E. Charles; Noon, Barry R.; Verner, Jared. 1990. *A conservation strategy for the northern spotted owl*. Washington, DC: U.S. Government Printing Office; 427 p.

Some Guidelines for Using the Report

The report consists of 13 chapters covering various aspects of the information needed for the assessment. Chapter 1 is an extended summary of Chapters 3-13, providing the bare essentials about key findings to establish the basis for our final conclusions, and presenting our recommendations. It is the essence of our assessment. Chapter 2 presents the consensus of the Technical Assessment Team's recommendations about what we think future efforts on the California spotted owl should be, and why. Readers can explore any or all of the remaining chapters, as needed or desired, for details on statements and conclusions summarized in Chapter 1. Chapter 3 presents the general background leading up to the present issue and summarizes what we know of the owl's distribution throughout California, and how the subspecies is being managed. The next seven chapters describe the owl's general biology and ecological relations, results of studies on its habitat associations, its demography and projections of population stability, and its major prey species. Finally, Chapters 11-13 consider how conifer forests in the owl's range came to be what they are today, review the fire history and current fuels problems in owl habitat, and identify projected trends in the forested habitats used by the owl. Four appendices conclude the report: Appendix A identifies the Technical Assessment Team and provides a brief chronology of Team activities leading to the report; Appendix B is a glossary of terms used in the text; Appendix C lists the common and scientific names of plant and animal species mentioned in the text; and Appendix D identifies authors of the various parts of the document.

We adopted some policies in the preparation of this report that we believe will ease the reader's task. Figures and tables are labeled by number for the chapter in which they appear, and by letter for their order in that chapter (for example, figure 4C is the third figure in Chapter 4). This procedure allows us to cross reference figures and tables from one chapter to another without confusion. In addition, a set of color photos of owl habitat taken during the Team's field trips are aggregated at the end of Chapter 5; these are identified as "colored photo 5-1," colored photo 5-2," and so on. We have substituted acronyms for several entities that are mentioned frequently in the text. Some are already familiar to most readers (for example, USDA = the United States Department of Agriculture), but in each chapter we define anew each acronym when it is first used. A list of many of the common acronyms appears after the Contents pages in this volume, for quick reference in case readers momentarily forget what one represents. All measurements are expressed in English units (for example, feet, acres, ounces) instead of metric units (meters, hectares, grams). This decision was made because English units are still used by Federal land-management agencies and by the forest industry, and because most of the general public still thinks in terms of English units, not metric units.

Acknowledgments

To complete this assessment, we have relied upon assistance, input, information, and general cooperation from literally hundreds of persons. To acknowledge each one is clearly not possible. We could not even rank them in order of the importance of their contributions. Certainly our biggest debt is to the many biologists from all the State and Federal agencies and private entities—both in management and research—who have spent countless hundreds of hours in the field, mostly at night, hooting for owls, searching for their nests, measuring nest trees and stands, locating owlets, recording data, and generally accumulating the wealth of information now available about the owl and its habitats. In particular, we thank the Forest and District Biologists from the National Forests within the range of the California spotted owl who have responded, again and again, to specific requests for information that we needed. They have met all of our requests unfailingly, pleasantly, and quickly.

Another major group of folks that worked largely behind the scenes, and essentially anonymously as far as we on the Team were concerned, were persons on the National Forests who compiled and mapped habitat information for us in electronic form. We have all learned much from this exercise, which should result in significant improvements in the way habitat information is collected, classified, and stored in the future.

Many others operated behind the scenes to implement data summaries, analyses, and syntheses, particularly at the Pacific Southwest Research Station's Redwood Sciences Laboratory in Arcata and Forestry Sciences Laboratory in Fresno. And a special thanks to folks in the California Department of Forestry's Forest and Range Resources Assessment Program, whose willing applications of their geographic information system made possible the mapping of all known California spotted owl sites and an assessment of high, medium, and low likelihoods of owls in riparian/hardwood forests in the Sierran foothills and Coast Ranges.

The administrative side of the Team's operation was made possible largely through the Regional Office of the Forest Service in San Francisco, which covered nearly all of the costs, and the Pacific Southwest Research Station in Albany, California. We were blessed by the wisdom of a couple folks in the Regional Office who saw and met a need to provide us with "scissors" to cut through the red tape that occasionally threatened to bring our progress to a temporary halt.

Technical Coordinators:

Jared Verner, Kevin S. McKelvey, Barry R. Noon,
R. J. Gutiérrez, Gordon I. Gould, Jr., Thomas W. Beck

Chapter 1

Assessment of the Current Status of the California Spotted Owl, with Recommendations for Management

Jared Verner, Kevin S. McKelvey, Barry R. Noon, R. J. Gutierrez, Gordon I. Gould, Jr., and Thomas W. Beck

Release of a proposed conservation strategy for the northern spotted owl in April of 1990 (Thomas et al. 1990) raised concern in Region 5 (R5) of the U.S. Department of Agriculture, Forest Service (FS) about the adequacy of their regional guides for managing the California spotted owl (Barker and Jay pers. comm.). This concern was amplified by a decision formally announced on 26 June 1990 by the U. S. Department of Interior, Fish and Wildlife Service (1990) to confer "threatened" status on the northern spotted owl throughout its range. Negotiations began shortly thereafter to undertake an assessment of the current status of the California subspecies. This process led to the formation of the California Spotted Owl Assessment Team Steering Committee, with members representing several State of California (Resources Agency, Board of Forestry, Department of Fish and Game, and Department of Forestry and Fire Protection) and Federal entities (U.S. Department of Agriculture, Forest Service; and U.S. Department of Interior-Bureau of Land Management, Fish and Wildlife Service, and National Park Service). Observers represented the California Farm Bureau, California State Association of Counties, California Forestry Association, National Audubon Society, Nature Conservancy, private timber companies, Sacramento Chamber of Commerce, and the Wilderness Society. The Steering Committee held its first meeting on 11 May 1991, in Sacramento, CA, and established two teams to implement the assessment--a Technical Assessment Team to be designated by the FS and a Policy-Implementation Team to be designated by State entities. The charter for the Technical Assessment Team specified submission to the Steering Committee of a report on the current status of the California spotted owl (the "CASPO Report"), following "accepted scientific standards and practices." The report would:

1. Present, analyze, and interpret relevant information currently available on the biology of the owl--its distribution, abundance, density, movements, breeding biology, diet, demography, habitat associations, and so on.
2. To the extent possible, characterize the attributes of various habitats used for foraging, roosting, and nesting by the owl throughout its range in California.
3. Evaluate current land-management practices throughout the range of the owl, recognizing that more detailed information may be available for some ownerships than for others.
4. Evaluate a range of options to achieve an amount and configuration of suitable habitat to provide for the long-term maintenance of the owl throughout its range.

5. Identify research, monitoring, and inventory programs needed to answer existing critical questions and to provide for adaptive management of the owl in the future.

The Technical Assessment Team consisted of a Core Group of six members (see Appendix A), consultants from the State and Federal entities represented on the Steering Committee, observers from the timber industry and the environmental community, and staff. This volume is the CASPO Report to the Steering Committee; this chapter synthesizes the Team's findings and presents its recommendations.

Producing the Technical Assessment

We established an agenda, schedule, objectives, and operating procedures (see chronology of Team activities in Appendix A). We spent 19 days on field trips throughout the range of the owl in the Sierra Nevada and southern California, including 5 days on private industrial timberlands. Arrangements were made for a professional photographer to accompany the Team on all field trips and to search archives for historical photos of locations that might be rephotographed now. Workshops were held to exchange information and explore concepts with agency biologists from throughout the State of California, with leading authorities in silviculture, and with some of the Nation's leading conservation biologists. Numerous other informational meetings were held with smaller groups and with more focused objectives. An extensive reference library, including most published literature and unpublished reports (from many very recent field studies of California spotted owls), was assembled and made available to the Team in its offices in Sacramento. We acquired all other relevant information currently available on the owl, its habitats, and its biology; reviewed the current-management situation; and identified the major factors leading to concern for the well-being of the California spotted owl throughout its range. The Team and staff analyzed and synthesized all information obtained from the variety of sources mentioned above. Various Team members and other specialists prepared the supporting chapters contained in this report.

Background and the Current Management Situation

As done for the northern spotted owl (Thomas et al. 1990, p. 12), we have subdivided the range of the California spotted owl into two major physiographic provinces, based on a variety of factors. These are the Sierra Nevada Province and the Southern California Province, with Tehachapi Pass as the dividing line between provinces. These regions are clearly distinct geographically; owl populations in the two provinces probably seldom exchange individuals; most owls in the Sierra Nevada Province prey mainly on northern flying squirrels, but all owls in the Southern California Province prey almost exclusively on dusky-footed woodrats (table 4A); the predominant threats to owl populations differ markedly between provinces; and feasible options for dealing with those threats also differ markedly between provinces.

The administrative history of the California spotted owl is closely tied to that of the northern spotted owl. Detailed research began in 1969, with studies on the northern subspecies, and early surveys for both subspecies of spotted owls in California were done in 1973 and 1974. Those surveys located owls at 159 sites (Chapter 3), primarily by visiting selected late-successional forests and areas with known historical sightings. Region 5 (R5) of the FS designated the spotted owl as a "Sensitive Species" on National Forests (NFs) throughout California in the late 1970s. In spite of this and increasing concern over the status of the northern spotted owl, FS surveys in the range of the California spotted owl did not begin in earnest until 1981.

Sierra Nevada Province

Primary concern for the status of the California spotted owl has been in regard to timber management on the seven westside Sierran NFs and on private industrial timberlands. The Sierra Nevada owl population is contiguous and fairly evenly distributed throughout its 400-mile length (figs. 4A and 4B) but is probably poorly linked to the southern California population. Connectivity may exist through the Tehachapi Mountains and the Liebre/Sawmill area east of Interstate Highway 5 (fig. 9A). The California spotted owl connects to the northern spotted owl in Shasta County (fig. 4A).

Standard survey and monitoring protocols have been established by the FS to locate owl sites; these protocols have been used by most other entities involved in owl inventories. An owl site is an area of unspecified dimensions where a single owl or a pair of owls has been located, usually repeatedly. In demographic and radio-tracking study areas, where efforts to locate all owls are more intense than elsewhere, most owl sites with single owls have eventually been found to have a pair. All owl sites have been mapped and given unique spatial references, so they can be tallied. Designation of an owl site makes no assumption about home-range or territory boundaries of the owls, although usually a center of activity can be identified by the location of a nest or a primary roosting area. The terms "owl site" and "site" are general and often used generically to refer to home ranges, territories, or to sites designated by agencies for special owl management (see glossary in Appendix B).

Surveys, inventories, and other field efforts produced an estimated 1,250 spotted owl sites in the Sierra Nevada during the period 1987-1991, 92 percent on public lands (table 1A). Pairs were confirmed at 697 of those sites (table 3B). Only 162 of the sites were in reserved lands [National Parks (NPs) and Wilderness Areas in NFs]. Biologists have estimated an additional 305

Table 1A—Known California spotted owl sites (1987-1991 surveys) and estimated acreages of suitable habitat, by ownership and physiographic province (see tables 3B and 3J).

Ownership	California spotted owl sites						Estimated acres of potential suitable habitat ¹	
	Sierra Nevada Province		Southern California Province		Statewide		Sierra Nevada	Southern California
	Known	Additional estimated	Known	Additional estimated	Known	Additional estimated		
Federal ownerships								
Forest Service	1,028	250	294	190	1,322	440	3,500,000	540,000
National Park Service	120	55	0	0	120	55	461,000	0
Bureau of Land Management	1	?	1	?	2	?	68,500	7,600
Subtotal of Federal	1,149	305+	295	190+	1,444	495+	4,029,500	547,600
State of California	3	?	7 ²	14 ²	10	14+	26,000	25,000 ²
Private ownerships	98	?	37	?	135	?	2,408,000 ³	? ⁴
Native American Nations	0	?	4	?	4	?	? ⁴	? ⁴
Grand total	1,250	305+	343	204+	1,593	509+	6,463,500	572,600

¹ Acreages are based on forested land currently known to be suitable habitat (dominant tree size ≥ 12 -14 inches in diameter at breast height, with ≥ 40 percent canopy cover) or land that is currently not suitable but has high timber-producing capability, providing for a relatively rapid return to suitable habitat.

² Includes some local governmental ownerships.

³ Figure is only for known forested lands in private ownership in the Sierra Nevada; an unknown amount of that is unsuitable.

⁴ The quantity of suitable habitat on private ownerships in southern California and on Native American Nations' lands has not been determined.

sites, based on unsurveyed areas in habitats considered to be suitable (tables 1A and 3B). We have assigned owl sites in the Sierra Nevada Province to one of five general habitat types, based primarily on tree-species composition:

1. *Foothill riparian/hardwood forest*--This type generally occurs at low elevations in the Sierran foothills. It includes denser stands of hardwoods immediately adjacent to streams, as well as denser stands of hardwood forests on the adjoining slopes. Tree species along streams include cottonwood, California sycamore, interior live oak, California buckeye, Oregon ash, and occasionally white alder. Tree species on the adjoining slopes include blue oak, interior live oak, and digger pine.
2. *Ponderosa pine/hardwood forest* (montane hardwood)--This habitat blends with the upper elevations of riparian/hardwood forests. In the southern Sierra Nevada, ponderosa pine at its lowest elevation generally occurs with interior live oak, canyon live oak, and black oak, with incense-cedar and white fir coming into stands at slightly higher elevations. In the northern Sierra Nevada, tanoak and Pacific madrone commonly contribute to the hardwood component of this type.
3. *Mixed-conifer forest*--This type is the predominant timber-producing forest of the Sierra Nevada, consisting of various mixtures of white fir, ponderosa pine (at lower elevations), incense-cedar, sugar pine, black oak, and red fir (at higher elevations). Douglas-fir is an important component from Yosemite NP northward, and giant sequoia occurs in widely scattered localities.
4. *Red fir forest*--This type blends with the higher zones of mixed-conifer forest. It is dominated by red fir, with increasing amounts of white fir at lower elevations until it becomes mixed-conifer forest. At upper elevations it often includes some lodgepole pine and occasionally quaking aspen.
5. *Eastside pine forest*--This type occurs generally east of the Sierran crest and is dominated by ponderosa and/or Jeffrey pine.

Most known spotted owl sites (82 percent) on Federal lands in the Sierra Nevada are in mixed-conifer forests. Indeed, about 62 percent of all California spotted owl sites on Federal lands are in Sierran mixed-conifer forests, making this by far the most significant habitat for the subspecies (table 1B).

Approximately 8.6 million acres of forested or potentially forested lands occur in the Sierra Nevada; 71 percent are on public lands. Of these lands, 6.5 million acres are either suitable or potentially suitable owl habitat, and about 4 million acres are owned by the public. Because we lack a full understanding of all attributes that comprise suitable owl habitat, however, we cannot determine the exact amount of suitable habitat for the owls on any ownership.

Forest Service

NFs of the western Sierra Nevada with major owl populations have a total land base of 6,978,900 acres; about 5,260,611 acres are forested and about half of that is current or potential habitat for spotted owls (Chapter 3). An estimated 1,028 spotted

owl sites, probably most capable of supporting a pair of owls, have been located on NFs in the Sierra Nevada (table 1A). About 80 percent of those are in the zone of mixed-conifer forests, about 10 percent in red fir forests, and about 7 percent in ponderosa pine/hardwood habitats. The remaining 3 percent are in eastside pine forests and foothill riparian/hardwood habitats in the western Sierran foothills (table 1B).

In July 1981, the Regional Office of R5 notified Forests with the California spotted owl to provide in their Land Management Plans (LMPs) a strategy for maintaining viability of the owls. This led to the designation of Spotted Owl Habitat Areas (SOHAs) in a "network" on each of the westside Sierra Nevada NFs with owl populations and major timber-management programs. The network concept was patterned after a similar approach adopted by the FS in Washington and Oregon to manage for northern spotted owls. SOHAs are designated stands of habitat to be managed to maintain suitable owl habitat. They may occur singly, in pairs, or in triplets. If single, they may be no more than 6 miles from at least two other SOHAs, edge-to-edge; if pairs or triplets, they may be up to 12 miles from other SOHAs. Management direction for SOHAs is to maintain at least 1,000 acres of suitable owl habitat within a 1.5-mile radius of the known or potential nest site. Suitable habitat is described as mature timber stands having (1) multi-storied canopies with 70 percent or greater total cover, (2) 40 percent or more of the total canopy in trees at least 21 inches in diameter at breast height (d.b.h.), and (3) extensive decadence-cavities, broken tops, snags, and so on (Chapter 3).

Directions for Sierran Forests resulted in the designation of 264 SOHAs in approved or draft Forest LMPs (Lassen 40; Plumas 54, Tahoe 33, Eldorado 32, Stanislaus 36, Sierra 29, and Sequoia 40). Of this number, 249 are on lands suitable and

Table 1B- Distribution by major habitat types of known California spotted owl sites, based on 1987-1991 surveys in National Forests and National Parks (see tables 3A and 3I)¹

Forest type	Known sites	Percent of province	Percent of total
Sierra Nevada Province			
Mixed-conifer	959	81.5	62.4
Red fir	114	9.7	7.4
Ponderosa pine/hardwood	79	6.7	5.1
Foothill riparian/hardwood	19	1.6	1.2
Eastside pine	6	0.5	0.4
Subtotal	1,177	100.0	76.6
Southern California Province			
Live oak/bigcone Douglas-fir	147	40.8	9.6
Riparian/hardwood	116	32.2	7.6
Mixed-conifer	95	26.4	6.2
Redwood/California-laurel	2	0.6	0.1
Subtotal	360	100.0	23.4
Grand total	1,537		100.0

¹ Subtotals and totals do not match those in table 1A because values given here were based only on numbers supplied by National Forests and National Parks. The figures occasionally include habitat descriptions from sites on private lands within NF boundaries and from single owl locations. We believe the percentages shown here correctly display the relative proportions of owl sites in these habitat types.

otherwise available for timber management. The total allocation for the 264 SOHAs is about 454,000 acres, of which about 110,000 acres would be managed under low-yield, even- or uneven-aged management (Chapter 3).

Other Public Ownerships

Lassen, Yosemite, Kings Canyon, and Sequoia NPs occur within the range of the California spotted owl in the Sierra Nevada. These have a total land base of 1,719,039 acres, but only about 28 percent of that is judged to be suitable owl habitat, and only 120 owl sites are known to occur in the four NPs combined (table 1A). Even though the NPs experience high recreation impacts in local areas, NP management has not been an issue, because the emphasis in the Parks generally is believed to be compatible with habitat needs of the owls.

The Bureau of Land Management (BLM) administers scattered public lands along the foothills and lower slopes of the Sierra Nevada and southern Cascades, some with forests, woodlands, and riparian habitats that are potentially suitable for California spotted owls. About 68,500 acres of BLM lands are potential for spotted owls (table 1A). Although owls have been observed at a few sites on BLM lands, a general lack of inventory precludes an estimate of the total number.

Seven State Parks (SPs) total an estimated 16,580 acres in the Sierra Nevada, with perhaps as many as six sites suitable for owls. Because all wildlife and plants are protected in SPs, habitat for any owls there is probably secure. Two State Forests (SFs) in the Sierra Nevada, totaling 13,830 acres, are managed for demonstration of forestry practices and to support cooperative research with other agencies. Uneven-aged silviculture is featured on these lands, which may have three or four pairs of owls. In addition, the University of California administers the 3,000-acre Blodgett Forest in El Dorado County and the 320-acre Whittaker Forest in Tulare County. About 2,000 acres at Blodgett are suitable owl habitat and typically one or two pairs nest in the area (Chapter 3).

Private Lands

Industrial timberlands total 1,451,000 acres and miscellaneous private timberlands total 957,000 acres in the Sierra Nevada (table 3D). The latter group includes both large landowners, such as utilities and water districts, and small landowners. About 58 percent of the combined total of these private lands are surrounded by NF lands, much in the form of alternating sections of private and public lands in "checkerboard" pattern, especially in the Tahoe and Eldorado NFs. Significant additional parcels of private timberlands, not in checkerboard arrangement, are included within boundaries of the Lassen, Plumas, and Stanislaus NFs. Most of the best forest-growing lands in the Sierra Nevada are owned by commercial timber companies in the mixed-conifer zone. The majority of the private land has not been inventoried for owls yet, but it is apparent that some industry lands with a long history of logging have spotted owls comparable in density to adjacent NF lands. Other private lands lack nesting owls, however, even though nest sites occur in adjoining NF lands (Chapter 5). Decisions are still pending on

possible enactment of forestry reform legislation to provide new rules for logging on private lands in California. Although we cannot now assess the effects of any new forestry regulations on the capability of private lands to support spotted owls, we believe that any new regulations would be more beneficial for owls than past policies.

At the north end of the Sierra Nevada, private timberlands along the east side of Shasta County provide an essential habitat linkage for movement back and forth by both northern and California spotted owls, between the Lassen and Shasta-Trinity NFs. Maintenance of this connection is believed to be essential to the long-term conservation of both subspecies of spotted owls (Dawson et al. 1987, Thomas et al. 1990).

Spotted owls breed in dense stands of hardwoods along stream channels at low elevations on the western edge of the Sierra and Sequoia NFs. These habitats, generally not classified as commercial timberlands, are similar in most respects to habitats commonly used by spotted owls in southern California. Similar habitats occur along riparian zones west of the boundaries of all NFs in the Sierra Nevada. Livestock grazing, type conversions, firewood cutting, and logging in and adjacent to riparian zones have affected these habitats. Many are now being affected by an increasing trend of residential developments in the foothills. These potential habitats have not been adequately surveyed for spotted owls, although they may support many pairs (see fig. 4D).

Areas of Concern

Our over-riding concerns for spotted owls in the Sierra Nevada conifer zone involve potential impacts of logging practices on their habitat (details in Chapter 13) and the extent to which selective logging and aggressive fire suppression in this century have created incendiary conditions in a majority of the low- to mid-elevation conifer forests (details in Chapters 11 and 12). In addition, we have identified several conditions that will bear further study and evaluation (table 3G, fig. 3A). These involve bottlenecks in the distribution of habitat or owl populations, gaps in the known distribution of owls, locally isolated populations, fragmented habitats, and areas with low densities of owls.

Concerns for spotted owls in foothill riparian/hardwood forests in the western Sierra Nevada primarily involve increasing development of residential properties. This is the case for dispersed, rural homesites and growth of existing communities in the foothills. Both potentially impact spotted owls directly by reducing the amount of owl habitat and by bringing dogs and cats into potential contact with fledgling owls that may spend some period of time on the ground before they are capable fliers. These developments would also affect the owls indirectly by reducing the area suitable for woodrats. Grazing in the foothills may also impact owls by influencing shrub cover needed by woodrats. We cannot evaluate possible effects on owls that may result from the increasing need for surface and ground water to provide for residential developments in the foothills. None of these potential impacts has been studied.

Southern California Province

Spotted owls occur in all major mountainous areas of southern California, but they are not continuously distributed like those in the Sierra Nevada. Instead, we believe that each major mountain range has a relatively isolated subpopulation of birds that is separated from its nearest neighboring subpopulation by distances ranging from 6 to 45 miles (fig. 9A, table 9A). Inventories in these mountains since 1987 have produced a total count of 343 known owl sites; 295 of these are on Federal lands (table 1A). Estimates by biologists of additional sites in southern California range from 155 to 254 (table 3J); taking the midpoint of these gives an estimate of 204 additional sites or an estimated total of 547 spotted owl sites in southern California. This is not out of line with an independent estimate of 578 (known + potential) owl sites in southern California by Stephenson (1991). We have assigned owl sites in southern California to one of four general habitat types, based primarily on tree-species composition:

1. *Riparian/hardwood forest*-This type varies considerably in different parts of southern California. In deep canyons in the Los Padres NF, for example, it occurs in narrow strips adjacent to permanent or near-permanent streams. Common tree species include coast live oak (near coast), canyon live oak (interior locations), California sycamore, white alder, California-laurel, and cottonwood. In shallower canyons in the Cleveland NF, these forests may consist almost exclusively of coast live oak.
2. *Live oak/bigcone Douglas-fir forest*-This habitat occurs in a narrow band mostly at mid-elevations in mountains of all four NFs in southern California. Dominant tree species are canyon live oak, coast live oak, and bigcone Douglas-fir.
3. *Mixed-conifer forest*-This type is best developed at relatively high elevations in the San Gabriel and San Bernardino Mountains, and on Mount San Jacinto. Species composition is similar to that of Sierran mixed-conifer, although Coulter pine occurs and bigcone Douglas-fir occasionally occurs at lower elevations. Red fir, Douglas-fir, and giant sequoia are missing.
4. *Redwood/California-laurel forest*-These forests are restricted to the coast range, where coast redwood, California-laurel, tanoak, Pacific madrone, red and white alder, coast live oak, Santa Lucia fir, and bigleaf maple form various mixtures.

About 41 percent of the owl sites in southern California are in live oak/bigcone Douglas-fir forests, 32 percent are in riparian/hardwood forests, and 26 percent are in mixed-conifer forests, mainly in the San Bernardino Mountains (table 1B). Southern California has an estimated potential of about 573,000 acres of suitable owl habitat (table 1A), but we still cannot characterize the full range of conditions that comprise suitable habitats there.

Federal and State Lands

Regional direction for the four NFs in southern California is to protect all known spotted owl sites and to manage the habitat based on local information about suitability and availability. One owl site is known on BLM lands, where only about 7,600 acres of potential owl habitat occur; habitats are managed for wildlife, riparian habitat quality, water quality, and dispersed recreation. Camp Pendleton probably had spotted owls in the past, but long-term effects of military training activities have degraded habitat to an extent that little exists today. State Parks have several thousand acres of potential owl habitat, perhaps enough for 13-15 pairs.

Other Lands

Over the past 5 years, 41 owl sites have been found on private and Native American Nation lands in southern California (table 1A). Most private lands are at lower elevations than "traditional" spotted owl habitat.

Areas of Concern

Several significant factors threaten the long-term maintenance of spotted owl populations in these relatively isolated mountain ranges in southern California. Probably of most concern is the likelihood of a decline in the capability of landscapes between the mountains to support owls that would otherwise disperse from one subpopulation to another. Only in this way can the decline in one subpopulation be offset naturally by immigration from other subpopulations (so-called demographic "rescue effects"). As urban and residential areas expand in the valleys between mountains, the suitability of dispersal habitat may decline to the point that successful dispersal is too restricted for demographic rescue. Subpopulations must then survive demographically on their own or decline to extinction (Chapters 8 and 9). We are similarly concerned about what appears to be a tenuous linkage between owls in the southern Sierra Nevada and owls in the Transverse Ranges (see fig. 9A).

In addition to maintaining connectivity, the integrity of each habitat "island" must be maintained. An additional concern, therefore, is a decline in the amount, or an increase in fragmentation, of currently suitable habitat within any of the many isolated mountain ranges.

Direct surface-water diversions and "mining" of ground water for human needs deplete water in permanent or near-permanent streams, threatening the associated riparian woodlands. Loss of the woodlands would mean the loss of spotted owls and numerous other riparian species found in these habitats. Stand-destroying fires, and increasing concentration of recreational activities in prime owl habitat are additional threats to spotted owls in southern California. Maintenance of a viable population of spotted owls in southern California may be impossible without changes in land-use policies on private lands, especially those that adjoin public lands.

Assessing the Owl's Status: The Sierra Nevada

Determining the owl's status depends on answers to three fundamental questions: (1) Is the California spotted owl's population declining in all or part of its range? (2) Is the California spotted owl a habitat specialist? (3) If the answer to question 2 is yes, then is the habitat upon which the California spotted owl specializes declining? We have endeavored to answer these questions by attempting to falsify the implied null hypotheses:

H_0 : California spotted owl populations in demographic study areas are not declining.

H_0 : California spotted owls use all habitats in proportion to their availability.

H_0 : Habitats used in excess of availability by California spotted owls are not declining in abundance.

All sources of information available to us have been important in this effort, including common sense, professional judgment, empirical data, widely accepted concepts and theories, and mathematical modeling.

Failure to falsify a null hypothesis does not necessarily mean that it is true. When data are insufficient to provide a powerful test of the hypothesis, we are likely not to falsify the hypothesis even when it is false. This is known to statisticians as a type-II error. In all cases where it was possible, we have estimated the power of tests that failed to reject a null hypothesis. This information is critical to the conclusions and recommendations we have made in this report.

Is the Owl's Population Declining in All or Part of Its Range?

Demographic studies of California spotted owls are currently underway in five locations-Lassen NF (2 years), Eldorado NF (6 years), Sierra NF (2 years), Sequoia/Kings Canyon NPs (4 years), and San Bernardino NF (5 years). Owls are captured and color-banded with unique band combinations that can be identified in the field without recapturing the birds. In this way, a history of each color-banded bird can be accumulated for as long as it remains in the study area. Sex is determined by voice, and age (up to 2 years) can be determined by plumage characteristics. Critical parameters needed to determine whether a population is stable, increasing, or decreasing are stage-specific birth rates and death rates. The parameter we need to estimate is lambda (λ), the finite rate of population growth ($\lambda = 1.0$ indicates a stable population; $\lambda > 1.0$ indicates an increasing population; and $\lambda < 1.0$ indicates a declining population). Lambda is computed from estimates of three classes of parameters: age at first reproduction, age-specific survival rates, and age-specific fecundity (for simplicity in modeling population trends, we use a females-only model, so fecundity is defined here as the expected

number of female fledglings produced per female of age x per year). In the Lefkovitch stage-projection matrix model (Lefkovitch 1965) used for this assessment, the value of lambda indicates the annual rate of change in the size of a population.

Results

Owl banding has been underway long enough to compute estimates of lambda for only three study areas-Eldorado NF, Sequoia/Kings Canyon NPs, and San Bernardino NF. We could estimate juvenile survival rate only for the San Bernardino study area, because data were insufficient for the Eldorado and Sequoia areas. Consequently, the San Bernardino value was used as a reasonable approximation for the other two locations. It was in line with estimates of juvenile survival rates from studies of northern spotted owls (Chapter 8), and lambda was not especially sensitive to variations in juvenile survival rate (figs. 8C and 8D). Results from the Eldorado and Sequoia/Kings Canyon studies follow; results from the San Bernardino are deferred to the section dealing with southern California.

Eldorado Study Area-The estimate of lambda for the Eldorado population was 0.947, suggesting about a 5 percent annual rate of population decline during the period of study (1986-91). This value was not significantly <1.0 ($\alpha = 0.05$, $P = 0.1271$), however, so we cannot reject the null hypothesis that the population is not declining. The test, however, had a power of only 0.30. Even if the population were truly declining at 5 percent per year, we would fail to detect that decline 70 times in every 100 studies of equivalent size. The low power resulted from a relatively small number of marked birds, and the large standard errors of parameter estimates (table 8E). The correct inference to draw from this result is that we are uncertain about the true trend of this population. The power of the test is much too low to infer that the population is stable.

Sequoia/Kings Canyon Study Area-The estimate of lambda for this population was 0.969 (table 8F), suggesting about a 3 percent annual rate of population decline during the period of the study (1988-91). As in the Eldorado study, the statistical test ($\alpha = 0.05$, $P = 0.2709$) failed to reject the null hypothesis of no decline in the population. The power of this test-0.30-was identical to that for the Eldorado study, so we must infer again that we are uncertain about the trend of this population.

Is the California Spotted Owl a Habitat Specialist?

Results from Landscape Studies

This question was explored in several ways and at three scales, with details given in Chapters 5 and 6. We know, for example, that California spotted owls use forested habitats almost exclusively, although they occur and breed in a greater variety of habitats than does the northern spotted owl. Within forested landscapes, we found that 45 percent of all nests of California spotted owls in the conifer zone of the Sierra Nevada were in M4N and M4G stands, significantly more than expected based on availability (table 5A) [table 1C explains codes designating timber strata, or see "timber strata" in the glossary (Ap-

pendix B)). All other habitat types that we evaluated were used less than or equal to their availability (table 5A). These results indicated that, for nesting, the owls selected stands with relatively large trees and closed canopies.

Densities of owl sites in 1:24,000 U.S. Geological Survey quadrangles were significantly related to the percentage of forests having medium-sized and larger trees and high canopy closure. These results generally corroborated those of the previous analysis.

Results from Home-Range Studies

At a home-range scale, attributes in nest stands were compared with those in randomly selected stands in the general forest matrix. Significant differences were found for several attributes, most or all of which were consistent with the previous conclusion that the owls tended to select stands of large, old trees with closed canopies for nesting. Results of identical analyses in roost stands produced parallel results. Nest and roost stands showed consistent, often significant differences from random locations in the forest in having higher canopy cover, greater snag basal area, greater total basal area of live trees, and greater softwood basal area (tables 5B and 5D). Mean values for canopy cover ranged from about 75 to 96 percent in the different studies; similarly these studies suggested a range for total basal area of live trees from 185 to 350 square feet per acre, and basal area of large snags (>15 inches in d.b.h. and >20 feet tall) from 19 to 31 square feet per acre in nest and roost stands ("Recommendations" in Chapter 5). Many of these parameters varied considerably, and not all measures of habitat used by spotted owls and at random locations differed significantly within a given study. The data were, however, consistent and mutually supportive among all studies. California spotted owls in these various studies chose to nest and roost in stands that were denser than average and that contained a large-tree component. Most nest sites were selected in dense mixed-conifer stands with average quadratic mean diameters of canopy trees >24 inches in d.b.h. We know of no studies that consistently contradicted these findings.

Table 1C-- Explanation of codes used to designate timber strata in the Sierra Nevada.

Attribute	Code used	Identification	
Timber type	M	Mixed-conifer	
	P	Ponderosa pine	
	R	Red fir	
Tree size-class ¹	2	<12 inches	
	3	12-23.9 inches	
	4	>24 inches ²	
Canopy closure	P	Poor	0-39 percent
	N	Normal	40-69 percent
	G	Good	>70 percent

¹ Mean diameter at breast height of dominant trees.

² Code 5 has been used to designate larger size-classes, and code 6 has been used to designate multi-layered stands; most National Forests in the Sierra Nevada no longer make these distinctions in their timber inventories.

Results of similar analyses at foraging locations indicated that the owls foraged in stands characteristic of nest and roost sites, as well as in a wide variety of other habitats having lower canopy cover and a greater range of tree sizes and ages. Nonetheless, in comparison with random locations within the forest, owls tended to forage in sites with higher canopy closure; greater basal areas of live trees combined and of softwoods; greater basal areas of snags; and more dead-and-downed wood (tables 5G and 5H). In general, they foraged in forests of intermediate to old age, typically with >40 percent canopy closure.

Results from Studies at Nest Locations

Data from 276 nests located throughout the range of the California spotted owl provided the most conclusive evidence of selection by the owls of very large, old trees. In Sierran conifer forests, for example, nest trees averaged about 96 feet in height and 45 inches in d.b.h., with a surrounding canopy cover of about 75 percent (table 5K). A prevalence in these forests of cavity nests (66 percent) and nests on broken-topped trees (10 percent) showed that most nest trees were not only large but also old and decadent. For example, many of the natural cavities used for nests were created when decay invaded a wound on the side of the tree where a branch tore out of the trunk. These cavities must have room to accommodate an owl's nest, the female, and her (usually) two nestlings, so only very large trees have branches and trunks of sufficient size to produce such cavities. Not only were the diameters of nest trees significantly larger than the average tree in today's conifer forest (fig. 5K), but also they exceeded the mean diameter of trees in plots sampled in the Sierra Nevada at the turn of this century. The owls are apparently nesting today in a legacy of very large, old trees that were present in 1900 and before.

Results from Radio-Tracking Studies

Radio-tracking studies of California spotted owls in the Lassen NF and the Sierra NF provide some insights into habitat selection in conifer forests of the Sierra Nevada. Studies of this nature have shortcomings that can lower our ability to draw inferences from them, however. First is the need for a large number of owl locations during a brief period of the year (for example, the breeding period or the winter period). But to meet assumptions of independence in the locations, required by statistical tests, locations should be recorded only about every 2-3 days. In the 6-month period that approximates the breeding cycle of the spotted owl, only about 72 locations could be obtained without violating assumptions of independence. Second is the fact that a small sample size results in low power of the tests to detect habitat selection. A mean of 57 locations was available for the radio-tagged spotted owls reported in the home-range studies (Chapter 6) upon which the following summary is based. The power of statistical tests ranged from about 15 to 80 percent, so failure to detect significant overuse or underuse of habitats, based on availability, probably resulted from low power in many cases. This means that any consistent pattern in habitat selection among birds with samples large enough for tests with ample power should be given additional

weight when evaluating the suitability of habitats for spotted owls from studies of radio-tagged birds.

Habitat selection was more consistent and more pronounced for canopy closure than for tree size-class among radio-tagged California spotted owls in the Sierra Nevada. Chi-square values were consistently higher for canopy closure, and more owls had significant tests of habitat use for canopy closure than for tree size-class in 18 site-by-season comparisons. Differences between total and dominant canopy closure were minor (Chapter 6). Because more owls showed selection for cover of the dominant trees in a stand, however, it appears to be a better measure of habitat quality for California spotted owls than total canopy cover.

The amount of medium and large sawtimber in individual home ranges did not appear to be a good indicator of the amount of habitat needed to sustain the owls, unlike the case for the northern spotted owl (Chapter 6). Most owls did not have significant tests of habitat use for tree size-class. Nearly all owls in the Sierra NF used size-classes in proportion to their availability; patterns were stronger in the Lassen NF during the breeding season, where about half of the birds used medium and large sawtimber greater than expected.

Based on overall use by radio-tagged owls of habitats with ≥ 40 percent canopy cover and those with ≤ 39 percent canopy cover, stands with ≥ 40 percent canopy cover should generally be considered suitable owl habitat. Stands with ≤ 39 percent canopy cover should generally be considered unsuitable (Chapter 6). The data show that owls exhibited lower selectivity for habitats when foraging than they did when roosting (Chapters 5 and 6).

Results from Studies in Foothill Riparian/Hardwood Forest

Results of habitat studies and home-range use by owls in lower-elevation, riparian/hardwood forests and adjacent stands of oak-pine woodlands in foothills of the Sierra Nevada generally agree with those in conifer forests. The birds nest and roost in stands with mean canopy cover of about 89 percent and in trees generally large for those habitats (mean d.b.h. = 29.5 inches, table 5K).

Is the Habitat Used Selectively by the California Spotted Owl Declining?

Having concluded that California spotted owls are not habitat generalists, particularly for nest stands, we next must determine whether any evidence indicates a decline in the amount of habitat used more than expected by the owl. Forests of the Sierra Nevada have been markedly impacted in a variety of ways by human intervention, especially during the past 150 years (Chapter 11). The first major perturbation was grazing by millions of sheep from about 1860 to the first decade or so of this century; peak numbers occurred in the early 1870s. Coincident with sheep grazing was extensive early logging, mainly at low elevations near towns, mines, and along transportation routes. Timber production in billions of board feet reached a peak about 1950, dropping some from that level but remaining relatively

high in most years since. Fire suppression began in the early part of this century and has become increasingly effective and aggressive since.

With removal of sheep and some measure of fire control in place, forest stands became subject to ingrowth of shade-tolerant conifers such as white fir and incense-cedar (Chapter 11). A combination of logging and natural attrition of the old forest led to a decline in the number of large, old trees. Past logging activities that concentrated on removal of the largest, most valuable trees broke up the patchy mosaic of the natural forest, further encouraging the development of dense conifer regeneration. These developments, especially in the ponderosa pine and mixed-conifer forests of the Sierra Nevada, reduced large-diameter trees in many areas to small remnant populations. Concurrently, surface fuels have been accumulating in forest stands and the extensive ingrowth of shade tolerant trees has resulted in vertical fuel ladders that essentially connect the surface fuels to the dominant tree crowns over much of the Sierra Nevada. These changes have not occurred to the same degree in the red fir type, where fires were less frequent historically, and logging was generally uncommon until recent decades.

Because of current stand structures and excessive fuel loadings in much of the Sierran mixed-conifer type, fires that escape initial suppression efforts—usually those occurring during extreme weather conditions—tend to become large and severe. Fire trends in the Sierra Nevada can be expected to continue along their current trajectories. As the human population increases in Sierran forests and woodlands, the presence of so many houses within the forest will shift further the emphasis of suppression from one of saving forests to one of saving property. The fuels will also continue to accumulate, with the recent drought-induced bark beetle infestations contributing a major pulse of new fuels over the next few decades. We expect the net result to be a much higher incidence of stand-destroying fires in the future than was characteristic of the Sierran fire regime prior to this century. And with those fires we will continue to lose remnant, individual old trees, stands of old trees, and other old-growth attributes.

Timber cutting trends also point to a continuing decline in the number of old trees and remnant old-growth stands. Sixty-five percent of the forested acres on all Sierran NFs are classified as suitable for timber production (Chapter 13). If we discount forested acres that cannot produce timber commercially because they are too poor in quality, they cannot be successfully regenerated, or they have unstable soils, 74 percent of the lands that can potentially produce timber will be harvested in some manner (table 13A). Seventy-two percent of the timber volume removed from these lands will be taken through even-aged systems—mostly clearcuts. Of the 528,474 acres of suitable timberlands on the Tahoe NF, for example, 68 percent will be managed for even-aged silviculture (24 percent long rotation, 44 percent short rotation) (Chapter 13). On the Plumas NF, 52,000 acres are scheduled for even-aged cutting per decade, with 8,000 acres in selection cutting methods.

Clearcut, seed-tree, and shelterwood cutting techniques all have the same goal: produce even-aged stands. In this regard,

seed-tree and shelterwood systems can generally be thought of as two-stage (sometimes three-stage) clearcuts. In all of these cutting systems, the original stand will be totally removed before the new stand is scheduled to be cut. In terms of owl biology, the primary impact of traditional, even-aged harvesting practices lies in the creation of simple stand structures and, probably more importantly, the removal of all large trees from vast areas of the forest. Even if prescriptions are modified so that snags and live culls are left at the first cutting, no provision is made for a predictable recruitment of replacement trees for these relics when they fall. This, in turn, will lead to a loss of large-diameter downed woody material important for production of the fungi that are a primary food source for flying squirrels—the main prey of spotted owls in the Sierra Nevada (Chapter 4). Log slash can create much small-diameter woody debris, but it cannot replace the large logs. In an even-aged system, these old-growth features can be created only by an extreme extension of the rotation interval. Even if the rotation is extended to 150 years, for instance, no trees will match the average age of the forest at the beginning of this century (Chapter 11). Decadent features in stands are functions of age, not just d.b.h. (fig. 13G); and any animals that depend on decadent features (cavities, broken-tops, snags), or the large woody debris that they create, will simply drop out of these forests (see Chapters 4, 5, and 10 for examples specific to the spotted owl and its prey species). The rate of conversion to even-aged systems in the western Sierra Nevada is estimated by the LMPs to be 229,000 acres per decade.

Even on lands planned for selection harvest (about 80,000 acres/decade), we have no guarantee that harvest prescriptions will leave any of the large, old trees. Ideally, stands managed for individual selection are harvested in a manner that brings the diameter distribution in the stand into conformity with an idealized distribution, which is characterized by a declining exponential function (in forestry referred to as an inverse "J"). The number of large trees in the stand is dictated by the slope of this curve and the designated diameter of the largest tree. In selection-logging systems, timber is removed from all diameter classes as required to maintain this diameter distribution. Little evidence exists, however, that historical patterns of partial cutting have followed the classic single-tree theory. "Selective" harvest in the Sierra Nevada has, in the past, primarily targeted the large trees. This system, sometimes called "pick and pluck," will not produce the simple, even-aged structures that characterize clearcutting techniques, but its effect on the presence of large, old trees is similar. If the large trees are removed and no stocking control is done on the smaller stems, replacement trees in these diameter classes will be produced very slowly, if at all, and they will consist primarily of the more shade-tolerant species. Even with classical single-tree selection, a gradual loss of shade-intolerant species would be likely.

The future forest of the Sierra Nevada, as projected by the LMPs, will very likely be split between areas of even-aged plantations and areas of dense and increasingly small-diameter stands. Given these projections, it seems most likely that the forest to be generated by adherence to current LMPs will be susceptible to fire disturbance, nearly devoid of large, old trees, and depauperate in terms both of plant and animal species that

depend on attributes of the older forests that were common last century. We conclude that the key elements of spotted owl nest and roost stands, under current LMPs, will decline sharply over most of the Sierra Nevada in the next few decades. If they disappear, a hiatus of well over 100 years will pass before more can be grown to take their place. In the process, the spotted owl would probably be markedly reduced in numbers over most of the Sierra Nevada, but probably with viable subpopulations surviving in Yosemite and Sequoia/Kings Canyon NPs.

Conclusions

Is the Sierran population declining? We cannot be certain. Failure to detect significant declines in the two Sierran study areas must be interpreted cautiously, because the power of both tests was very low. We know nothing about the normal, long-term fluctuations of spotted owl populations in the Sierra Nevada. If the California spotted owl has experienced gradual declines in habitat quality in these mountains, the effects may be subtle and difficult to detect. Because we lack adequate, historical inventories of spotted owls in the Sierra Nevada, we have no basis for comparison with our current knowledge. Their current distribution and abundance, however, do not suggest that they have declined either in their overall distribution in the Sierra Nevada or that they have declined markedly in abundance within any forest type.

Selective logging of the largest trees from the most productive sites in the Sierra Nevada has resulted in significant changes in diameter distributions of trees, leaving relatively few very old, large trees that are clearly selected by the owls for nesting (Chapter 5). Consequently, we are far from comforted by results from the demographic studies. Before reaching a final conclusion on this matter, we need to continue these studies until the power of their tests on lambda is greatly increased.

Do Sierran owls exhibit selective use of habitats? Yes. The overwhelming weight of evidence is that California spotted owls in the Sierra Nevada select habitats differentially from among all habitats available to them. Selectivity is strongest for nesting and roosting habitats, weaker for foraging habitats. Even for foraging, however, we conclude that a target for suitable owl habitat should include at least 40 percent canopy cover in stands with trees averaging at least 11 inches in d.b.h. Data from direct measures of foraging stands further suggest that suitable foraging stands have snags, dead-and-downed woody debris, and some large trees (Chapter 5).

Are key habitat elements declining in the Sierra Nevada? Yes. Of greatest concern to us at this time is the rapid disappearance of the large, old, and generally decadent trees that are the focus of nesting by spotted owls. Given projections from approved and draft LMPs for NFs in the western Sierra Nevada, where the vast majority of Sierran owls occur, these important stand components will disappear at a rapid rate over the next few decades. They cannot be replaced quickly.

Considering the present state of our knowledge about spotted owls in the Sierra Nevada, we can identify eight major factors of concern about owl habitats there (table 1D). These have resulted from a combination of selective logging removing

Table 1D-Summary of major factors of concern in habitats of California spotted owls in the Sierra Nevada, reasons for those factors, and their impacts on the owls.

Factor	Reason(s) for the factor	Impact on spotted owls
Decline in abundance of very large, old trees	Selective logging of the largest trees from stands	Loss of the owl's preferred nest sites
Long recovery period for spotted owl habitat after logging	Selective logging of the largest trees from stands	Less of total landscape in suitable owl habitat at any given time
Ingrowth of shade-tolerant tree species, creating unnaturally dense stands with ground-to-crown fuel ladders	Selection harvest; aggressive fire suppression; sheep grazing, which created ideal seedbeds for conifer germination late last century	Increased threat of stand-destroying fires
Excessive build-up of surface fuels	Aggressive fire suppression over the last 90 years, leading to higher densities of trees, more competition for space and water, so a higher death rate of trees	Increased threat of stand-destroying fires
Loss of large-diameter logs from the decaying wood source on the ground	Intentional fires by sheepherders; selective logging of largest trees; piling and burning logs after logging; domestic fuel-wood removal	Potential decline in flying squirrel densities via loss of fungi that are a dietary staple for the squirrels
Decline in snag density	Selective logging of the largest trees from stands; salvage logging; fuel-wood removal	Loss of potential nest sites for owls; loss of den sites for flying squirrels; loss of a source of large logs for decay needs on the ground
Disturbance and/or removal of duff and topsoil layers	Sheep grazing; mechanical disturbance from logging equipment, skid trails, and so on; increased surface fuels that burn hot enough to destroy duff layer	Potential decline in flying squirrel densities via loss of fungi that are a dietary staple for the squirrels
Change in composition of tree species (fewer pines and black oaks, more firs and incense-cedar)	Selective logging of the largest trees, particularly pine species, from stands; aggressive fire suppression	Some loss of nest sites; other effects unknown

mainly the largest trees from stands, aggressive fire suppression beginning shortly after the turn of this century, and the combination of human-ignited fires and extensive sheep grazing in the Sierra Nevada during most of the last half of last century.

Assessing the Owl's Status: Southern California

Here we summarize available evidence for the spotted owl in southern California as it relates to the three fundamental questions, and null hypotheses, posited for Sierran owls. Less is known about the habitat relations of spotted owls in southern California, but we can say much about the likely stability of the owl population there in relation to its pattern of distribution-in relatively isolated blocks with potentially hostile habitat between them, through which the owls must disperse.

Does Evidence Indicate a Decline in the Southern California Population?

Yes. The estimate of lambda for the San Bernardino demographic study area was 0.827 (table 8G), suggesting about a 17 percent annual rate of decline in the resident, territorial population during the study period (1987-91). The statistical test ($\alpha = 0.05$, $P < 0.0001$) strongly rejected the null hypothesis of a nondeclining population. The correct inference for this population is that it has been in a steep decline for at least the past 5 years.

We do not know the reason(s) for this decline. Much logging occurred there in the 1960s, but we doubt whether that disturbance can explain the current decline. Chronic air pollution in southern California may be directly or indirectly linked to the declining population of owls, for example by way of the plant foods important to woodrats. A more plausible hypothesis involves either direct or indirect effects of the drought in southern California, where precipitation from 1984 through 1990 averaged about 60 percent of normal at one weather station and about 67 percent of normal at another near Big Bear Lake, near the center of this demographic study area. Precipitation was below normal in all 7 years at one station and above normal in only 1 of the 7 years at the other (figs. 8A and 8B). In 1991,

when precipitation was above normal, it exceeded the long-term average by about 10 percent. Most of this came in a series of strong storms that coincided with the laying period for most owl pairs that attempted to breed that year.

One working hypothesis is that numbers of dusky-footed woodrats, the primary prey of the owls in the San Bernardino Mountains (Chapter 4), have declined as a result of the drought. If the decline in owl numbers is related in some way to the drought, it suggests that the owl population there is subject to high levels of environmentally induced variation in its demographic parameters. As the population declines, individuals may be lost from marginal habitats, where survival and reproduction are possible only during "good" times (Chapter 8). Individuals that survive, and even reproduce, during the decline may be those occupying better, more stable, habitats, as where more mesic conditions prevail (for example, riparian areas). Such refuges would be critically important to the species' long-term persistence, and any destabilization of them by logging, water diversion, depression in ground-water levels, excessive development of recreational activities, or further development of communities and dispersed housing could pose a significant threat to the owl's survival.

Do Spotted Owls in Southern California Exhibit Selective Use of Habitats?

Yes. The same basic patterns found at the home-range scale for Sierran owls have been observed in studies of habitat use by spotted owls in southern California. The most detailed study was done in the San Bernardino Mountains (table 5C). Compared to randomly located sites, nesting and roosting stands had significantly higher canopy cover, total live basal area, hardwood basal area, softwood basal area, and snag basal area. Nest trees were very large for the area, averaging 37 inches in d.b.h. and 88 feet in height. The mean age of nest trees in the San Bernardino Mountains was 230 years based just on the core length that could be extracted from the trees (table 5M).

Are Key Habitat Elements Declining in Southern California?

We do not know. We were not able to bring quantitative information to bear on this question. Little commercial logging occurs in southern California, but "timber-sale improvements" and firewood cutting have negative impacts on owl habitat there. In addition, wildfires occasionally burn through suitable owl habitat, rendering it less suitable, or even useless. The extent to which these events result in a net loss of suitable owl habitat is unknown, however. We also know that urban and dispersed residential expansion is occurring in suitable owl habitat in southern California, especially at lower elevations between relatively isolated subpopulations of the owl. Those are the places where dispersing owls must move from one subpopulation to another, and such dispersal is the only method whereby a decline in one subpopulation can be compensated by "rescue" via immi-

grants from another. We also know that many owl pairs in southern California, especially in the southern portion of the Los Padres NF, occupy narrow strips of riparian/hardwood forest. These forests will survive there only as long as the stream system from which they get their water survives. In some of these areas, water mining in the forms both of diverting surface water and drilling into underground aquifers threatens to dry up streams to the point that they will lose their riparian forests.

Stability Properties of the Spotted Owl Metapopulation in Southern California

Spotted owls in the Southern California Province have an insular population structure, ranging in size from about 1-4 pair sites to about 125 pair sites, distributed among discrete mountain ranges (fig. 9A, table 9A). This distribution of habitat islands is discontinuous across the landscape, reflecting natural discontinuities in vegetation structure and composition, in topographic conditions, and in the effects of extensive human-induced habitat disturbance and fragmentation. The largest population is in the San Bernardino Mountains, with considerably lower population sizes in the other areas. This "archipelago" is estimated to have 376 pair sites (table 9A), with an approximate population of 300-350 pairs at any point in time. Based on theory and limited empirical data, we believe the ultimate stability of this metapopulation will depend on several factors, including the persistence of one or more populations of sufficient size to avoid negative effects of demographic stochasticity, and with demographic characteristics that result in production of excess individuals to serve as potential colonists for other local populations (Chapter 9).

The sensitivity of the southern California metapopulation to a variety of perturbations was tested by performing multiple simulations, using a spatially explicit model developed to examine effects of spatial aspects of the distribution of the northern spotted owl (Chapter 9). Interpreting model results in a visual and spatially explicit way allows insights into areas of the landscape that are especially vulnerable to local extinction events, as well as those areas that represent sources for immigrants to other local populations. We did not, however, project extinction likelihoods from the model runs.

The arrangement of owls and owl habitat across the landscape shows that most of the population is concentrated in the San Gabriel/San Bernardino Mountain complex. Smaller populations in the archipelago will continue to function as a part of the larger metapopulation only if they remain connected through dispersal. If these smaller populations become increasingly isolated, via reduction in size of their habitat islands or creation of barriers to dispersal, the likelihood of their extinction increases. Although these small, isolated populations will be the first to go, even the largest, most continuous ones will experience increased risks as smaller populations drop out of the metapopulation.

The many factors discussed earlier—for example, wildfires, urban and dispersed residential expansion, water mining, and increased recreational use of riparian areas that are prime owl habitat—can all add their seemingly insignificant, individual bits

of erosion into the existing population of spotted owls in southern California. To the extent that this leads eventually to fewer pairs overall, fewer pairs in individual "islands," greater distances between pairs, and reduction in the rate of successful dispersal between populations (to maintain smaller ones), the spotted owl population in southern California appears to be fragile.

On the other hand, we know that inventories of spotted owls in southern California have not been completed. If more pairs were known to occur in some of the habitat islands, it could markedly increase estimates of the stability properties of those subpopulations. Particularly important in this regard are the possibilities of more pairs in and near the Cleveland NF and in and near the San Rafael Wilderness in the Los Padres NF. Increasing cluster size (number of pairs with essentially shared home-range boundaries) to 45 or 50 pairs in each of these areas would have a strong stabilizing effect on the metapopulation in southern California.

Conclusions

Several uncertainties are associated with the status of spotted owls in southern California. The only population studied demographically has been declining at a high rate for at least 5 years, but this has all taken place during the recent drought. We cannot separate the possible effects of the drought from other

possibilities. Indeed, no other explanations are immediately evident. It is possible that some subtle, even unsuspected phenomenon is the real cause of the decline. Although the owls in southern California use only a subset of all available habitats, we do not know if those selected types are undergoing a net decline. Our modeling suggests that the metapopulation structure of the owls, there is especially sensitive to diminishing sizes of smaller, local populations. And it is also especially sensitive to any reduction in the effectiveness of dispersal by owls among the various "island" populations. We have identified several factors that could be, and probably are, affecting the sizes of the "island" populations and the effectiveness of dispersal among them. For this reason, we believe that more inventories and research are needed on the spotted owl metapopulation in southern California.

Considering the present state of our knowledge about spotted owls in southern California, we have identified seven major areas of concern about owl habitats there (table 1E). These have resulted from a combination of two major factors: (1) The overall population is naturally fragmented into small, relatively isolated subpopulations by the topography, precipitation patterns, and fire regime. (2) Extensive growth in the human population in the Los Angeles basin, and in other valley and foothill areas within commuting distance of Los Angeles, is encroaching on owl habitat.

Table 1E--Summary of major factors of concern in habitats of California spotted owls in southern California, reasons for those factors, and their impacts on the owls.

Factor	Reason(s) for the factor	Impact on spotted owls
Fragmented distribution of suitable owl habitat into small, relatively isolated "islands"	Mainly a natural result of topography, precipitation patterns, and fire regime in southern California	Creation of a metapopulation structure overall population is fragmented into numerous relatively small populations
Small population units are relatively unstable	Demographic stochasticity (random events in breeding, such as most or all young in a given year being males)	Increased likelihood of local extinction of small population units
Extent of demographic rescue of small populations by immigration of owls from other populations is relatively impeded	Distances between isolated populations, and the nature of the habitat between them, directly affect the likelihood of successful dispersal among populations by owls	Increased likelihood of local extinction of small population units
Wildfires	Natural fire regimes in southern California; additional human-caused fires; difficulty of fire suppression in rugged, remote terrain	Loss of suitable habitat will exacerbate problems of small owl populations and restricted dispersal among populations
Expansion of communities and dispersed housing developments in suitable owl habitat, especially in dispersal areas between isolated owl populations	Human population growth in southern California	Further decline in effective dispersal among isolated owl populations; possible loss of suitable breeding habitat
Increasing recreational impacts in owl habitats	Human population growth in southern California	Possible loss of additional owl habitat; possible disturbance effects inducing owls to leave otherwise suitable habitat
Surface and subterranean mining of riparian water sources	Human population growth in southern California	Loss of suitable owl habitats in riparian/hard wood forests

An Assessment of Current Management

Forest Service Lands

Regional Policy-The SOHA Network

Based on available information, we estimate that 83 percent of all California spotted owls occur on NFs, overall; 65 percent of the total are on NFs in the Sierra Nevada (table 1A), and only 4 percent of those are on reserved lands. All known spotted owl sites on NFs in southern California are to be protected. We were not able to assess the extent to which the implementation of this policy is adequate for those owls, because we have incomplete knowledge of the range of habitats in which the birds can maintain self-sustaining populations. In general, we agree with the policy. We are concerned, however, about the current level of information on owl sites in southern California, as well as with the ability of the FS to manage habitat to provide adequate protection from fire and other factors. We recommend that current policy be reviewed periodically to determine (1) that it is being implemented adequately, and (2) that measures taken to implement it reflect the latest information available on the owls in each locality.

The FS's Regional policy for maintaining a viable population of California spotted owls in the Sierra Nevada is the network of SOHAs described in a previous section of this chapter. Because SOHAs provide habitat for only one to three owl pairs in a unit, separated by 6-12 miles from other units, the Interagency Spotted Owl Scientific Committee (ISC) that proposed an alternate strategy for the northern spotted owl (Thomas et al. 1990) concluded that the SOHA strategy had an unacceptably low likelihood of maintaining the owl population over the next 50 to 100 years. We agree that a SOHA strategy, culminating in a network of small, relatively isolated "islands" of older forest suitable for breeding by spotted owls and separated by a "sea" of younger, less suitable or unsuitable habitat, is not a workable strategy to assure long-term maintenance of spotted owls. The underlying principles are the same whether for the northern or the California spotted owl:

1. Every empirical study available on the persistence of bird populations in relation to the number of pairs in the population shows that the likelihood of extinction increases dramatically with decreasing numbers of pairs in a block of habitat. Isolated pairs exhibit excessively high extinction rates. Modeling studies show the same thing. Consequently, we expect that owl pairs in SOHAs would disappear at a relatively high rate, leaving the SOHAs unoccupied and at least temporarily nonfunctional. This loss would considerably exacerbate dispersal problems. Replacement of members lost from pairs would occur very slowly because recruits would have to search extensive areas of unsuitable landscape before locating a vacancy in an isolated SOHA.

2. Social interactions among pairs of owls almost certainly increase calling frequency where several pairs of birds are clustered. If this were not true, observers should not be able to elicit calling from silent owls by imitating their calls. The increased calling rate in clusters of several pairs should provide a sort of "vocal guidance" that would help dispersing birds locate other owls of the opposite sex in good, occupied habitat. This effect would be minimal at SOHAs because calling neighbors could be too far away to hear, and thus to stimulate counter-calling (see Thomas et al. 1990, appendix O).
3. Although SOHAs must provide at least 1,000 acres of suitable owl habitat, and some specified amount of replacement habitat, this can be (and usually is) accumulated by summing acreages of several smaller patches. A result is that SOHAs have a high ratio of edge to area. Some studies indicate that fundamental changes occur in the microclimate of a forest interior, at about 525 feet from an edge (Harris 1984, Franklin and Forman 1987). A 20-acre circular patch, therefore, is essentially all "edge." A 100-acre circular patch has a core of only 32 acres that would be sheltered from edge effects. In addition, allowing a SOHA to consist of several small patches of habitat, instead of a single large one, results in each patch being more susceptible to blowdown of trees around its edges.
4. Being relatively small, SOHAs are vulnerable to small-scale catastrophes. Destruction of a SOHA removes it from the network for perhaps 80 to 150 years and increases the mean dispersal distance between remaining SOHAs, further reducing the chance of nonterritorial owls finding unoccupied but suitable sites.
5. Floaters (nonterritorial birds) behave toward populations of breeding birds in ways that seem unlikely toward isolated pairs of breeders. We believe SOHAs would fail to provide sufficient conditions for recruitment of floaters into a breeding population, because the extent of suitable habitat in a SOHA is too limited to accommodate much more than a nesting pair.

All of the above problems are markedly reduced if owl populations are maintained in relatively large clusters in extensive landscapes where most or all owl pairs have one or more adjoining neighbors (Thomas et al. 1990).

Cumulative Effects Analysis

In 1991, the FS implemented a cumulative effects analysis (CEA) to evaluate green timber sales and other projects within the range of the California spotted owl in the Sierra Nevada. Its objective is to maintain a full range of options for managing spotted owls in the future, while still allowing logging. First, all known and probable spotted owl sites for pairs or resident singles are identified that could be directly or indirectly affected by a project that might remove or affect owl habitat. Directly affected sites are those in which project activities will occur; indirectly affected sites are those in which owl use areas during the breeding period adjoin directly affected sites. The analysis area generally corresponds to the combined use areas of the known and probable owls that are determined to be directly and

indirectly affected by a given project. The outer boundary of this combined area may be constrained on one or more sides by topographic barriers or unsuitable vegetation types.

The process next calls for mapping all nesting and foraging habitat available within the analysis area before the project is done, using the most current information. This can include recent aerial photography, Landsat imagery, LMP database, timber stand inventory, and especially ground verification. All components of suitable habitat—total canopy closure, dominant overstory trees, multi-storied canopy structure, decadence, dead-and-downed wood, and hardwoods—are considered. The amounts of suitable nesting and foraging habitat that will remain in each owl use area after completion of the proposed project are then mapped. Effects of other actions that are reasonably foreseeable are also considered (for example, other sales under contract, other projects with signed decision notices, timber harvest plans, or predictable actions on private lands that will remove suitable habitat). The amounts of suitable foraging and nesting habitat that will remain after project completion are next evaluated against that determined to be needed by the owls in that locality, using the best available information from research and other sources. If the proposed action would reduce the total suitable owl habitat below levels needed to support the current estimated number of owls in the analysis area, adjustments are made in the project. These may include deleting portions of the sale, modifying prescriptions so that suitable habitat remains after logging entry, or moving sale units into unsuitable habitat. If the project would leave the needed amount of suitable foraging and nesting habitat per owl use area, it may proceed subject to any other Forest standards and guidelines that apply.

We have reviewed this process and believe that it will accomplish its objectives in many cases. We are concerned, however, that it lacks specific guidance for retaining the very large trees that are selected for nesting by the owls. Although the procedure calls for at least half of the canopy cover retained in the project area to be in the dominant overstory, which would undoubtedly spare many larger trees in a project area, it would not necessarily spare the largest or the oldest trees. The process also lacks specific guidance for retaining snags and maintaining some quantity of dead-and-downed woody material in specific size-classes. Finally, the CEA process has no provision to retain important habitat attributes in areas not now classified as suitable nesting or foraging habitat, even though these may have the potential to become suitable at varying times in the future—some sooner and some later. Results presented in Chapter 5 of this report could be used to craft specific recommendations for these attributes.

Other Public Ownerships

Only 130 owl sites located from 1987 to 1991 were on SPs and NPs, where management appears to be consistent with maintaining their habitat. The single known owl site on BLM lands certainly underestimates the true number of owl pairs, present, although the final count is not likely to be large. Logging occurs on much of the forested land managed by the BLM. Even though BLM's stated management emphasis will shift

toward managing for old-growth, wood products, stand maintenance, and to meet wildlife and vegetation objectives, we cannot be certain that this will suffice to maintain the number of owl pairs that probably occur now on BLM lands. The matter needs to be addressed in detail along lines recommended in later sections of this chapter. A similar approach should be taken for State-owned forests where logging occurs.

Private Timberlands

Timberlands in the Sierra Nevada that are owned by commercial timber companies and miscellaneous private parties exceed 2 million acres. Presumably much of this acreage has habitat suitable for spotted owls. Inventories have not been completed on most of these lands, and we have not been provided with full information about results of some inventories that have been done. It is clear, however, that much commercial timberland still supports breeding pairs of spotted owls, even though that has not been an objective. Breeding pairs are missing from other private timberlands, however (Chapter 3). Management across all private timberlands is consistent to the extent that policies and practices mandated by the State Forest Practices Act are followed on all private lands. Even with these constraints, however, we cannot easily characterize timber management on private ownerships because practices differ markedly among them. The fact that some private timberlands have breeding pairs of owls, while others do not, suggests to us that existing State regulations do not assure maintenance of owl sites on private lands. The difference lies in the different policies and practices of individual land owners. Whether or not new forest management practices will be enacted by the State of California remains to be seen, as does their contribution to the maintenance of breeding pairs of spotted owls on private lands.

Management Recommendations for Southern California

We regard the status of the spotted owl in southern California as serious and meriting annual attention into the foreseeable future. We are deeply concerned that the largest subpopulation in southern California, in the San Bernardino Mountains, has been declining at an average annual rate of about 17 percent, at least since 1987. Of equal concern is the fact that the overall population is fragmented into many smaller populations. This metapopulation structure is mainly a natural result of vegetation patterns created by topography, precipitation, and fire regimes. Consequently, we are unaware of significant management opportunities to create additional, large areas of suitable dispersal habitat between the isolated populations, or to add markedly to the amount of suitable breeding habitat within those population areas. Our modeling studies strongly suggest that the stability of

the entire southern California metapopulation depends on the populations in the San Bernardino and San Gabriel Mountains (Chapter 9). If they collapse, the entire metapopulation will collapse with them. Although the observed steep decline in the San Bernardino population may be related to current drought conditions, and so be transitory, this is not a certainty (Chapter 8). The large number of factors leading to concern for the owls in southern California (table 1E) only add to our concern for what appears to be a very fragile balance for the spotted owl metapopulation. Accordingly, we recommend the following:

1. Immediately implement a program to complete inventories of spotted owls in the remainder of their range in southern California (Chapter 2). If inventories and assessments of total populations, based on our understanding of habitat, have led us to markedly underestimate the number of owls occurring in various parts of their range, it could significantly change conclusions from our modeling.
2. Continue to monitor the demographics of the San Bernardino population annually, and implement at least two additional demographic studies—one centered on Palomar Mountain and the other in an area with reasonable road access in the Los Padres NF. These additional demographic studies would help (1) to determine whether our conclusion from modeling is correct that owl subpopulations in these locations depend for their maintenance on immigrants from the San Bernardino and San Gabriel subpopulations, and (2) if so, to establish the rate of immigration from other subpopulations needed to maintain them.
3. Continue existing management direction on FS lands, and extend that policy to other Federal lands and to State lands, to maintain all known pairs of spotted owls in southern California. To the extent possible, implement the same policy on private lands.
4. Finally, we recommend that a team of specialists be assembled immediately to formulate guidelines that they believe would best assure maintenance of owl pairs in various parts of their distribution in southern California. This team should include biologists with the most knowledge of spotted owl biology and habitats in southern California, silviculturists, specialists in fuels management and wildfire suppression, county planners, and probably others.

Management Recommendations for Private Timberlands in the Sierra Nevada

Management of private timberlands in California are regulated by the State, which appears to be in the process of promulgating new policies in this arena. We hope that some of the information provided in this full report may influence the final form of those new policies.

Recently, some of the larger private timber companies have begun to develop guidelines for their lands that they contend will maintain populations of breeding spotted owls. We laud those efforts and believe they should be encouraged, but under the provision that results are carefully studied and documented using standard, scientific methods, including scientific peer review, and that they are shared openly with the public at least annually. Specifically, for private timberlands, we recommend the following:

1. Private timber companies that have developed management practices that they contend will maintain nesting or foraging habitat, or both, for spotted owls, should be permitted to test those practices, contingent upon submission of detailed plans to, and subsequent approval from, the State Board of Forestry. It would be the Board's responsibility to determine whether a particular plan has reasonable merit, vis-à-vis spotted owl biology.
 - A. These plans should clearly identify how resulting forest structures and configurations are likely to provide owl habitat, as it is presently understood, or additional information presently known only to a given timber company should be made public, in detail, for evaluation.
 - B. Approval of a plan by the State Board of Forestry would be contingent upon the concurrent implementation by the timber company of a long-term demographic study (see Chapter 8) over a large enough sample of its ownership to determine whether or not its management leads to predicted results. Such a demographic study would follow the same standards and protocols already established for spotted owls, and results would be open for scrutiny, at any time, by the public.
2. Operations on other private timberlands should continue to be regulated by existing State policies.
 - A. All information about spotted owls on these lands should be shared openly with all adjoining ownerships. Indeed, this needs to be a two-way street so that all parties can maximize the efficiency of their planning and the evaluation of their land management, vis-à-vis the owls.
 - B. Further, overall plans for management of spotted owls need to result from coordinated efforts with adjoining landowners, including all public ownerships. This recommendation is not leveled as a criticism of private landowners. On the contrary, we believe that all parties—public and private—share equally in the general failure to work cooperatively to develop solutions to common problems.

Management Recommendations for Public Timberlands in the Sierra Nevada

A successful strategy for the California spotted owl in the Sierra Nevada must be designed to ameliorate the negative effects on owls of several important trends that have been underway for at least the past 100 years (table 1D). Furthermore, if the FS moves ahead with its current generation of LMPs, the dramatic shift toward clearcutting would add considerably to the fragmentation of Sierran forests. This would lessen the ability of spotted owls to find mates and increase the distances that the birds would need to fly to find sufficient food. In addition to ameliorating the several negative trends itemized in table 1D, a successful long-term strategy for spotted owls in the Sierra Nevada must result in the clustering of pairs such that many occur as neighbors with overlapping home ranges in the same general area. This is the same reasoning advanced by the ISC in the case of the northern spotted owl (Thomas et al. 1990), which recommended multiple Habitat Conservation Areas (HCAs) large enough to provide habitat for at least 20 pairs of owls.

Evaluation of an HCA Strategy for the California Spotted Owl

Both the northern and California spotted owls select forest conditions commonly associated with very old forests. Consequently, logging is responsible for much of the concern about long-term maintenance of the populations of both subspecies. As two of our five peer reviewers pointed out, the ISC strategy proposed for the northern spotted owl (Thomas et al. 1990) set new precedents in conservation biology, so it should not be lightly dismissed as an option for the California spotted owl. We agree. In five important ways, however, the current situation for the California subspecies differs from that of the northern subspecies.

First, by some estimates the numbers and distribution of the northern spotted owl have been reduced by about 60 percent as a direct result of logging, land clearing for agriculture, urbanization, and other human developments (Thomas et al. 1990, p. 20). We have no evidence of similar declines in the number or distribution of California spotted owls, however, either in the Sierra Nevada or in southern California. In spite of the fact that logging has occurred over nearly all of the conifer forests of the Sierra Nevada in the past 100 years, and especially in the past 50 years, spotted owls continue to be widely distributed throughout most of the conifer zone. Indeed, spotted owls may be more abundant in some areas of the Sierra Nevada today than they were 100 years ago. Late last century, sheep and sheepherders so depleted the understory vegetation and the supply of dead-and-downed wood at some locations in the Sierra Nevada

that flying squirrel populations may have been depressed. We would expect owl numbers to decline proportional to the decline in numbers of flying squirrels (see table 4A), unless the owls preyed mainly on other species in the latter part of last century. With the burst of regeneration that followed removal of the sheep and introduction of reasonably effective fire suppression (fig. 11I), stand densities increased markedly and this led to an increase in the amount of decaying wood on the ground. The absence of periodic fires also permitted greater accumulations of duff and decaying wood.

Second, clearcutting is still held by many foresters and silviculturists to be the prescription of choice for most of western Washington and Oregon, west of the Cascade crest. Partial cutting there leads to extensive blowdown of remaining trees, and regeneration of preferred timber species is poor after partial cutting compared with clearcutting. The result is a scant record of experience with partial cutting in most of the Pacific Northwest, and certainly no experience with how to maintain spotted owls in logged forests by applying a variety of partial-cutting prescriptions. As a result, the ISC opted for a strategy that separated HCAs from areas where logging could occur, and they prudently held that experience with silvicultural procedures that could both generate timber volume and maintain owls should be acquired outside of HCAs. On the other hand, partial cutting has been the predominant method over most of the Sierra Nevada for decades. We know that stands there do not "fall apart" when partially cut. We also know that most of what has been done there has not yet excluded spotted owls from Sierran forests.

Third, because clearcutting practices have dominated silviculture in the Pacific Northwest, most forests there today are either relatively undisturbed or they are in various stages of regeneration from clearcuts done mostly within the past 50 years. Consequently, distinguishing between suitable and unsuitable owl habitat in the Pacific Northwest was relatively easy, compared with the same task in most of the range of the California spotted owl. Tallying total acres of suitable owl habitat, although not easy, was nonetheless feasible over most of the range of the northern spotted owl. This has not been the case throughout the range of the California spotted owl for three primary reasons: (1) Logging practices in the Sierra Nevada and southern California have not typically involved the creation of nonforests where once forests stood. Instead, logging's impacts have been incremental. (2) We have no studies to show what sorts of forest stands can support *self-sustaining* populations of California spotted owls. (3) Nearly all of the quantitative research done on the California spotted owl began in 1987 or later—the same time the present drought began (fig. 4H). Therefore, all results must be interpreted against that background.

Fourth, fire is not a major threat to most existing stands west of the Cascade crest in Oregon and Washington (Agee and Edmonds 1992). Setting aside large blocks of forested land to be left nearly intact, with little or no logging or other stand-altering activities, does not entail a big risk that fires will destroy major portions of those blocks at an unacceptable rate. We have little confidence that the same is true in the Sierra Nevada. Sierran mixed-conifer forests, where most California spotted owls oc-

cur, are drier and, given the effects of fire exclusion, much more prone to stand-destroying fires than are most forests in western Washington and Oregon. This creates a challenge when trying to establish procedures for maintaining spotted owls in Sierran conifer forests. An HCA strategy there could deal with the uncertainties associated with logging, but HCAs would sometimes be reduced in extent by stand-destroying fires. Prescribed fires and other methods of fuel treatment can be used to reduce the excessive fuel loads that are now so common in Sierran forests (Chapter 12). These procedures are costly, however, and we believe it is folly to imagine that sufficient funds would be forthcoming to implement an effective fuels management program in HCAs excluded from logging. Furthermore, regulations on air quality standards are making it increasingly difficult for agencies to obtain the burning permits needed to implement effective prescribed burning programs.

Fifth, the northern spotted owl is considerably more numerous than the California spotted owl. This contrast is even greater, of course, for the Sierra Nevada—the only area where an HCA strategy might be considered for the California spotted owl (see prior discussion of the southern California case). Thomas et al. (1990, p. 20) stated that "...results indicate about 2000 pairs located during the last 5 years, representing some unknown fraction of the true number of pairs. Because a census of the total population is not available, we have no statistically reliable population estimate. Recent claims of actual counts of some 6000 birds in 1989 are not out of line with other information from monitoring and inventory efforts." The HCAs recommended by the ISC were estimated to set aside habitat for 1,743 pairs of northern spotted owls (Thomas et al. 1990, p. 33). "In a worst-case scenario, we estimate that the strategy could result in a 50 to 60% reduction in current owl numbers," stated Thomas et al. (1990, p. 34). Given the relatively large number of northern spotted owls, and the extensive distribution of HCAs throughout the range of the subspecies, the ISC believed that such a reduction in total population would not preclude attaining a stable, equilibrium population within 100 years.

We expect that an HCA strategy in the Sierra Nevada could be implemented only on Federal lands, where we have estimated 1,454 known and possible owl sites (table 1A). If 75 percent of the owl sites have pairs at any given time, and assuming that an HCA strategy in the Sierra Nevada might result in only a 40 percent decline in the number of owl pairs, we would expect only about 650 pairs of owls to be protected by HCAs (which would be structured to include reserved lands-NPs and Wilderness Areas). This number may be sufficient to maintain a viable population of owls over the short- to mid-term in the Sierra Nevada, depending on the sizes and positioning of the HCAs. But the number is small enough to introduce additional risks associated with catastrophic events, such as stand-destroying fires in HCAs. Because fire events and subsequent impacts on owl numbers are inevitable, we must maintain a balance between the rate of habitat loss to fires and the rate of habitat recovery from fires.

From the above considerations, we believe an HCA strategy for the Sierra Nevada has as many faults as it has benefits. It

should not be undertaken lightly, and evidence of the need for such a strategy must be compelling. Here we briefly summarize that evidence.

Although both study populations suggest the possibility of population declines, evidence of declining owl populations in the Sierra Nevada was inconclusive. Because the power of the test of the null hypothesis of no decline was very low in both cases, the correct inference to draw from results is that we are uncertain about the status of these populations. Condition this inference, however, with the additional facts that (1) one of the two demographic studies was done in Sequoia/Kings Canyon NPs, where logging and other habitat disturbances have not occurred, and (2) the second demographic study was done in an area of checkerboard ownership where owl density was considerably less than in areas of continuous public ownership in the Sierra Nevada, and where no nests and few roosts of owls were found on the private timberlands that were part of the checkerboard. Even if this population actually declined during the period of study, it may not have been representative of owl populations occupying areas of more contiguous, suitable habitat in Sierran conifer forests.

As for northern spotted owls, strong evidence from several sources indicates that California spotted owls select nest and roost sites in stands with very large, old trees, high canopy closure, and snags. Clear evidence from past logging practices and from the LMPs for Sierran NFs indicates that most of these stands will soon be gone if the direction of forest management in Sierran conifer forests is not changed. At the present time, however, the owls are widely and evenly distributed throughout nearly all of the westside conifer forests on NF lands. We know less about their occurrence on private lands, but we do know that owls occur on many of them. Apparently, even though the total amount of old-growth forest has been markedly reduced in the Sierra Nevada during the past century, enough very old trees remain today, widely distributed, that the owls do not exhibit major gaps in their distribution that can be clearly attributed to logging.

Given these circumstances, we do not find a case sufficiently compelling at this time to recommend setting aside large blocks of Sierran forests as HCAs for the California spotted owl. Instead, we believe the situation calls for several steps needed during an interim period to preserve for the future significant management options for owls in the Sierra Nevada. These are aimed primarily at saving the older forest elements that the owls appear to need for nesting and roosting, and at reducing the excessive build-up of surface and ladder fuels.

A Recommended Interim Approach

We believe the current status of the California spotted owl in the Sierra Nevada is more amenable to improved management practices throughout public lands (Federal and State) than it is to any of the variety of reserved block designs we have examined. Because spotted owls are still widely and fairly evenly distributed throughout the conifer forests of the western Sierra Nevada, we favor an alternative strategy that maintains that number and distribution at least for an interim period. Management of the

forests during this interim should not foreclose options for whatever long-term management scenario may be adopted for the owl at the end of the interim period. The desired objective, of course, would be to determine how to maintain spotted owls throughout Sierran conifer forests in a manner compatible with some sustainable level of timber production. The advantages of such a strategy are many. No decisions must be made about the number of owl pairs needed in blocks of habitat or how far apart to space blocks, because most of the Sierran conifer forest would be suitable for foraging by owls, and nesting and roosting habitat would be widely available. Commodity production associated with maintenance of suitable owl habitat would result in funds for fuels management. And much of the fuels management problem could be approached physically as part of the strategy to maintain suitable owl habitat by removing the dense surface and ladder fuels that now facilitate stand-destroying fires. Finally, we contend that such a strategy is more likely to sustain viable populations of most or all other plant and animal species in the Sierra Nevada than is any block strategy.

Whatever interim strategy may be adopted, it should accomplish three primary objectives: (1) protect known owl nest stands (or main roost stands if nest stands are not known) from any significant degradation; (2) protect very large, old trees throughout Sierran conifer forests; and (3) begin to cope with the excessive fuels problem. The duration of the interim period will depend on how quickly we can determine, with certainty, the status of the owl population in the Sierra Nevada and attain a relatively full understanding of the range of habitats in which the owls can maintain self-sustaining populations. We recommend an initial period of 5 years, although whatever period is chosen must extend well past the present drought into the next "normal" or "wet" climatic period.

General Recommendations

1. Maintain all existing SOHAs, as presently specified in LMPs, until a long-term strategy is implemented. Although the SOHAs do not, by themselves, constitute a viable strategy for the owls, we cannot anticipate what role they may play, if any, in a long-term strategy.
2. Continue to monitor the demographics of spotted owls in the Lassen NF, Eldorado NF, Sierra NF, and Sequoia/Kings Canyon NPs. Enlarge these studies enough that the power of their tests of lambda can provide a reasonable likelihood of detecting real population declines when they occur (Chapter 8).
3. Implement ecological studies of the primary prey species of spotted owls in the Sierra Nevada Province, especially the northern flying squirrel in the conifer zone and the dusky-footed woodrat at lower elevations (Chapter 2). The objective should be to develop a full understanding of the key ecological linkages among trees, soil, water, prey, and owls (Chapter 4).
4. Undertake an extensive inventory of potential spotted owl habitat in riparian/hardwood forests and adjoining woodlands in the foothills of the western Sierra Nevada and in the

inner coast ranges to estimate the number of nesting pairs there (Chapter 2).

5. Through coordination between managers and researchers, initiate a program of experimental forestry in Sierran NFs within the interim period, as recommended in Chapter 2 and elucidated in Chapter 13, so that we may observe these modified forest systems and determine their effects on spotted owls.
6. Develop a time schedule that identifies specific, annual accomplishments that can be monitored to assure satisfactory progress toward attaining information needed to craft a longer-term strategy for the California spotted owl.

Specific Recommendations

The following guidelines (table 1F) should not preclude options for the future. The protections afforded to owl sites and preferred nesting habitat are intended to stabilize owl habitat acreage in the short-term. Taking a longer look, the basal area retention in larger tree size-classes will ensure that old-growth elements will not be lost from these systems. Existing Experimental Forests and Demonstration Forests are expressly exempted from all of the following recommendations.

Spotted Owl Sites on Public Lands

1. Establish a *Protected Activity Center* at all known California spotted owl sites in the Sierra Nevada. Locate owl sites using the California Department of Fish and Game's database, and identify the activity center in each, defined either by a known nest site or by what is judged by a Forest Biologist knowledgeable about owl biology to be the best roost location in the site. Delineate an area of 300 acres around this activity center (see "Size of Activity Centers" in Chapter 5) following boundaries of known habitat polygons and topographic features such as ridgelines, as appropriate. The *intent* here is to include in the 300 acres the best possible owl habitat available, blocked up into as compact a unit as possible. Ideally, each unit would consist of 300 acres of P4G, M4G, or better stands (M5G, M5N, M6) (see table 1C for code definitions), but this will likely not be possible in all instances. To assure that the unit includes the best owl habitat available, augment the acreage of P4G, M4G, or better with the following timber strata, arranged here in descending order of priority: M3G, P3G, M4N, M3N, P3N, R4G, R4N, P4P, and M2G (see table 5A and fig. 5B, and the discussion of ponderosa pine strata under the heading "Selective Use of Forest Types" in Chapter 5).
2. Undertake no stand-altering activities within *Protected Activity Centers*, other than light underburning.
3. Light underburning in these stands would be permissible, given careful review by biologists and fuels management specialists, on a case-by-case basis. Any underburning should be done in a manner that minimizes removal of duff and large woody debris.
4. Remove no snags or large culls from *Protected Activity Centers*.

Table 1F-Summary of primary recommendations for stand retention and special stand treatments to maintain options for spotted owls on public timberlands in the Sierra Nevada during an interim period.

Attributes	Protected ¹ Activity Centers	Selected ² Timber Strata	Other ³ Timber Strata
Large, old trees Basal area	No logging	Retain 40 percent basal area from the largest healthy trees and culls	Retain 30 percent basal area from the largest healthy trees and culls Retain at least 50 square feet basal area per acre
D.b.h. ⁴	No logging	Retain all live trees ≥ 30 inches in d.b.h.	Retain all live trees ≥ 30 inches in d.b.h.
Percent canopy cover	No reduction	≥ 40 percent	No restriction
Snags	No reduction	Save the largest snags ≥ 30 inches in d.b.h., to a maximum of eight snags per acre; if this is < 20 square feet basal area per acre, save snags < 30 inches in d.b.h., from the largest down, to a total of eight snags per acre or 20 square feet basal area per acre, whichever comes first; need not retain snags < 15 inches in d.b.h. or < 20 feet tall	
Downed woody material	Reduction only in relation to light underburning	Beginning with the largest downed logs (by volume), sequentially retain pieces of downed wood until an average of <i>at least</i> 10-15 tons/acre are retained over a cut unit. Do not include pieces < 11 inches in diameter to meet the tonnage limit. The intent here is to retain as many as possible of the existing large pieces of decaying wood present on a site before any treatment (for example, a timber sale or prescribed burn). Cull logs created by a sale should be left at or near where they fall and be included when totalling the downed wood to be retained	
Fire threats	Light underburning	Positive fuels management	Positive fuels management

¹ Block of 300 acres of suitable nesting/roosting habitat delineated around nest site or primary roost site in all known spotted owl sites in the Sierra Nevada, as identified in the California Department of Fish and Game database.

² Timber strata selected for nesting by spotted owls in the Sierra Nevada (P4G, M4N, M4G, and better-strata codes explained in table 1C).

³ Other timber strata used for nesting by spotted owls in the Sierra Nevada (MG, P3N, P4P, M2G, M3P, M3G, M3N, M4P, R3P, R3G, R4G, R4N-strata codes explained in table 1C).

⁴ Diameter at breast height, in inches.

Other Forested Public Lands

1. **Selected Timber Strata:** Stands shown to be selected for nesting by the owls (P4G, M4G, M4N, M5G, M5N, M6--see table 5A and section on "Selective Use of Forest Types" in Chapter 5) may be entered only once for commercial logging prior to implementing a long-term strategy for managing the California spotted owl on public lands. Remove no live tree ≥ 30 inches in d.b.h. Retain 40 percent of the basal area, consisting of the largest of the healthy trees and culls in each cut unit, using the following steps:

A. Do not rely on current timber inventories to determine stand strata. Base this determination on field verification of each cut unit during stand inventories in preparation for sales. When a cut unit is borderline between two timber strata (for example, between M4N and M3N, between M4G and M3G, or between M4N and M4P), assign it to the stratum with higher canopy cover and/or larger stem diameter. Develop diameter distributions of live trees (including culls) from the inventory data for each cut unit separately, by 2- to 4-inch d.b.h. groupings.

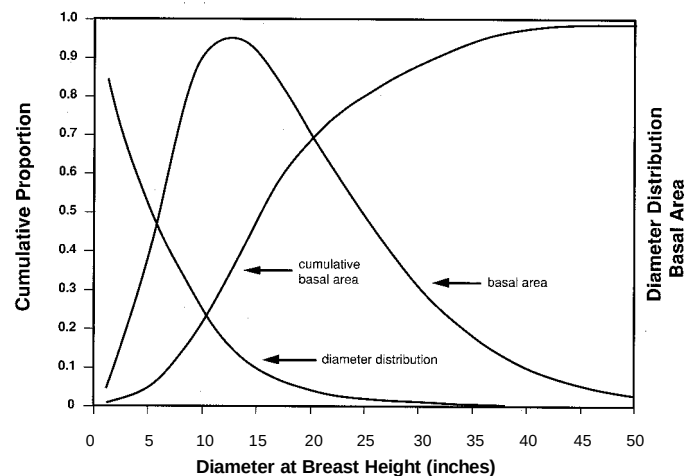


Figure 1A-Diameter distribution (stems per acre), basal area distribution (square feet per acre), and cumulative basal area distribution of a hypothetical, uneven-aged stand of trees.

- B. For each cut unit separately, construct basal-area distributions for live trees.
- C. Next form *cumulative* basal-area distributions for live trees in each cut unit (see fig. 1A), and draw a horizontal line from the 0.6 proportion on the y axis to the cumulative basal-area distribution curve. From that point, draw a vertical line down to the x axis (see fig. 1B).
- D. Cut no live trees with diameters equal to or larger than the diameter intersected by the line perpendicular to the x axis.

Maintain an average crown closure ≥ 40 percent in the remaining overstory. If the largest live trees retained in the cut unit do not yield a canopy closure ≥ 40 percent, make up the difference with stems 12-24 inches in d.b.h. Treat surface and ladder fuels as necessary to create a mosaic of fuel profiles that will minimize the probability of extensive, stand-destroying wildfires. Fuel profiles should consider other objectives of land management, including the needs for site productivity and for habitat of species other than spotted owls.

2. *Other Timber Strata*: Stand types used for nesting by the owls, but not significantly selected based on availability (P3G, P3N, P4P, M2G, M3P, M3G, M3N, M4P, R3P, R3G, R3N, R4G, R4N-table 5A), may be entered only once for commercial logging prior to implementing a long-term strategy on public lands. Remove no live tree ≥ 30 inches in d.b.h. Retain 30 percent of the basal area, consisting of the largest of the healthy trees and culls in each cut unit, following the same steps described for *Selected Timber Strata*. In this case, begin the horizontal line to the cumulative basal area distribution curve from 0.7 on the y axis (fig. 1B). Live trees remaining in these stands must have a cumulative basal area of at least 50 square feet per acre. Remove surface and ladder fuels that would threaten to carry fire into the crowns of remaining trees, and undertake on the sale unit other fuels treatments that are considered necessary.
3. *Snag Retention*: Retain all snags in Protected Activity Centers. In all other habitat that is currently or potentially suitable for foraging, roosting, and/or nesting by spotted

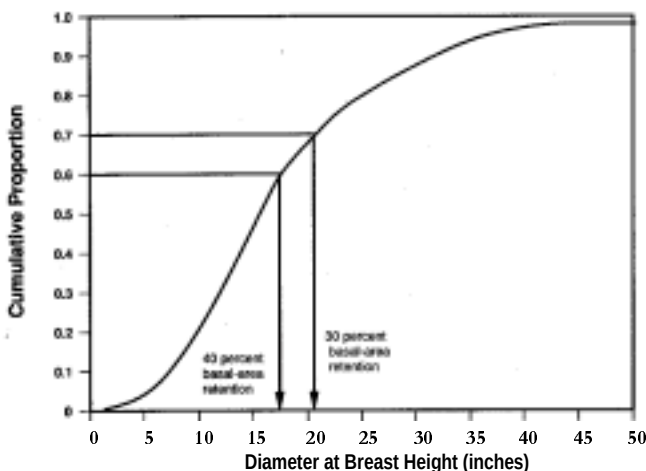


Figure 1 B-A cumulative basal-area function from a hypothetical stand, showing how to relate the proportion of the total basal area subject to logging to the diameter limit of the trees to be retained.

owls, including salvage sales and instances of catastrophic stand loss, use the following guidelines: Save the largest snags ≥ 30 inches in d.b.h. (starting with the largest snag and working down) to a maximum of eight snags per acre, averaged over the cut unit. If this guideline does not result in at least 20 square feet basal area of snags per acre, continue adding snags, from the largest ones remaining, down to a total of eight snags per acre or 20 square feet basal area, whichever comes first. Snags < 15 inches in d.b.h. or < 20 feet tall need not be retained.

4. *Downed Wood Retention*: In all habitat that is currently or potentially suitable for foraging, roosting, and/or nesting by spotted owls, use the following guidelines: Beginning with the largest downed logs (by volume), sequentially retain pieces of downed wood until an average of *at least* 10-15 tons/acre are retained over a cut unit. Do not include pieces smaller than 11 inches in diameter to meet the tonnage limit. The intent here is to retain as many as possible of the existing large pieces of decaying wood present on a site before any treatment (for example, a timber sale or prescribed burn). Cull logs created by a sale should be left at or near where they fall and included when totalling the downed wood to be retained. For the mass calculation, assume a specific gravity of 0.4.
5. *Exceptions to Guidelines 1 and 2*: Guidelines 1 and 2, above, require that large, live trees be left where they are found. In certain cases, based on concurrence between wildlife biologists and silviculturists, compelling reasons may exist to reduce the areas of tree crowns and roots in portions of a cut unit. These include the need to break up a uniform distribution of leave trees to allow regeneration of shade intolerant species, to reduce the spread of dwarf mistletoe from the overstory to regenerating conifers in the understory, or to protect dense leave patches from bark beetle attack by killing high-risk trees. In such cases, we recommend the following guidelines:

If the total basal area of snags ≥ 30 inches in d.b.h. is less than 20 square feet per acre, live trees greater than the diameter limit for *Selected Timber Strata* or *Other Timber Strata*, as appropriate, may be girdled to create snags. Add the basal area of the girdled trees to the snag basal area, but leave an equivalent live basal area in the dominant and codominant tree classes to compensate for the loss in basal area of large live trees that were girdled. A maximum of 10 square feet basal area per acre, or one stem per acre if that stem contains ≥ 10 square feet basal area, may be girdled. As with all other retention figures, the evaluation is averaged over the cut unit, which means that a minimum of 40 trees may be treated in this manner on a 40-acre cut unit. The following steps would serve to implement this strategy:

- A. Develop a diameter distribution and mark leave trees in a given cut unit.
- B. Determine whether the stand is deficient in large snags.
- C. If more large snags are desirable, mark desired snags as "wildlife" trees and measure their diameters at breast height.
- D. After all "wildlife" trees have been selected, mark to leave enough additional live trees from the dominant

Table 1G-Estimates of the effects of leaving the largest trees in stands, accumulating to various percentages of total stand basal area, for four timber strata, using actual mean stand-diameter distributions from the Tahoe NF. When the value in column seven ("Percent of basal area retained by 30-inch limit") exceeds the corresponding value in column one ("Percent basal-area retention"), the 30-inch limit is more constraining. Similarly, when the value in column five ("D.b.h. of smallest tree left") is larger than 30, the 30-inch limit is more constraining than "Percent basal-area retention."

Percent basal-area retention	Strata ¹	Initial basal area	Basal area left after logging	D.b.h. of smallest tree left ²	Mean d.b.h. of trees remaining	Percent of basal area retained by 30-inch limit	Number of trees left per acre with basal-area rule
Stands affected by the 40-percent retention rule							
20	M4G ³	254.61	50.92	34	37	27	6
25	M4G ³	254.61	63.65	31	37	27	7
30	M4G	254.61	76.38	29	36	27	10
35	M4G	254.61	89.11	27	34	27	14
40	M4G	254.61	101.84	25	32	27	18
45	M4G	254.61	114.57	23	30	27	23
50	M4G	254.61	127.30	22	30	27	26
Stands affected by the 30-percent retention rule							
20	M4P ^{3,4}	126.45	25.29	32	38	24	5
	M3G ^{3,4}	213.43	42.69	34	38	26	4
	M3P ⁴	138.06	27.62	30	38	19	3
25	M4P ⁴	126.45	31.61	30	38	24	4
	M3G ³	213.43	53.36	31	38	26	6
	M3P ⁴	138.06	34.52	28	35	19	5
30	M4P ⁴	126.45	37.94	26	35	24	6
	M3G	213.43	64.03	29	37	26	8
	M3P ⁴	138.06	41.39	26	33	19	7
35	M4P ⁴	126.45	44.26	24	33	24	7
	M3G	213.43	74.70	27	35	26	11
	M3P ⁴	138.06	48.32	25	32	19	9
40	M4P	126.45	50.58	22	30	24	10
	M3G	213.43	85.37	25	32	26	15
	M3P	138.06	55.33	24	31	19	10
45	M4P	126.45	56.90	21	28	24	13
	M3G	213.43	96.04	24	31	26	17
	M3P	138.06	62.13	22	29	19	13
50	M4P	126.45	63.23	20	27	24	14
	M3G	213.43	106.72	22	30	26	21
	M3P	138.06	69.03	20	28	19	16

¹ Strata codes defined in table 1C.

² Diameter at breast height, in inches.

³ Does not satisfy the 30-inch d.b.h. rule, which then takes effect.

⁴ Does not satisfy the rule of retaining a basal area of at least 50 square feet.

and codominant classes to equal the basal area of trees to be girdled.

- E. Girdle the marked "wildlife" trees after the sale. If trees marked to leave were inadvertently removed during harvest, make up for the lost basal area by NOT girdling some of the "wildlife" trees.

A Rationale for the Recommendations

Having decided that a major part of an interim strategy for spotted owls in the Sierra Nevada needed to save the largest, oldest trees, we then had to determine what level of retention would be sufficient. For this, we obtained plot-level data from timber-strata inventories in the Tahoe NF. From these data we defined diameter-distribution and basal-area functions for each stratum in the mixed-conifer group. We then generated cumulative distributions for each stratum, determined the diameter limits, and computed the number of trees per acre that would

remain for basal-area retentions between 20 and 50 percent (table 1G). Evaluation criteria were based on the need to leave both the large, old trees and to leave sufficient "dominants" as replacement trees so that these structures would be retained into the future. Because we wished to establish a limit, not a target, we aimed to set minimum retention values.

An additional objective for *Selected Timber Strata* was to leave such stands in or near a structural condition corresponding to suitable foraging habitat for spotted owls. For these stands, it is clear from study of values for M4G strata in table 1G that basal-area retentions of <30 percent would not accomplish our main objective of retaining large, old trees AND providing a succession of replacement trees for them. The smallest of the large trees under 20-percent retention would be 34 inches in d.b.h.-too large to be considered candidates for replacement of the large, old trees when they die and fall. Only six large trees per acre would remain with 20-percent retention, but the 30-inch

d.b.h. rule takes over in this case and leads to retention of 10 trees per acre. A 40-percent retention nearly doubles the number of trees retained per acre, and the smallest of the large trees would be 25 inches in d.b.h. Trees of this size can easily be produced in less than 100 years on most commercial timberlands in the Sierran mixed-conifer zone, providing ample replacements for the large, old trees that range upward in age from 200 years.

A challenge arises with stands having a very high proportion of very large trees. Even with a 40-percent retention rule, the smallest of the large trees retained could be too large to qualify as a replacement tree. For this reason, we added a recommendation to retain all trees ≥30 inches in d.b.h. When the basal-area retention rule fails to include such trees, the 30-inch rule is more constraining and determines the smallest stem diameter to be retained.

The criteria outlined above for retaining large trees will result in unique residual stand structures. In contrast to the uniform spacing of trees common to seed-tree and shelterwood methods, we expect large trees to be irregularly distributed in a stand and to exhibit varying degrees of clumping. This pattern of distribution would result in some large openings in the canopies of units logged following the retention guidelines, and thus promote the regeneration of shade-intolerant species like ponderosa pine and black oak. Our next concern was with the final canopy closure in these stands, which should be ≥40 percent to be within the range of suitable owl foraging habitat. Given 18 trees per acre with a 40-percent retention, and assuming an average crown diameter of 30 feet, final canopy closure would be <30 percent. This led to our final recommendation of retaining sufficient trees 12-24 inches in d.b.h. to bring total canopy closure up to ≥40 percent. Not only would this provide adequate canopy closure, but also it would provide an intermediate range of tree sizes as later candidates for replacement of large, old trees.

The thought process was similar for *Other Timber Strata*, represented by M4P, M3G, and M3P stands (table 1G), although it was not our intention that these should qualify structurally as suitable foraging habitat for owls after logging. Retaining 30 percent of the total basal area in the largest tree sizes would maintain some trees <30 inches in d.b.h., which would provide replacements for the largest trees. As added protection for very sparse stands, we have recommended a minimum basal area of 50 square feet per acre, accumulated from the largest trees in the stand. For the M3P and M4P stands (table 1G), approximately 40 percent of the basal area must be retained to leave 50 square feet per acre, and 10 of the largest trees per acre would remain.

As described in Chapter 5, under the section entitled "Selective Use of Forest Types," we lacked data to analyze whether or not spotted owls select nest sites in various ponderosa pine strata in excess of expectation. Because we have strong reason to believe that at least P4G strata would be selected, however, we recommend a cautious approach in treating ponderosa pine types during the proposed interim period, especially because NFs are likely to classify them as unsuitable owl habitat for lack of sufficient crown closure, even though they may have plenty of hardwood cover in the understory. Accordingly, we recommend that P4G stands, so classified *after* hardwood and understory conifer components have been included in an assessment of

Table 1H Summary of major factors of concern in habitats of California spotted owls in the Sierra Nevada, and which of the recommended actions are intended to ameliorate effects of those factors.

Factor	Recommended actions
Decline in abundance of very large, old trees	Saving live trees ≥30 inches in diameter at breast height; saving the largest trees in stands, by percentage of basal area
Long recovery period for spotted owl habitat after logging	Emphasizing retention of largest, trees shortens the recovery period after logging
Ingrowth of shade-tolerant tree species, creating unnaturally dense stands with ground-to-crown fuel ladders	Thinning; emphasizing removal of small-diameter trees; clearing fuel ladders from around largest trees
Excessive build-up of surface fuels	Implementing aggressive fuels management program, especially to reduce amount of downed wood <10 inches in diameter
Loss of large-diameter logs from the decaying wood source on the ground	Retaining the largest trees and snags in stands, which will eventually be recruited as logs; meeting guidelines for large-diameter logs on the ground
Decline in snag density	Retaining at least 20 square feet basal area per acre of the largest snags in stands; in addition, sparing the largest trees will assure a continuing source of large snags and downed logs
Disturbance and/or removal of duff and topsoil layers	Reducing surface fuels so ground fires burn cooler; reducing mechanical impact of logging and other projects on top soil and duff layers
Change in composition of tree species-fewer pines and black oaks, more firs and incense-cedar	Leaving largest trees and removing smaller trees should result in many openings large enough for germination by shade-intolerant species

stem diameter and canopy closure, should be treated as "*Selected Timber Strata*" during the proposed interim period. P3N, MG, and P4P, again as classified after inclusion of their hardwood components, should be treated as "*Other Timber Strata*."

Evaluation of the Recommendations in Relation to the Problem

Our recommendations address all factors in Sierran conifer forests that we believe have negative effects on California spotted owls (table 1H). Of the eight factors identified, six would be alleviated by a strategy that saves the largest trees in stands and removes some significant proportion of the smaller trees. In effect, the approach recommended here tends to invert silvicultural practices of the last 100 years. What has been characterized as "top down" logging (concentrating on the largest trees) would become primarily a "bottom up" approach (leaving the largest trees and concentrating on the smaller trees). Although not

excluding certain kinds of silvicultural prescriptions that are sometimes associated with clearcut logging, the steps recommended here preclude "clearcutting" in the sense that much of the public perceives it-as creating unsightly patches of land from which all trees have been removed. It also prevents the high-grading of scattered remnant trees.

We do not contend that the approach recommended is without risks. No approach is risk-free. The guidelines suggested for *Other Timber Strata* are not so restrictive that they would guarantee stand conditions suitable for owls immediately after logging. We have focused on setting strong rules to retain stand components that are most at risk and hardest to replace. For instance, to replace large logs in late decay-classes after clearcutting, we first must grow large-diameter trees, allow them to become snags, fall over, and subsequently rot. This is a process measured in centuries. On the other hand, a clearcut site can return to a dense stand of small to medium sawlogs in a few decades (see figs. 11P-11S). We are therefore more concerned about the former than the latter. The spotted owl population in the Sierra Nevada persists despite 100 years of logging injurious to its habitat, and it is still widely and relatively evenly distributed. We thus believe the recommended changes in traditional silvicultural practices in Sierran forests are unlikely to significantly degrade spotted owl habitat over the short-term, and they may even improve habitat over the long-term.

In contrast to the case for *Other Timber Strata*, recommendations for *Protected Activity Centers* should maintain existing nest/roost habitats in a condition suitable for continued use by the owls for those purposes. And guidelines for *Selected Timber Strata* should at least maintain suitable foraging habitat, as recommendations would retain all structural attributes associated with foraging owls (Chapters 5 and 6). We know, for example, that spotted owls regularly used some stands, but not others, that had been recently logged in the Lassen NF (Chapter 7). We would not be surprised to find that a brief period (probably less than 5 years) elapses after logging operations before the owls resume foraging in *Selected Timber Strata*. This is a primary question to be studied through radio-tagged owls (see recommendation in Chapter 2). If the approaches recommended here can be implemented faithfully and studied carefully, we are hopeful that they might lead us to a feasible, long-term solution to the owl problem and to many other problems that follow from the loss of attributes associated primarily with forests in late seral stages.

The recommendations DO NOT REPRESENT TARGETS. Instead, they should be viewed as limits that allow a wide range of silvicultural options. Their main purposes are to arrest the decline of very large, old trees; to save younger, "dominant" trees as replacements for older trees as they die and fall; to reduce risks of catastrophic fire; to promote recruitment of shade-intolerant tree species; and to retain large-diameter dead-and-downed woody materials. These goals can be achieved, in most cases, by leaving *more* trees than the guidelines suggest. For instance, guidelines proposed for *Selected Timber Strata* would be perfectly acceptable for *Other Timber Strata*. Examples of some silvicultural options compatible with the recommendations are described in Chapter 13.

Most or all biomass sales (see glossary) are probably also consistent with the guidelines. In particular, these sales can deal effectively with the serious problem of accumulating surface and ladder fuels. This situation strikes us as being akin to the general deterioration in the nation's infrastructure-bridges, highways, railroads, and so on. We have enjoyed relative luxury while postponing the inevitable costs of maintaining these structures. Someday, someone must pay for this negligence, and it will certainly cost more in the long run than it would if we simply dealt with maintenance needs as they arise. In the case of the current, serious fire threats to conifer forests of the Sierra Nevada, the money spent to suppress just one very large, stand-destroying fire would go a long way toward lessening the threat of such fires if it were spent in an aggressive fuels management program. Instead, we continue to behave like a person who fails to see the wisdom of owning fire insurance on an expensive home.

Conclusions

We suspect that some of the interim guidelines proposed here-those intended to retain various stand attributes found most often in older forests-would also be a necessary part of any strategy to maintain California spotted owls over the long-term. The best long-term solution for the owl in the Sierra Nevada would be to maintain the population in its current, relatively even distribution throughout the forests of the western slopes. If that distribution can be maintained, no need may arise to block up numerous areas large enough to contain many pairs of owls that can share home-range boundaries, as proposed for the northern spotted owl (Thomas et al. 1990). Such a policy in the Sierra Nevada would bring with it a high risk of stand-destroying fires (Chapter 12) that was not a major concern over most of the range of the northern spotted owl. Further, if an acceptable way can be found to maintain attributes of older forests generally throughout the Sierra Nevada, such a plan might go a long way toward meeting the needs of most or all other plant and animal species that thrive in older forests. The spotted owl issue is only the first in a potentially long list of such species awaiting our attention.

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Chapter 2

Future Directions for the California Spotted Owl Effort

Jared Verner and Robert J. Taylor

The chapters that follow summarize most of what we presently know about California spotted owls—their biology and general ecology, their habitat requirements, their demography, and so on. Most chapters contain references to information still needed and suggest further studies and inventories of California spotted owls—their habitat associations, their prey, and their demography. Here we offer tentative directions for proceeding with these tasks, which we believe will speed our progress compared with the past. This chapter is intended to satisfy item #5 in the Charter that established the Technical Assessment Team for the California Spotted Owl: "Identify research, monitoring, and inventory programs needed to answer existing critical questions and to provide for adaptive management of the owl in the future." The need to continue any phase of the effort to fully understand the current status of the owl must be conditioned on the extent to which remaining areas of uncertainty will lead to incorrect decisions. The objectives of this chapter are to identify remaining areas of uncertainty that can be reduced by further inventory, monitoring, and research work, and to recommend at least a broad approach for moving forward with these efforts in a more systematic and coordinated way than has been the case in the past.

Major Uncertainties About California Spotted Owls

Inventory

Significant areas of uncertainty still preclude conclusive recommendations about how best to manage for California spotted owls. For example, inventories have not yet been completed over much of the range of the owl in southern California. Our present information indicates that the largest area of fairly clustered owl sites in the Cleveland National Forest (NF) and adjacent areas has only 37 sites. Similarly, the largest group anywhere west of the San Gabriel Mountains in southern California contains only 25–30 sites. Sites in both localities are not tightly clustered, so they would not function efficiently to foster internal recruitment of dispersing juveniles. The numbers of sites in both are also near the lower limit of stability for isolated populations

(see fig. 9G). Consequently even small increases in numbers of pairs there can be expected to have large, positive effects on estimates of stability properties of the populations in those two areas and of the entire metapopulation in southern California.

Further, we know little about the full extent of winter use or the presence of breeding owls in riparian/hardwood habitats in foothill woodlands of the western Sierra Nevada or other parts of the owl's distribution in the Coast Ranges (Chapter 4). This information is critical for two reasons. First, significant numbers of breeding pairs in these habitats, combined with owls in the adjacent conifer forests, would markedly increase the overall size, and thus the stability, of these owl populations. Second, their presence and importance there would merit serious consideration in planning for residential expansion into those localities. We know little about the possible impacts of current land uses in relevant hardwood habitats on spotted owls or their prey species. These are major uncertainties that need resolution. Inventories in these hardwood types could be planned in a way that tests, on a sample basis, habitat suitability models developed by Steger and Greenwood (pers. comm.) to estimate the possible distribution and abundance of spotted owls in foothill woodlands (fig. 4D).

Finally, the presence of California spotted owls along the central coast of California is well-established as far north as Monterey County, where they occur in mixed conifer-hardwood habitats and coast redwood/Douglas-fir forests. Similar habitats occur to the north, especially in the coastal mountains from the Santa Cruz area northward at least into San Mateo County. Inventories are needed there to determine whether the coastal arm of the California spotted owl's distribution extends northward beyond Monterey County.

Monitoring

A detailed monitoring procedure was designed to detect declining trends in the occupancy and breeding status of territorial spotted owls in the SOHA network (see Chapter 1) on Forest Service lands in California. In the range of the California subspecies, this procedure was implemented in 1987, 1988, and 1989. Analyses done in the course of developing a proposed conservation strategy for the northern spotted owl, however, showed that this monitoring procedure was relatively insensitive to declines in the overall population (Thomas et al. 1990, appendix M). This was the case because of two significant lag effects that accompany habitat-induced declines in the number of territorial owls.

The first lag effect arises from the fact that spotted owls can live for 10-20 years. Even in a SOHA that has declined in suitability to the point that a pair of owls can no longer breed successfully there, the pair may survive for a long time, still be counted as a viable pair, but never replace themselves. Spotted owls often do not breed annually; they may even fail to do so for several successive years. For this reason, little concern is raised when a pair does not nest in a given year. Furthermore, the monitoring protocol does not always detect nesting when it does occur. Consequently, a gradual decline in habitat quality could be overlooked and, over the short term, the overall population would be judged to be stable.

The second lag effect results from the fact that only the resident territorial population is monitored. Floaters (nonterritorial birds) are an integral part of the total owl population (Chapter 4), but they are seldom or never detected by any standard sampling protocols. When territorial adults die in the vicinity of floaters, their places are quickly filled, leaving no indication that the total population has actually declined. This continued occupancy of pair sites would last as long as required to exhaust the floater population. Only then would we expect to see a decline in the territorial component of the total population. This may be the reason why 1991 was the first year in the several years of studying the declining population of spotted owls in the San Bernardino Mountains that the number of occupied territories showed a marked drop (LaHaye pers. comm.).

Modeling work done for the northern spotted owl (Thomas et al. 1990, appendix M) indicated that the combination of these lag effects might delay by as much as 15-20 years the period before a significant decline could be detected in the territorial component of a population of spotted owls. By that time, conditions might already have worsened to a point that some critical threshold in the amount or quality of suitable habitat could have been crossed, resulting in a precipitous decline in the owl population with little chance of recovery. For these reasons, Thomas et al. (1990, appendix R) recommended that the emphasis of the monitoring program be shifted from tracking trends in the occupancy rate and breeding status of owls in SOHAs to detailed monitoring of birth and death rates, turnover rates (replacements of territorial birds lost from the population), and finite rates of population change (λ -see Chapter 8) of spotted owls in several demographic study areas. Only in this way could we know whether a population is reproducing with sufficient success to maintain itself.

We are still uncertain about whether the Sierran population has been declining during the years since demographic studies began (Chapter 8). λ was <1.0 in two populations in which it could be estimated (Eldorado NF and Sequoia/Kings Canyon National Parks), but not significantly less. The power of the tests on λ , however, were so low that we were not likely to detect a significant decline even had it been occurring. Furthermore, even if the test results had suggested that a significant decline had taken place, it would be impossible to infer whether the population decline resulted from changes in the amount or quality of available habitat or because of ecological relations mediated by the present drought (fig. 4H).

Research

Habitat Capability for Spotted Owls

Explicit characterizations of superior, suitable, marginal, or unsuitable habitats for California spotted owls still elude us. This contrasts sharply with the case for the northern spotted owl, for which most land capable of growing forests in the Pacific Northwest could easily be identified as either suitable or unsuitable for the owls—most was either regenerating from clearcuts less than 50 years old, or it had been altered little or not at all from its pristine condition. Either it was or it was not suitable habitat.

The past 150 years or so of forest management in the Sierra Nevada, where most California spotted owls occur, have involved relatively little clearcutting, especially on lands presently within NF boundaries (Chapter 11). The present character of these forests resulted from combined effects of (1) the natural fire regime before European settlement (Chapter 12), (2) massive overgrazing by sheep over a 50-year period beginning in the early 1860s, (3) increasingly effective fire suppression since about 1900, and (4) extensive selection logging in the past 5-6 decades. Currently, most of these forests are unnaturally dense, have large components of young and intermediate-aged trees but few surviving older trees, have extensive vertical fuel ladders linking ground fuels with crowns, and are highly susceptible to stand-destroying fires (Chapters 11, 12, and 13). But these same forests have a relatively uniform density of spotted owls, dispersed in a mostly even pattern over the forested landscape. At the landscape scale, we see little in the overall distribution pattern of California spotted owls to suggest how we might distinguish between suitable and unsuitable habitat (but see Chapter 5).

We have learned much about particular stand attributes that are used selectively by California spotted owls (Chapters 5 and 6), but we have been unable to connect them with studies of the owl's reproductive success—or failure. We still are uncertain about what levels of canopy cover, tree densities and sizes, snag densities and sizes, quantities and sizes of downed woody debris, and so on, are found where owls reproduce consistently and well. Only by linking demographic rates with habitat attributes can we eventually distinguish among superior, suitable, marginal, and unsuitable habitats.

Owl/Prey Relations

Studies of many owl species from around the world suggest that variations in available prey affect their breeding behavior in many ways (table 4B). We contend that the spotted owl is typical in this regard and that an essential component of suitable owl habitat is a consistent abundance of available prey. We know much about the diets of California spotted owls, but no studies have been done on relations between the availability of prey species and the presence, density, or reproductive success of California spotted owls. Only one definitive study of this sort has been completed on northern spotted owls (Carey et al. 1992). Carey et al. found evidence that the area used for foraging by northern spotted owls increased as the densities of their primary prey species declined. Our ultimate understanding of why some

habitats tend to be superior for the owls, while others are only marginal, may depend on knowledge of this sort. It remains as a major uncertainty.

In addition, we know little about the ecologies of the prey species that dominate the owl's diet in different parts of its range. For example, it is generally unknown if the primary prey species show cyclic variation in response to either endogenous or exogenous factors, or to what extent their populations track environmental variation. Furthermore, understanding how prey availability differs with changes in habitat structure is essential if we are to indirectly manage spotted owl populations by increasing suitable habitat for their prey.

Addressing Uncertainties

Additional Inventories

Deficiencies in our knowledge about the presence and reproductive status of California spotted owls in localities like the hardwood zone of the Sierran foothills, or in large parts of southern California, can be met with relative ease and speed, and at a modest cost compared with other major uncertainties. The needed inventory work can follow established protocols and draw upon a wealth of prior experience in such endeavors. Planning for it should begin immediately to assure that field work is completed no later than September 1993. If inventories show that a substantial number of owl pairs breed in these hardwood habitats, studies will be needed to investigate the range and scale of the impacts on owls and their prey that result from the variety of current uses of these lands by humans. Such studies are almost certainly needed in relation to where migrant owls from the conifer zone spend their winters.

Results of complete inventories in potential habitats throughout the range of the spotted owl in southern California will probably require additional modeling efforts to ascertain the stability properties of that metapopulation.

Monitoring

Population Trends

We recommend that the direction of the monitoring program for California spotted owls be shifted to demographic studies. Using this approach, uncertainties about population trends can be resolved more quickly and with a better chance to identify cause-and-effect relations than would be the case with simple measures of occurrence or breeding by owls at selected sample points.

Existing demographic studies in the Sierra Nevada must continue and be enlarged (see recommendations in Chapter 1). It is critical that the continuity of these be maintained, because just a single year's interruption in the series of years needed to

estimate vital demographic rates means that the study essentially must begin anew. Generally, 5-6 consecutive years of banding all territorial owls in a demographic study area are required to attain a reasonable estimate of the vital rates, assuming that the study area is large enough that a sufficient number of birds is banded and reobserved each year (see Chapter 8). Enlarging the studies to include more owls in each year's sample can shorten the time needed to attain accurate and precise estimates of lambda. For example, if current vital rates remain stable and the study is not enlarged, we would need 9 more years of banding in the Eldorado Study Area to attain a statistically significant estimate of the population's trend. On the other hand, by enlarging the study to double the number of banded owls, we might confidently estimate the population trend in only 4-5 more years. In any case, demographic studies in these populations need to continue well beyond the current drought cycle before we will have a chance to fully understand the significance of observed birth and death rates, turnover rates, and estimates of lambda.

The demographic study in the San Bernardino Mountains must also be continued, especially considering the modeling results indicating that the collapse of this population would probably result in the extinction of the entire population of spotted owls in southern California (Chapter 9). Banding in the San Bernardino study area has been done for 5 years, so the study is just getting to a stage that payoffs from its continuation become especially significant. In addition, we need to enlarge the effort in the San Bernardino to include studies of those owl sites where breeding is most consistent and successful. If the present drought is causing the significant decline in the population there, sites that still allow successful breeding are certainly the ones most in need of protection. They are the "sources" of birds that can maintain this population through the "crunch" of the present drought (Chapter 9).

Additional demographic studies are needed to broaden our monitoring sample in southern California—one centered on Palomar Mountain and one in the southern block of the Los Padres NF (Chapter 9). These would also serve to test our current hypothesis that these subpopulations depend for their maintenance on immigrants from the relatively large population center in the San Gabriel and San Bernardino Mountains. If that proves to be the case, the studies would also provide quantitative measures of the rates of immigration needed to maintain each subpopulation.

Effects of Logging

Monitoring the effects of various logging prescriptions on the foraging, roosting, and nesting activities of spotted owls is an especially high priority. Analyses reported in Chapter 7 provide one model of how such studies can be done. If recommendations proposed in Chapter 1 are implemented to maintain options for spotted owls in the Sierra Nevada during some interim period, we consider it essential to monitor owl activities and movements before and after logging operations that follow those recommendations. This can be done on a sample basis, following a study plan developed jointly by managers and researchers. It will require studies of radio-tagged owls, although some concern

exists about possible effects of radio tags on breeding and survival of the owls. Using the latest tail-mounted radio transmitters, however, should reduce impacts on the owls compared to back-pack models used in earlier studies.

Research

Uncertainties About Habitat Capability

Because an accurate determination of the suitability of owl habitat must be linked to the birds' reproductive success (specifically, demographic rates), we believe that advances in dealing with these uncertainties will be most rapid when habitat studies are coupled with demographic studies. The specific details of what habitat parameters should be measured, how they should be measured, and at what scale, need to be given a thorough review by a team of experienced owl biologists, foresters, silviculturists, and others. Implementing these efforts should be contingent upon developing a fully interactive Geographic Information System (GIS) for each demographic study area, with layers for all relevant attributes (for example, vegetation types, locations of owl nests and roosts, hydrographic features, topography, and so on).

Uncertainties About How Silvicultural Systems Affect Owl Habitat

Current Land Management Plans (LMPs) of the various NFs propose to emphasize silvicultural methods and to attain levels of timber removal that will result in significant changes in forest structure. Conversion of most of the lands suitable for timber production to a regulated state will largely result in even-aged plantations and areas with dense, and increasingly smaller-diameter stands (Chapter 13). The LMPs make no reference to the natural conditions of forest ecosystems when proposing the timber programs leading to regulated forests, but the short- and long-term effects of these changes are unknown. No certainty exists that ecosystem processes, whether the population dynamics of spotted owls or the successional trends of multi-species plant communities, will be maintained in regulated forests. We propose that the FS move away from its goal of regulating forests and develop, instead, the knowledge to manage for more natural stand structures, compositions, and functions. Given incomplete knowledge of natural forest conditions and, once known, the uncertainties of how to produce such stands, this is clearly an area for high-priority research.

To the extent that spotted owls nest in stands that retain remnants of historical structure (Chapter 5), data available from habitat-capability studies can provide a useful starting point. In this regard, extensive studies within NPs of stands occupied by owls may prove particularly valuable. We propose that quantitative characterizations of the structure and composition of stands used by owls be expanded and that these data be made available to research silviculturists.

Uncertainties About the Role of Prey

First in priority, we need to know whether prey availability is a primary causative factor in whether or not the owls breed in

a given year. If that proves to be the case, as we believe is likely, we will then need to understand better how we might manage habitats to assure sufficiently dense (and available) prey populations. As with studies of habitat suitability, studies of prey ecology and owl-prey relations would be best done within the boundaries of demographic study areas. For this reason, some decisions about where to initiate additional demographic studies could be determined according to perceived needs to study prey relations.

Several approaches might be suggested to falsify the null hypothesis that the availability of prey is unrelated to the likelihood that a pair of owls will or will not breed in a given year. The hypothesis might be tested by measuring densities of key prey species in many owl home ranges over some period of time (probably a few years) and comparing prey densities available to pairs that did and did not breed. We believe this approach is unfeasible. We know from experience, for example, that it can cost as much as \$50,000 to \$100,000 per year to obtain reasonably precise estimates of prey densities in just a few owl home ranges. A second option might be to supplement artificially the prey available to various pairs of owls in a set of pair-wise comparisons among owl pairs randomly selected from the population. The latter experiment might be more direct and less costly than the former, but it may also prove to be unfeasible for a variety of reasons. Other alternatives need to be considered before we move forward with research on this question. This example points up the need to establish a coordinated effort and a rigorous process for deciding what the major uncertainties are that we need to study, and what are the most efficient ways to reduce those uncertainties.

Establishing a Process

Coordinating studies of owl demographics, habitat attributes, and prey relations promises to significantly streamline research and to speed answers to critical questions needed for a more definitive assessment of the owl's status. Simultaneously, we should learn more about the spatial scales at which these components of the overall system should be considered and how differences in functional scales can best be dealt with in management plans. For example, frequent disturbance events in pristine forests, resulting from fire, insect outbreaks, and wind storms, probably affected relatively small areas ranging from 0.5-2 acres (Chapters 12 and 13). The result was a relatively fine-grained pattern of variability in the vegetation, modified by topography, at a landscape scale. Logging and fire suppression have changed the scale of frequent disturbance to one of about 5-30 acres. Spotted owls, on the other hand, operate in home ranges of hundreds of acres (hardwood habitats where woodrats dominate the diet) to thousands of acres (conifer habitats where flying squirrels dominate the diet) (Chapters 4 and 6). As a result, their home ranges generally incorporate a mosaic of stand structures,

the distribution of which may determine habitat quality. Finally, owl prey populations probably respond to variation in vegetation at scales more like those of pristine forests.

Research Approaches

The style of research best suited to issues at hand is a fusion of two emerging trends in wildlife science. First is an emphasis on hypothesis testing (Romesburg 1981, 1989, 1991; Bailey 1982; MacNab 1983; Eberhardt 1988; Keppie 1990; Murphy and Noon 1991; Nudds and Morrison 1991; Sinclair 1991). Second is adaptive management (Holling 1978, Walters 1986, Walters and Holling 1990).

Hypothesis Testing

Experimentation is the essence of the hypothetico-deductive method. It may be done in many ways, not all requiring direct manipulation of a system under study (Sinclair 1991). It requires formulation of null hypotheses, based on application of common sense to observed natural phenomena and stated in terms that can be falsified. For example, the null hypothesis that the population of spotted owls in the San Bernardino Mountains did not decline from 1987 to 1991 was falsified by estimates of demographic rates from the area. Problems with routine experiments in wildlife biology are many: the scale of the landscape is often immense; variability in data may be too large to reveal treatment effects; replication may be difficult or impossible. These challenges are not insurmountable, but they require that careful attention be given to experimental design.

No style of experimental research has been more effective than a protocol called "strong inference" (Platt 1964). Strong inference is simple in principle. The phenomenon to be explained is described and defined thoroughly. An exhaustive set of explanations (hypotheses) is then devised, which constitutes the core of the process. All hypotheses must be initially plausible, and they should be as diverse and complete as possible to avoid the common pitfall of premature commitment to a single explanation (Chamberlin 1965). They must lead to precise, falsifiable predictions. This process is facilitated if the hypotheses can be stated as quantitative predictions. The predictions are examined and compared until natural circumstances are found that can, if studied, discriminate among hypotheses.

These circumstances define the conditions of a traditional "crucial experiment" (Romesburg 1991). The experiment may involve only the taking of a set of measurements in the field without causing disturbance; the important feature of the experiment is not that it is manipulative but that it allows alternative hypotheses to be compared in a definitive way. In principle, only one hypothesis will survive the tests and comparisons. In practice, however, crucial experiments are seldom perfectly unambiguous (Hempel 1965). Their design and conduct come under attack. More often, the "exhaustive" set of alternative hypotheses is found to be missing a reasonable new idea. In spite of its logical flaws, this style of research has proven to be remarkably productive in those sciences, such as chemistry and physics, where it is routinely practiced.

Platt's (1964) paper on strong inference is widely cited and equally widely misunderstood. In particular, strong inference is not equivalent, as Sinclair (1991) claimed, to the hypothetico-deductive method—it is a subset of that method. To illustrate the difference, the rejection of the null hypothesis that California spotted owls use lakes in their home ranges in proportion to their availability is a reasonable application of the hypothetico-deductive method. The fact that it is a trivial null hypothesis, the rejection of which does not really advance our understanding of the owl's habitat needs, renders this research far from strong inference.

A strong-inference approach to habitat selection would consist first of compiling a list of alternative hypotheses that span the range of possible cause-and-effect relations. The only constraint on these hypotheses is that they must be consistent both with what is known of owl biology and with previous research in animal ecology. This list might contain, for example, a physiological hypothesis (owls choose habitats that minimize thermal stress), a foraging hypothesis (owls require a mosaic of habitats that support their preferred prey), and a cover hypothesis (owls choose habitats that minimize risks of attack by great horned owls and goshawks). The hypotheses are not necessarily mutually exclusive, and thus may allow the possibility of multiple causation. Some set of predictions from the hypotheses, however, must differ so that all predictions cannot be jointly true (Romesburg 1991).

Implementing tests of these hypotheses would require some quantitative assessment of specific attributes of both spotted owls and their territories, resulting in sets of measurements collected across a range of occupied sites. Further, each hypothesis would need to be formulated in terms of specific predictions that discriminate among them. Data used to test the truth of these predictions could be collected from either observational (nonmanipulative) or manipulative studies, in which the researcher experimentally alters one or more components of the system. The design of such studies is difficult and requires much creativity, but those sciences in which it is taught and routinely practiced profit enormously from the exercise.

Adaptive Management

This is an emerging style of management planning that provides an intelligent response to uncertainty (Walters and Holling 1990). Its essence is the use of management decisions to gain knowledge, which may then be used to improve subsequent management decisions. In effect, it integrates management with research and uses feedback loops to progress from acquired knowledge to iteratively improve management paradigms. One might respond that this is not new, that the history of environmental management has always been "adaptive." In its precise meaning, however, the point of adaptive management is to progress from mere trial-and-error learning to a systematic and efficient process of acquiring new knowledge.

Adaptive management offers a major additional benefit deriving from the fact that most conflicts over environmental issues result as much from uncertainty as from fundamental differences in the social valuation of resources. If these uncer-

tainties are acknowledged and a systematic effort is begun to reduce them, most management conflicts tend to moderate.

Walters (1986, p. 9) suggested that adaptive management requires attention to four basic issues: "(1) bounding of management problems in terms of explicit and hidden objectives, practical constraints on action, and the breadth of factors considered in policy analysis; (2) representation of existing understanding of managed systems in terms of more explicit models of dynamic behavior, that spell out assumptions and predictions clearly enough so that errors can be detected and used as a basis for further learning; (3) representation of uncertainty and its propagation through time in relation to management actions, using statistical measures and imaginative identification of alternative hypotheses (models) that are consistent with experience but might point toward opportunities for improved productivity; (4) design of balanced policies that provide for continuing resource production while simultaneously probing for better understanding and untested opportunity."

The construction of models is central to the adaptive-management approach. Models are not new to wildlife biology, but Walters intended for them to be used in a novel way. If one can say that a model-building tradition exists in wildlife biology, then it is to build a single model that captures the essence of existing data and leads to the formulation of rational projections of a population, habitat, or whatever the variable of interest. This activity, usually the capstone on a series of empirical studies, is not what Walters intended. He meant for the scientific manager to identify areas of uncertainty and then build a set of models that both incorporate what is known and allow rational evaluation of the consequences of what is not known.

We contend that adaptive management, in its most elegant form, is the application of strong inference to environmental problems, with the additional constraint that experimental treatments are limited to management protocols that are at least minimally acceptable. That is, most treatments should involve some level of logging with positive economic value. In this light, adaptive management can be the best hypothetico-deductive science applied directly to a management problem.

The Next Phase

The question of how to implement an adaptive management approach is open to discussion. Holling (1978) and Walters (1986) advocated a workshop approach, which has both advantages and disadvantages. Its primary advantage is its contribution toward conflict resolution—if the owl is determined to be in trouble, conflicts will probably be intense. When all interested parties participate both in formulating the set of models considered as management alternatives and in identifying hypotheses to be tested, it strips the mystery from those activities and turns resulting products into common property. Most or all participants feel "ownership."

A problem with relying entirely on a workshop approach is that modeling is a difficult process under the best of circumstances, requiring much effort, time, and creativity. A workshop environment is far from the best arena—time is short, tensions may be high, and participants are often tired and irritable. We

contend, however, that a relatively structured "workshop" format is appropriate to formulate a program to proceed with management and research on the California spotted owl.

The process requires a team and a leader; the leader should not be affiliated with any of the entities involved. The team should include at least a computer scientist with GIS experience, a population biologist, a community ecologist, a forest ecologist, and a forest products economist. These theoreticians could come from the organizations with a stake in the outcome of the plan, with the stipulation that no single organization can be allowed to dominate the team. In addition, the team should have access to other experts, as needed, to deal with various phases of the planning. A central office/work facility should be provided, with a staff to implement routine duties. We envision seven steps in the overall process:

Step 1: Define Issues and Develop an Agenda

The initial stage of the effort should bring together representatives of all affected parties. Each must attempt to gain a clear understanding of the components of the problem and understand both objectives of and constraints on solutions. Existing datasets should be examined to assess their usefulness, and unavailable but needed datasets should be identified.

Step 2: Develop Alternative Models

This is a brainstorming exercise designed to identify as large a set of component processes, and alternative representations of each, as possible. These should be cast in symbolic form suitable for computer models. The modeling team must include the best available theoreticians in all important aspects of the problem. The resulting models should be compared with available data to see if the models are at least consistent with what is known. The necessary precision of outputs will almost certainly require that alternative models be cast in spatially explicit forms and be based upon GIS-derived, landscape descriptions. Parameters to which the models appear to be sensitive should be identified.

Step 3: Assess Uncertainty

This is an intensive workshop exercise to identify uncertainty, both socio-economic and physical-biological. Again, participants should represent all parties with a stake in the issue, and they need to be at ease with quantitative reasoning. They should be teamed with the model builders from Step 2 to forge a set of alternative models that bracket our range of ignorance.

Step 4: Design Experiments

Models coming from Step 3 should be tightened and analyzed by the model builders until they yield predictions that lead to crucial experiments. To the extent possible, the modeling team should focus on predictions that differ qualitatively and that do not require precise parameter estimates. Assuming that multiple experiments will emerge from this exercise, the participants have an added responsibility to prioritize them in rank order, listing first those likely to remove the most uncertainty from critical aspects of our ignorance about the owls in relation to their environment.

Step 5: Forge a Management Plan

Representatives of all groups involved in Steps 3 and 4 should meet to examine the models and the proposed crucial experiments. If the experiments seem plausible, the group should consider the practical problems of their implementation, determining how they can be done and ensuring that sufficient data are collected to discriminate among alternative models.

Step 6: Conduct Experiments

This task would fall to various scientists and study teams from among the entities cooperating in the effort. Success will depend to a major extent on the degree to which the several participating entities can cooperate: (1) to assure that funds are available on a sustained basis to see each experiment through to a logical conclusion; (2) to plan the total set of studies to assure that sensible priorities are followed; (3) to coordinate all studies to avoid needless duplication; (4) to standardize the data to be collected, the methods for collecting them, the forms used to record them, the computer filing and operating systems for manipulating them, and the methods used to analyze them; (5) to assure that political boundaries become as invisible to researchers and their respective affiliations as they are to the owls; and (6) to assure that all results obtained are freely and openly shared, discussed, and interpreted. The nature of the experiments, and their likely duration and cost, are impossible to predict. Ideally they would involve existing manipulations of habitats, but this must not be assumed *a priori*.

Step 7: Feedback Loops

Knowledge gained from the experiments and tests of hypotheses (models) feeds back to management, and the process goes through another iteration.

Completing the Tasks

It is no more likely that a single pass through this process will completely reduce uncertainty than it is that a few laboratory experiments will solve a major scientific question. These steps may need to be retraced a second or third time. The likelihood is high, however, that the process will identify a management solution much faster than current process-oriented research. In particular, the likelihood is high that a blend of strong inference and adaptive management will distill the extent of our uncertainty about the biology of California spotted owls and highlight areas of ignorance that matter the most.

Conclusion

The primary barrier to finishing what is needed to remove the remaining uncertainty about the status of the California spotted owl is administrative, not scientific. Before it can begin, much discussion is needed at the highest levels of the organizations involved to discover whether they are prepared, or even

legally able, to accept and implement the changes that will be needed. For example, if a crucial experiment requires designating as "experimental land" a substantial fraction of a forest--public or private, will support be there for retraining local managers and for temporary reorganization of management authority? Will permitting processes be re-examined? Will citizen and environmental groups refrain from pressuring local managers as experiments proceed? If the answers to these questions are "no," then the political will is missing for any sort of systematic hypothesis testing and adaptive management in forest/wildlife issues.

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Chapter 3

Background and the Current Management Situation for the California Spotted Owl

Thomas W. Beck and Gordon I. Gould, Jr.

The administrative history of the California spotted owl is closely tied to that of the northern spotted owl. Detailed research first began in 1969, with studies on the northern subspecies (Forsman 1976). Forest Supervisors in California were first alerted in 1972 by the Pacific Southwest Regional (R5) Office of the U.S. Department of Agriculture, Forest Service (FS) about concern for the owl in Oregon, based on logging-related habitat changes. Wildlife biologists were advised to seek information on the presence of spotted owls in their respective forests.

Administrative Events

1972-1980

Shortly before passage of the Endangered Species Act (ESA) of 1973, the spotted owl was designated by the U.S. Department of Interior, Fish and Wildlife Service (FWS) as a "threatened species," including the California subspecies. This designation was intended to stimulate interest, impart knowledge, and solicit information about wildlife that appeared to be endangered. With passage of the ESA, however, an official list of Threatened and Endangered Wildlife and Plants did not include the spotted owl (USDI, FWS 1973).

In 1973 and 1974, the PSW Region, the California Department of Fish and Game (CDFG), and the U.S. Department of Interior, National Park Service (NPS) jointly financed the first survey for spotted owls in California. Locations of historical observations and selected late-successional forests were chosen for surveys. Spotted owls were located on most National Forests (NFs) and were found to be much more abundant than previously known, with 159 owl locations documented within the range of the California spotted owl (Gould 1974).

The Oregon Endangered Species Task Force was formed in 1973, at a time when spotted owls had been located at only about 100 sites in that state. The Task Force recommended that 300 acres of old-growth be retained around each northern spotted owl location, as interim protection until permanent guidelines could be adopted. FS Region 6, Pacific Northwest Region (R6) and the Oregon State Office of the U.S. Department of Interior, Bureau of Land Management (BLM) rejected the recommendation (Thomas et al. 1990).

Concern over the status of the California spotted owl was slow in developing compared to that for the northern spotted owl in the Pacific Northwest. During the mid-1970s, additional surveys were done on individual Forests and Ranger Districts in the Sierra Nevada but not in response to Regional direction or policy.

Passage of the National Forest Management Act (NFMA) in 1976, and regulations pursuant to that Act, established the basis for maintaining well-distributed, viable populations of all native vertebrate species on NF lands. NFMA also required the use of Management Indicator Species (MIS) to guide management for certain wildlife groups or critical habitats. The spotted owl was designated as an MIS for wildlife requiring large areas of late-seral-stage conifer forests by all NFs in the western Sierra Nevada.

Early in 1977, the Oregon State Director of BLM and the Regional Forester for R6 agreed to protect northern spotted owl habitat in accordance with interim recommendations of the Oregon Endangered Species Task Force. This included protection of habitat where spotted owls and their nest sites had been found. Late in 1977, agency administrators agreed to the Oregon Spotted Owl Management Plan, which recommended clusters of 3-6 pairs, 300-acre core areas for each pair, pairs in a given cluster no more than 1 mile apart, and clusters no more than 8-12 miles apart, edge-to-edge. The plan was to be implemented through the land-management process and individual land-management plans for NFs and BLM Districts (Thomas et al. 1990).

In 1978, the Oregon-Washington Interagency Wildlife Committee replaced the Oregon Endangered Species Task Force with the Spotted Owl Subcommittee, to represent both Oregon and Washington. In 1979, a Washington Spotted Owl Working Group was established, and in 1980 the FS afforded the same protection to spotted owls in Washington that had already been provided in Oregon.

Because of the rapidly growing issue of logging vs. habitat management for the northern spotted owl, surveys to locate owls increased sharply in 1978 on NFs in Oregon, Washington, and northern California, but FS surveys in the range of the California spotted owl did not begin in earnest for another 3 years. The initiation of systematic surveys in the Sierra Nevada responded to the need to verify designated spotted owl territories for land management plans, as well as to provide wildlife input to planned timber sales. Designated spotted owl territories were later called Spotted Owl Habitat Areas, or SOHAs.

The spotted owl was designated a "Sensitive Species" on NFs throughout FS R5 in the late 1970s (Carrier pers. comm.).

CDFG, with jurisdictional boundaries almost identical to R5, classified both subspecies as "Species of Special Concern" in 1978 (Remsen 1978).

1980-1991

Based on study results by Forsman (1980, 1981), the Spotted Owl Subcommittee revised the Oregon Spotted Owl Management Plan in 1981, recommending that 1000 acres of old-growth forest within a 1.5-mile radius of the nest area be maintained for each pair. R6 agreed to the new recommendations only to the extent that they would "maintain the option" to manage for 1000 acres if further research proved it to be necessary. The BLM in Oregon continued to protect only 300 acres for managed pairs (Thomas et al. 1990).

In early 1981, R5 initiated a meeting on spotted owls that brought interested State and Federal agencies together for the first time. This included BLM, NPS, California Department of Forestry and Fire Protection (CDF), CDFG, and both the administrative and research branches of the FS. The purpose of this meeting was both to share information and to discuss development of management policies and research needs.

FS Regional planning direction for both subspecies of spotted owl in California was issued in June 1981 and closely followed the Oregon Spotted Owl Management Plan. The final revised direction issued in 1984 included the concept of replacement habitat, explained below. In July 1981, the Regional Office, R5, notified Forests with the California spotted owl to provide a strategy for maintaining viability in their Land Management Plan (LMP). This led to the development of designated SOHAs in a grid configuration or "network" on each of the seven westside Sierra Nevada NFs, and prompted those NFs to verify occupancy of the designated sites.

The Portland Regional Office of the FWS conducted a status review of the northern spotted owl in 1981 because of concerns about the effects of the decline of old-growth forest (USDI, FWS 1982). Although the species was described as "vulnerable," the FWS review concluded that the species did not meet the listing requirements of the ESA.

In 1982, the Washington Office of the FS analyzed and clarified existing national policy for management of Sensitive Species on NF lands. This policy was seen as a visible, preventive strategy with the following key objectives: (1) identify plant and animal populations that currently or potentially qualify for Federal or State listing as a result of NF management activities, and (2) develop a consistent, systematic, biologically sound strategy to manage these species and their habitats to provide for viable populations so Federal listing as Threatened or Endangered would not be required.

In cooperation with the BLM, R6 initiated the Old-Growth Wildlife Research and Development Program in 1982, which entailed field studies of old-growth wildlife species and their forest habitats in western Washington and Oregon.

In 1982, R5 recognized differences in vegetation patterns between the Sierra Nevada and Pacific Northwest forests. Considering these differences and the observed use of habitats by spotted owls, R5 speculated that home ranges of the California

subspecies might be smaller and owls might be using younger and more diverse timber stands than in areas where research had been done to date. Based on this concern, the FS and CDFG planned the first research studies for the California spotted owl. The first of these studies began on the Eldorado NF in 1982.

Throughout 1984, the R5 Regional Office approved the final spotted owl habitat networks for proposed LMPs on most NFs in northern California and the western Sierra Nevada. The policy was to implement Regional standards and guidelines for the networks in advance of LMP approvals to avoid losing management options. No Regional policy was set, however, for management of spotted owls outside of approved networks. Some NFs provided protection for 1000-acre "non-network" SOHAs to maintain options for full spotted owl management, but most provided minimal or no protection.

In 1985, the Deputy Assistant Secretary of Agriculture upheld an appeal against the R6 planning guide. The successful appeal contended that the standards and guidelines for northern spotted owls were inadequate and that an environmental impact statement (EIS) was required. Work on a supplemental EIS (SEIS) began in 1985 and was completed in 1988 (USDA, FS 1988).

The National Audubon Society established a "Blue Ribbon" Advisory Panel in 1985 to review the status of the spotted owl in Washington, Oregon, and northern California. The Panel's report was issued in 1986, with findings and recommendations for the northern spotted owl throughout its range, and for the California spotted owl in the Sierra Nevada portion of its range (Dawson et al. 1987). Recommendations on numbers, home ranges, and distribution relevant to the California spotted owl were: (1) Maintain no fewer than 1,500 pairs in the combined range of the northern subspecies and the Sierra Nevada portion of the California subspecies and discard the earlier view that 500 individuals could represent an effective breeding population; (2) maintain the current distribution with a network system similar to that being used by the agencies, but with maximum emphasis on having networks comprised of SOHAs with verified reproduction; and (3) provide at least 1,400 acres of late-seral forest habitat for each pair home range in the Sierra Nevada. Maintaining the population linkage through Shasta County, where the California and northern subspecies come together, was emphasized to be critically important. The Audubon Panel also recommended a well-designed program of intensive and extensive research on a sample basis to obtain reasonable estimates of the proportion of network home ranges supporting breeding pairs of spotted owls and to document reproductive rates in relation to population maintenance.

In 1987, the Old-growth Wildlife Research and Development Program of 1982 was supplemented by the Spotted Owl Research, Development and Application Program (the RD&A Program) for a period of 5 years. This was a cooperative effort of R6, R5, and the Pacific Northwest (PNW) and Pacific Southwest (PSW) Research Stations. The new spotted owl RD&A program, funded as a line item by Congress, had a mission to develop, apply, and integrate new and improved information into guidelines and procedures needed to manage suitable spotted owl habitat to assure maintenance of viable populations in California, Oregon, and Washington. Under the auspices of this

program, numerous studies of spotted owls, associated habitats, and old-growth wildlife species were done in Oregon, Washington, and California (Thomas et al. 1990), but most research funds went to studies of the northern spotted owl. The monitoring phase of the RD&A Program included the Sierra Nevada portion of the California spotted owl's range.

In early 1987, the FWS received a petition to list the northern spotted owl as an endangered species under the ESA. A new status review was done and the FWS determined that listing was not warranted. That decision was litigated by conservation groups in 1988 in the Seattle Federal Court. The court ruled that the FWS's decision was not biologically based and ordered the FWS to reconsider listing (Thomas et al. 1990).

In December of 1988, the Chief of the FS approved the SETS for spotted owls in R6. The selected alternative maintained the existing concept of network owl reserves but increased the sizes of the SOHAs in Washington and portions of Oregon to range from 1,000 acres in southern Oregon to 3,000 acres on the Olympic Peninsula (USDA, FS 1988).

In 1989 the California State Legislature passed AB 1580 to improve the analysis of the cumulative impacts of logging. The measure directed the CDF to develop a system to better track how harvest planning decisions are made, and to develop a scientific database on timberland habitats and wildlife species (Thomas et al. 1990).

In response to Federal court action, the FWS initiated another status review of the northern spotted owl in January 1989 to supplement the 1987 review. That review team concluded that the northern spotted owl warranted protection as a Threatened Species under the ESA (USDI, FWS 1989). As required under Section 7 of the Act, FS and BLM immediately began to confer with FWS regarding evaluation of timber sales. A FWS listing team began a review in 1989 of the proposal to list the owl. Its final recommendation, released in June 1990, was to designate the northern spotted owl a Threatened Species throughout its range. The listing became official on 23 July 1990 (Thomas et al. 1990).

An Interagency Agreement among Agency heads of the BLM, FS, FWS, and **NPS** was signed in August 1988; the intent of this agreement was to enable these four Federal Agencies to work together toward a common goal of population viability for the spotted owl throughout its range. Under authority of this agreement, the Agency heads acted upon a 1989 recommendation from the FS to establish an Interagency Scientific Committee (ISC) to address the issue of the northern spotted owl. The committee was officially chartered in October 1989 and given 6 months to "develop a scientifically credible conservation strategy for the northern spotted owl." The ISC's final report was released to Agency heads and Congress on 1 April 1990 (Thomas et al. 1990). It concluded that existing management for northern spotted owls on NF and BLM lands would lead to increasing loss and fragmentation of suitable owl habitat and imperil the continued existence of the owl. The ISC recommended an alternative conservation strategy that would designate large reserves, called Habitat Conservation Areas (HCAs), to be well-distributed over the range of the owl. Ideally, each HCA should provide sufficient suitable habitat for at least 20

pair-sites, with the lands between managed to facilitate -movement (dispersal) of owls among HCAs.

The implications of the ISC report for management of the California spotted owl became apparent immediately. In May of 1990, the R5 Regional Forester requested assistance from PSW Research Station in additional data collection and analysis for the California subspecies. Emphasis on Sierra Nevada NFs was changed from conducting a third year of RD&A monitoring to inventory of presumed owl habitats not previously surveyed. These habitats were primarily low-elevation oak woodlands, pine-oak forests, and high-elevation red fir forests.

In April of 1991, R5 and PSW Research Station began a cooperative venture with CDF and other State and Federal agencies to assess current information on the California spotted owl. A Steering Committee with representatives from various State and Federal agencies and other interested parties was formed to oversee the entire effort (Chapter 1). The Steering Committee established two teams. A Technical Assessment Team was designated to synthesize and interpret all current information available on the California spotted owl, and to evaluate various management alternatives for the subspecies. A Policy-Implementation Team was designated to evaluate impacts of the Technical Assessment Team's recommendations, to determine whether they fall within existing policies and regulations, and to propose least-cost/low-impact ways to implement them. The Steering Committee will make final recommendations to the responsible agency heads based on reports from the two teams. This report is the product of the Technical Assessment Team.

Current Management

The range of the California spotted owl is considered to include the southern Cascades south of the Pit River in Shasta County, the entire Sierra Nevada province of California, all mountainous regions of the southern California province, and the central Coast Ranges at least as far north as Monterey County (Grinnell and Miller 1944, Gould 1977). Within this range, the owl occurs on 13 NFs, the Lake Tahoe Basin Management Unit (LTBMU) administered by the FS, four National Parks (NPs), several State Parks and Forests, private timber lands, scattered BLM lands, and other minor ownerships (fig. 4A, 4B, and 4C). This includes a portion of the Toiyabe NF, which is administratively a part of the Intermountain Region of the FS.

One of two major subdivisions of the total California spotted owl population occupies the southern Cascades and the Sierra Nevada, an area roughly 400 miles long by 50 miles wide. The other occupies mountains of southern California, primarily the San Bernardino Mountains and isolated mountains southward nearly to the Mexican border, the San Gabriel Mountains, the Tehachapi and nearby mountains westward to the coast, and the central coastal mountains (fig. 9A).

Sierra Nevada Province

The Sierra Nevada Province, as used here, includes the conifer forests and foothill riparian/hardwood forests of the Sierra Nevada and the southern end of the Cascade Mountains. Most known California spotted owls and suitable habitat occur on public lands on the west slope of the Sierra Nevada, primarily in seven NFs and in Yosemite and Sequoia/Kings Canyon NPs. Spotted owls also occur on scattered BLM lands along the Sierran foothills, but few surveys have been done on those lands. Large blocks and scattered parcels of private timberland occur within most NFs within the range of the owl in the Sierra Nevada. Recent surveys by timber companies indicate considerable spotted owl use on some of those lands.

Since 1973, agency and public concern for the status of the California spotted owl has been in regard to timber management on the seven westside Sierra NFs and on private industrial timberlands. Even though the NPs experience high recreation impacts in local areas, NP management has not been an issue because the emphasis of the NPS generally is believed to be compatible with maintaining habitats needed by the owls.

The Sierra Nevada owl population is contiguous throughout the mountain range's 400-mile length but is probably poorly linked to the southern California population through the Tehachapi Mountains and the Liebre/Sawmill area east of Interstate Highway 5. The California spotted owl connects to the northern spotted owl in eastern Shasta County.

Forest Service, Pacific Southwest Region (R5)

From north to south, the Lassen, Plumas, Tahoe, Eldorado, Stanislaus, Sierra, and Sequoia NFs in the Sierra Nevada all have major populations of California spotted owls. These NFs have a

total land base of 6,978,900 acres, about 73 percent of which (5,093,600 acres) is forested. About 50 percent of this land base, or 3.5 million acres, are forest types considered current or potential spotted owl habitat (USDA, FS 1986b, 1988a, 1988c, 1988e, 1990, 1991a, 1991b). The major forest types comprising known and potential habitat are Sierran mixed-conifer, red fir, ponderosa pine/hardwood (montane hardwood), eastside pine, and foothill riparian/hardwood (Chapters 5 and 6) (descriptions in Chapter 1). Mixed-conifer is the most abundant type with the most owl sites; the others are less abundant and have far fewer owl occurrences (table 3A).

The LMP directions for Sierran Forests resulted in the designation of 264 SOHAs in approved or draft Forest LMPs (Lassen 40, Plumas 54, Tahoe 33, Eldorado 32, Stanislaus 36, Sierra 29, and Sequoia 40) (table 3B). Of the 264, 249 are on lands suitable and otherwise available for timber production. The other 15 are on lands unavailable for timber production, either because of Congressional classification (Wilderness or Wild Rivers) or because of other Forest LMP allocations. The total land allocation for these 264 SOHAs is about 454,000 acres, of which about 110,000 would be managed under low-yield, even- or uneven-aged management (USDA, FS 1986b, 1988a, 1988c, 1988e, 1990, 1991a, 1991b).

The management direction for SOHAs is to maintain at least 1,000 acres of suitable spotted owl habitat within a 1.5-mile radius of the known or potential spotted owl nest site. Suitable habitat is described as mature timber stands having (1) multi-storied canopies with 70 percent or greater total cover, (2) 40 percent or more of the total canopy in trees 21 inches or more in d.b.h., and (3) well-developed decadence (USDA, FS 1984).

Further, the direction calls for replacement of the suitable habitat over time, based on the certainty that forest stands un-

Table 3A—Known California spotted owl sites, by habitat type on National Forests and National Parks in the Sierra Nevada, 1987-1991.

Location	Eastside pine	Red fir	Mixed-conifer	Ponderosa pine/montane hardwood	Riparian/hardwood	Number sites sampled ¹	Breeding pairs found ²
National Forests							
Lassen		8	97			105	36
Plumas	3	9	195	15		222	56
Tahoe		11	135	8		154	38
Eldorado		10	149	1		160	53
Stanislaus		11	97	10		118	26
Sierra		41	86	23	10	160	25
Sequoia	3	9	95	12	9	128	22
Inyo		1				1	1
Lake Tahoe Basin Management Unit		2	1			3	
National Parks							
Yosemite		9	46	1		56	6
Sequoia/Kings Canyon		3	58	9		60	12
Grand total	6	114	959	79	19	1,177	275
Percent	<1	10	81	7	2	100	

¹ Data based on NF and NP information for all known owl sites where habitat information was available. (This included some single owl sightings not considered to be "owl sites.") Table 3B should be used for official, total count of spotted owl sites, as it is based on interpretation of NF data along with information from private lands to avoid duplication.

² Data on sites where young were produced provided by NFs and NPs.

Table 3B-Estimated numbers of California spotted owl sites in the Sierra Nevada, by ownership.

Land	Total known sites (known pairs)				SOHAs				Sites in reserved areas	
	1970-91		1987-91		Estimated additional sites	Total per National Forest	Number with pairs ¹	Total number of pairs ²	1970- 1991	1987- 1991
National Forests	Federal Lands									
Lassen	111	(73)	111	(73)	26-31	40	36	42	23	1
Plumas	228	(113)	228	(112)	38-50	54	39	46	53	4
Tahoe	150	(83)	118	(75)	46-57	33	28	33	2	2
Eldorado	180	(125)	177	(123)	10-21	32	28	41	0	0
Stanislaus	131	(47)	118	(49)	15-25	36	23	23	3	3
Sierra	175	(86)	157	(81)	50-52	29	16	20	153	12
Sequoia	127	(77)	114	(71)	32-41	40	27	31	223	17
Lake Tahoe Basin Management Unit	3	(1)	2	(1)	?	0	0	0	0	0
Toiyabe	2	(0)	0	(0)	?	0	0	0	0	0
Inyo	5	(3)	3	(1)	0	0	0	0	2	1
Subtotal	1112	(608)	1028	(586)	217-277	264	197	236	51	40
National Parks										
Lassen	5	(2)	4	(2)	?				5	4
Yosemite	56	(17)	56	(16)	26-41				56	56
Sequoia/Kings Canyon	60	(42)	60	(41)	20-22				60	60
Subtotal	121	(61)	120	(59)	46-63				121	120
Bureau of Land Management										
All Lands	6	(3)	1	(1)	?				0	0
Total Federal	1239	(672)	1149	(646)	263-340				172	160
State of California										
State Parks	1	(1)	1	(1)	?				1	1
Other State	2	(1)	2	(0)	?				1	1
Private Lands										
Industrial forests	58	(32)	49	(29)	?					
Other private	67	(26)	49	(21)	?					
Total Sierra Nevada	1367	(732)	1250	(697)					174	162

¹ Number of SOHAs with at least one pair.

² Total number of pairs in all SOHAs (counting all pairs in each SOHA).

³ Indicates that FS data were augmented by information from CDFG's database.

dergo natural events such as fire, insect and disease attack, and windthrow that may render them unsuitable for spotted owls. The Forests were given a choice of three strategies for replacement: (1) no scheduled harvest, (2) uneven-aged management and (3) even-aged management. An option of no scheduled harvest requires that 650 additional acres of suitable or near-suitable habitat be designated to supplement the 1,000 acres, for a total of 1,650 acres for each SOHA. SOHAs selected for uneven-aged management must have replacement habitat of 1,000 acres and all 2,000 acres can be managed using selection harvests and an implied rotation period of 300 years. SOHAs selected for even-aged management must have 1,650 acres of replacement habitat, and the entire 2,650-acre SOHA is to be managed using clearcut and shelterwood prescriptions and an implied rotation of 240 years (USDA, FS 1984).

Most NFs have already designated management of their SOHAs, but a few will designate the management system as timber sales are planned. Essentially all SOHAs on the Lassen, Eldorado, Stanislaus, Sierra, and Sequoia NFs will be managed as "no scheduled harvest." SOHAs on the other NFs will be a

combination of management strategies. The Inyo NF and LTBMU have the same direction as westside NFs, but they were not required to establish SOHA networks because the LTBMU has no regulated timber program and the Inyo timber program is small. Both units have 1-3 spotted owl sites, and essentially all suitable habitat at these sites is protected. The Toiyabe NF, which is adjacent to the Inyo NF and LTBMU on the east slope of the Sierra Nevada is part of Region 4 of the FS. It has only 1-3 spotted owl sites and essentially all suitable habitat is protected (Coburn pers. comm.)

From 1981 to 1987, most spotted owl surveys done on NFs in the Sierra Nevada focused on verification of pairs in network SOHAs. Prior to 1987, this was generally done using a three-visit method without rigid survey requirements. In 1987, however, the Spotted Owl RD&A Program established strict protocols for monitoring SOHAs in R5 and R6. These protocols require up to six visits, methodical coverage of the SOHA and special nest-detection techniques that markedly increased the information acquired. In 1988 and 1989, NFs in the western Sierra Nevada participated in the RD&A Program by monitoring ran-

dourly selected SOHAs and Random Sample Areas (RSAs). Seventy-two SOHAs and 86 RSAs were selected as part of the sample in the Sierra Nevada. Verification of other SOHAs with little or no occupancy history was also made a high priority during this period. Many of those other SOHAs, especially at remote sites, had not been surveyed previously.

In 1988, RD&A monitoring of RSAs began to add information to a meager database of owl locations outside network SOHAs. In 1989, RS direction specified that field surveys be done for the preparation of biological evaluations for spotted owls in proposed timber sales. Surveys in 1989 and 1990 included improved coverage of project areas, similar to the RD&A monitoring method, but they required only three visits. Because of an extended drought affecting the Sierra Nevada, most NFs have had extensive insect mortality among conifers in the last few years, resulting in a much-expanded salvage sale program that involved large portions of the NFs. Spotted owl surveys for proposed green and salvage sales since 1989 have covered much more land outside SOHAs, and to a higher standard, than all previous surveys combined. In 1991 the protocol for project surveys for spotted owls was changed to match that used for the northern spotted owl. This entailed six visits with longer time periods between visits, ensuring a higher likelihood of detecting owls that might be present.

Protecting owl habitat in network SOHAs has been the policy since 1982 except where natural events have impacted the habitat to the extent that management actions to benefit the owl are justified. Direction for management of, spotted owl habitat outside network SOHAs, however, has not been as static. Sites outside network SOHAs received little or no protection before 1989. FS direction in 1989 on field surveys and biological evaluations for owl sites outside network SOHAs created concern and controversy in the NFs. Most Forests were hurrying to complete LMPs based on Regional Guidelines for networks intended to ensure viability. Emerging research on the northern and California subspecies cast doubt on the adequacy of that approach, however, and many biologists preparing biological evaluations concluded that many non-SOHA habitat areas might be needed to maintain viability of the California spotted owl. Release of the ISC report (Thomas et al. 1990) further eroded confidence in the efficiency of the SOHA network.

Protection was given to non-network spotted owls on a case-by-case basis in 1989 and 1990. Generally, more protection was given to pairs and nest sites than to single owls, but policies varied among Forests, Districts, and cases. Where extra measures were afforded, they usually involved habitat protection ranging from 40 to 300 acres and exclusion of sale-related activities between 1 March and 30 August for pairs known to be nesting. For insect salvage sales, protection entailed snag retention in the protected zone comparable to network SOHA standards. Occasionally, similar protection was given to some single birds where pairs were suspected.

In 1991, commensurate with higher standards for field surveys, RS established interim policy for evaluating and mitigating effects of timber sales on spotted owls not otherwise protected in the Sierra Nevada. The direction to NFs was to see that projects did not directly or indirectly affect spotted owls by removing

nesting or foraging habitat. This involved the use of home-range study data on the California spotted owl to estimate the territorial needs of known and potential owl pairs. The objective of the policy was to assure a full range of options for managing spotted owls by maintaining the population at current levels until the agencies could consider new directions based on recommendations of the Steering Committee.

Since 1970 biologists have identified California spotted owls at 1,112 sites (an area with either a pair or a single where a pair could be supported—see glossary) in NFs in the Sierra Nevada province. In the last 5 years (1987-1991) 586 pairs have been verified at 1,028 of these sites (table 3B). The NFs estimate a potential for approximately 250 more sites. Of the 264 network SOHAs identified in the LMPs that are managed exclusively for California spotted owls, pairs have been verified at 197 sites, including 107 sites where reproduction has been documented.

National Park System, Western Region

Four NPs are located in the southern Cascades and Sierra Nevada, within the range of the California spotted owl. Sequoia/Kings Canyon NPs, Yosemite NP, and Lassen Volcanic NP have land bases of 863,710 acres, 749,031 acres, and 106,298 acres, respectively, for a total of 1,719,039 acres. Thirty-six percent (315,933 acres) of Sequoia/Kings Canyon NPs is forested and within the elevational range of the owl, and 15 percent (133,561 acres) is considered suitable for foraging or nesting. In Yosemite NP, 75 percent (564,500 acres) is forested, and 35 percent (263,126 acres) is considered suitable for foraging or nesting by owls (Steger pers. comm.). Lassen NP is approximately 94 percent (100,100 acres) forested, but few surveys have been done there; about 60 percent (64,600 acres) of that is in yellow pine and fir forests (Husari 1990), and may be suitable spotted owl habitat.

The NPS manages the Parks to emphasize preservation and maintenance of natural communities and ecological processes. Their policy states that "Natural processes will be managed with a concern for fundamental ecological processes as well as for individual species and features. Managers and resource specialists will not attempt solely to preserve individual species (except threatened or endangered species) or individual natural processes; rather, they will try to maintain all the components and processes of naturally evolving park ecosystems, including the natural abundance, diversity, and ecological integrity of the plants and animals" (USDI, NPS 1988).

In addition, the NPS "will identify all state and locally listed threatened, endangered, rare, declining, sensitive, or candidate species that are native to and present in the parks, and their critical habitats. These species and their habitats are considered in NPS planning and management. Based on an analysis of the status of state and locally listed species throughout their native ranges and throughout the national park system, the National Park Service may choose to control access to critical habitats or to conduct active management programs similar to activities conducted to perpetuate the natural distribution and abundance of federally listed species."

The spotted owl is recognized as a special status species by the NPS, but specific management direction has not been devel-

oped. Resource management plans for the NPs will be revised as each unit determines what special management, if any, is needed (van Wagtenonk pers. comm.).

Known owl sites since 1986 total four in Lassen Volcanic NP, 56 in Yosemite NP (Roberts et al. 1988), and 60 in Sequoia/Kings Canyon NPs (Roberts 1989, Steger pers. comm.) (table 3B). We estimate that the NPs may contain owls at another 55 sites. Most of the information for Yosemite and Sequoia/Kings Canyon NPs was obtained by the CDFG and PSW Research Station in special surveys and studies done since 1988. Yosemite and Sequoia/Kings Canyon NPs are considered critical by the CDFG and FS as reserves for maintaining population viability and for movement by spotted owls between NFs in the Sierra Nevada.

Bureau of Land Management, California Office

The BLM administers scattered public lands along the foothills and lower slopes of the southern Cascades, Sierra Nevada, Transverse Ranges, central Coast Ranges, and southern California mountain ranges. Some of these support forest, woodland, and foothill riparian/hardwood habitats that are potentially suitable for California spotted owls. Commonly, potential owl habitat on BLM land occurs in small tracts (less than a section) and may be located adjacent to NFs or intermingled with private timberlands. Along the Merced, Tuolumne, American, Yuba, Stanislaus, and Mokelumne Rivers, however, their lands are concentrated in blocks of several thousand acres (Saslaw 1991).

In the northern Resource Areas, forest management includes green timber sales, thinning for timber stand improvement, fire and insect salvage, and forest sanitation. Forested lands of the BLM in California are managed primarily under uneven-aged prescriptions that remove 40 to 60 percent of the volume and up to 30 percent of the stems. Between 1981 and 1990, 25,691 acres were logged under a partial-cut prescription, and 238 acres (1 percent) were logged as clearcuts, generally between 2 and 4 acres in size. Many unharvested locations were within riparian buffer areas, usually 100 feet on each side of the stream, and may be within special recreation management areas along major streams. Future management in the Folsom Resource Area is expected to be custodial, with forest management prescriptions designed to meet wildlife and vegetation objectives. Emphasis will be on managing for old-growth, special wood products, and stand maintenance. Logging will be directed to fire and insect salvage and forest sanitation. Forest management on the Redding, Alturas, and Eagle Lake Resource Areas will continue to use uneven-aged methods.

Potential suitable habitat has been mapped based on BLM forest operation inventories, Timber Production Capability Classification maps, CDF oak woodland maps, BLM vegetation surveys, and records of owls from the CDFG and nearby NF lands. About 68,500 acres of BLM land are considered to be potential habitat for the California spotted owl, based on habitats they are known to use elsewhere in the Sierra Nevada (Saslaw 1991) (table 3C).

Inventories for California spotted owls on BLM lands were initiated in 1989 for forest management or land exchange proposals that could potentially affect spotted owl habitat. Because the BLM has only recently begun systematic inventories for

spotted owls, information on their distribution and numbers is unavailable. This precludes an estimate of the number of California spotted owls inhabiting BLM lands. They have been observed at six sites on BLM lands in the Sierra Nevada, however, and we believe there is potential for more.

California State Parks

Seven units of the California Department of Parks and Recreation with known or potential spotted owls occur in the Sierra Nevada. Management on State Park (SP) lands is similar to that of the NPs. All wildlife and plants are protected and sensitive species receive special care. Most units are designated as State Parks (SPs) and State Historical Parks (SHPs), with a total area of 16,580 acres. The SPs with the most potential for spotted owl are Plumas-Eureka SP with about 3,000 acres of conifer forest, Malakoff Diggins SHP with 1,500 acres of conifer forest, South Yuba River Project with 1,500 acres of conifer and oak habitats, and Calaveras Big Trees SP with 5,750 acres, mostly in old-growth conifer forest (Bakken pers. comm.). Spotted owls have been found on adjacent NFs and Calaveras Big Trees SP (2 pairs), Malakoff Diggins SHP (single owl) and Growers Hot Springs SP (single owl). Surveys, none of which are recent, have been conducted only at Calaveras Big Trees and Growers Hot Springs SPs and the potential exists for owls at the other larger units.

California State Forests

Mountain Home State Forest (SF) and Latour SF are State-owned forests managed by the CDF for demonstration of forestry practices and to support cooperative research with other agencies. Uneven-aged silviculture is featured in both SFs, including both single-tree and group-selection methods on a sustained yield basis. Other multiple uses are also emphasized, primarily recreation. Known owl activity centers would be protected from planned projects through review and advice from the CDFG.

Located in Tulare County, Mountain Home SF includes 4,807 acres, with Sierran mixed-conifer and giant sequoia stands that provide potential owl habitat on the entire property. About 960 acres of old-growth forest remain. Surveys have been done only around the edges of this SF by FS biologists, but they provide evidence of use by spotted owls. Probably two or three pairs occur there (Dulitz pers. comm.).

Table 3C--Potential suitable habitat for California spotted owls on Bureau of Land Management lands.

BLM District Resource Area	Acres
Susanville	
Alturas	13,337
Eagle Lake	18,936
Ukiah	
Redding	12,250
Bakersfield	
Folsom	24,000
Total	68,523

Latour SF is located in Shasta County and encompasses 9,033 acres. It was surveyed for spotted owls in 1990 and 1991, with one pair discovered in 1990 (McNamara pers. comm.). This SF has 7,000 acres of mixed-conifer and fir forest that are potential owl habitat, but only 2,000 acres have significant large-tree components (6+ trees per acre at least 32 inches in d.b.h.).

University of California

Blodgett Forest Research Station, located in Eldorado County within the Eldorado NF, is a 3,000-acre facility owned and operated by the University of California, Berkeley. It provides a setting for research on all aspects of forest management in Sierra Nevada mixed-conifer forests, especially research done as part of the forestry program at the University. Blodgett Forest has approximately 2,000 acres of suitable habitat for California spotted owls and typically one or two pairs nest in the area (Heald pers. comm.).

Whitaker Forest is a 320-acre unit located between the Sequoia NF and the General Grant area of Kings Canyon NP. Most of it is suitable owl habitat including giant sequoia stands. The property is used for research, with emphasis on sequoia natural history (Gasser pers. comm.). This unit has a long history of spotted owl observations and has supported at least a single owl over the last 5 years.

Private Lands

Private lands in the Sierra Nevada that are classified as timberland and have the potential to grow forest habitats used by California spotted owls encompass about 2.4 million acres, much of which is currently in suitable condition. Of this, 1.45 million acres are owned by industrial private timber companies (IPs) and

0.96 million acres are owned by miscellaneous private parties (MPs) not primarily engaged in commercial timber production (Colclasure et al. 1986, Hiserote et al. 1986, Lloyd et al. 1986) (table 3D). The latter group includes both large landowners, such as utilities and water districts, and many small landowners.

NFs in the Sierra Nevada include approximately 1.4 million acres of private land within their administrative boundaries (USDA, FS 1986b, 1988a, 1988c, 1988e, 1990, 1991a, 1991b) (table 3E). The other 1 million acres of IP lands are outside of NF boundaries. NF inholdings are much greater in extent in northern NFs (especially the Lassen, Plumas, and Tahoe) than in the southern Sierra Nevada. The Tahoe NF, with about 375,000 acres, includes the most private inholdings, and the Sequoia NF (with about 54,000 acres) has the least.

The spatial arrangement of private lands within NFs varies. Much of the private lands within the boundaries of the Lassen, Plumas and Stanislaus NFs tend to be in contiguous blocks, leaving NF lands also fairly contiguous. Most private lands on the Tahoe NF are in "checkerboard" ownership-alternating sections of private and NF ownership-and the Eldorado NF has a combination of checkerboard and contiguous block patterns. The checkerboard pattern is a vestige of Federal land policies used to stimulate development of the Nation's railroad system prior to establishment of the NFs. The Sierra and Sequoia NFs have relatively little interior private lands, and the four NPs have negligible amounts.

Except for historical railroad holdings, most lands belonging to IP companies were acquired with consideration for growth and yield potential. Therefore, they occupy most of the best tree-growing lands in the Sierra Nevada. Most IP timberlands are at middle elevations, in the mixed-conifer zone, but some are higher and farther east, in red fir and eastside pine zones. Almost all are within the elevation and geographic ranges of the California spotted owl. About 12 major companies have relatively large holdings in timberlands of the Sierra Nevada with eight owning at least 75,000 acres (Swing pers. comm.) Table 3D shows the total amount of IP and MP timberlands by county.

Systematic surveys for owls have not been done on most private lands, although several timber companies conducted surveys, using established FS protocols, starting in 1989, 1990, or 1991. Locations of owls found are not always available from timber companies, but it appears that some IP lands with a long

Table 3D--Acres of forest lands owned by commercial timber industries and miscellaneous private parties in the Sierra Nevada, by county, within the range of the California spotted owl.¹

County	Forest industry	Miscellaneous private
Shasta	194,000	54,000
Lassen	267,000	42,000
Tehama	120,000	19,000
Plumas	215,000	82,000
Butte	135,000	92,000
Yuba	26,000	23,000
Sierra	49,000	44,000
Nevada	60,000	137,000
Placer	95,000	79,000
El Dorado	121,000	117,000
Amador	25,000	31,000
Calaveras	68,000	71,000
Tuolumne	60,000	50,000
Mariposa	1,000	40,000
Madera	5,000	12,000
Fresno	10,000	22,000
Tulare	Trace	16,000
Kern	0	26,000
Total	1,451,000	957,000

¹ From Colclasure et al.1986, Hiserote et al. 1986, and Lloyd et al. 1986.

Table 3E---Approximate acres of private lands within National Forest boundaries (data from Forest LMPs as listed in references)

National Forest	Private land
Lassen	230,000
Plumas	226,000
Tahoe	375,000
Eldorado	190,000
Stanislaus	195,000
Sierra	109,000
Sequoia	54,000
Total	1,379,000

history of logging have a substantial number of owls, comparable in density to adjacent NF lands. We also know from one study that some IP lands with a history of intensive logging lack nesting owls, even though nest sites occur in adjoining NF lands (Bias and Gutiérrez 1988).

The public has recently attempted to pass forestry-reform initiatives for California, and the Legislature and Board of Forestry are also moving to provide new rules for logging on private lands. Emergency Regulations were recently in effect for IP timberlands in California, with the expectation they would be replaced with permanent policies. These policies will probably include requirements for sustained yield, less clearcutting, riparian protection, and special requirements for older forest stands. Although we cannot now assess the effects of new forestry regulations on the capability of private lands to support spotted owls, we believe those regulations will be more beneficial than past policies.

At the north end of the Sierra Nevada, a relatively continuous block of private timberlands in eastern Shasta County provides the habitat linkage for movement between populations by both northern and California spotted owls. Maintaining this connection is considered to be critical to the long-term conservation of both subspecies of spotted owls (Dawson et al. 1987, Thomas et al. 1990).

Owls are known to inhabit dense stands of hardwoods along stream channels at low elevations on the western edge of the Sierra and Sequoia NFs. These habitats resemble, in most respects, habitats used by many spotted owls in southern California. Similar habitats, with sparse stands of digger or ponderosa pine over denser stands of mixed hardwoods, occur along riparian zones west of NF boundaries from the Stanislaus NF north. Generally, these areas are not classified as commercial timberland. Livestock grazing has been the primary activity in these low-elevation habitats in the past, and type conversions, firewood cutting, and logging in and adjacent to riparian zones have also occurred. An increase in residential developments in the Sierra Nevada foothills is now impacting many of these potential owl habitats. The combination of residential development and indirectly related increased fire potential represent growing threats to habitat for both year-round and wintering spotted owls (Chapter 13). These areas have not been adequately surveyed for owls, although we suspect that they support many pairs.

Over the last 20 years, spotted owls have been located at 58 sites on IP lands and at 67 sites on MP lands in the Sierra Nevada. Twenty-nine and 21 pairs have been verified on IP and MP lands, respectively, in the last five years (tables 3B and 3F). There is no estimate of the potential number of spotted owl sites on private lands because of the small percent of those lands which have been surveyed and the lack of specific habitat information which could be used to estimate the distribution and numbers of spotted owls in lower elevation habitat types. We expect that these areas contain many owl sites but we estimate, based on the gross mapping of hardwood types, that number to be no more than one-third the total number of sites in conifer types.

Areas of Concern: Sierra Nevada

Spotted owl distribution in the Sierra Nevada Province is characterized by its continuity and relatively uniform density (fig. 4B). The ability of existing habitat to support owls does not appear to be a major problem except at the peripheries of the subspecies' range. This condition is normal for animal populations, however, and is not a concern unless the range begins to shrink. Five conditions give rise to some concern for the integrity of the California spotted owl's range in the Sierra Nevada: (1) bottlenecks in the distribution of habitat or owl populations; (2) gaps in the known distribution of owls; (3) locally isolated populations; (4) highly fragmented habitat; and (5) areas of low crude density of spotted owls. Areas occur throughout the length of the Sierra Nevada where one or more of these conditions currently limit the owl population; it might be of critical concern if conditions were exacerbated, or if they limit our knowledge of the owls there. This might lead to erroneous or more risky management decisions (fig. 3A, table 3G). These conditions may be caused solely or jointly by fire, land-ownership patterns, natural or human-caused fragmentation of suitable habitat, and by natural geographic features that control vegetation patterns. Rather than reflecting current negative effects on spotted owls, areas of concern identified in figure 3A simply indicate potential areas where future problems may be greatest if the owl's status in the Sierra Nevada were to deteriorate.

Areas A and B (fig. 3A) are bottlenecks in distribution where even relatively small losses of habitat could sever the interchange between adjacent populations of owls. In Area A, this would decrease the likelihood of interchange between the California and the northern spotted owl populations. This area of concern was identified for its importance by the Audubon Society's Spotted Owl Advisory Panel (Dawson et al. 1987) and by the Interagency Scientific Committee for the northern spotted owl (Thomas et al. 1990).

Areas A, B, 1, 4, 5, 7, and 8 are characterized by habitat fragmentation that decreases the density of owl pairs, makes successful dispersal more difficult, and reduces the likelihood of quick replacement of owls in vacated habitat.

Area 2 is a gap in the known distribution of spotted owls from the western to the eastern edge of the owl's range in the northern Sierra Nevada. If few birds and little habitat exist in this area, north-south dispersal could be impeded. This area and others (for example, areas 4 and 5) where few surveys have been done are, however, capable of producing owl habitat and may not be breaks in distribution.

Areas 5 and 6 also have low population densities. As in areas with fragmented habitat, low densities make dispersal more difficult and less likely to result in reoccupation of vacated sites.

Area 8 is characterized, in part, by small isolated populations that are more vulnerable to extinction by local stochastic or catastrophic events.

Table 3F—Estimated numbers of owl sites (confirmed pairs) on private lands in the Sierra Nevada, by county.

County	Industrial lands				Other private			
	1970-1991		1987-1991		1970-1991		1987-1991	
Shasta	5	(0)	5	(0)	4	(0)	3	(0)
Lassen	0		0		3	(1)	3	(1)
Tehama	6	(4)	6	(4)	0		0	
Plumas	8	(5)	7	(4)	10	(4)	10	(5)
Butte	9	(0)	5	(0)	7	(4)	5	(4)
Sierra	3	(2)	3	(2)	2	(0)	2	(0)
Yuba	0		0		3	(1)	1	(0)
Nevada	7	(6)	7	(6)	3	(2)	3	(1)
Placer	3	(3)	3	(3)	5	(1)	2	(1)
El Dorado	13	(8)	9	(6)	8	(3)	7	(2)
Amador	0		0		1	(0)	1	(0)
Calaveras	0		0		5	(0)	1	(0)
Tuolumne	4	(4)	4	(4)	7	(3)	3	(0)
Mariposa	0		0		4	(2)	3	(2)
Madera	0		0		0		0	
Fresno	0		0		4	(4)	4	(4)
Tulare	0		0		0		0	
Kern	0		0		1	(1)	1	(1)
Totals	58	(32)	49	(29)	67	(26)	49	(21)

Southern California Province

Spotted owls in southern California occur in 11 major mountain ranges and mountain complexes, predominantly on NF lands. These ranges and areas are the Santa Ana, San Diego (including the Laguna, Cuyamaca, Pine Hills/Vulcan, and Palomar mountain areas), San Jacinto, San Bernardino, San Gabriel, Liebre/Sawmill, Tehachapi, Tecuya Mountain area, Los Padres, southern Santa Lucia Mountains, and northern Santa Lucia Mountains (fig. 9A). Movement between these major ranges and complexes may be uncommon to nonexistent (Stephenson 1991). Within a given range, however, separate blocks of suitable habitat are relatively close together. For instance, the San Diego ranges include five of the mountain ranges mentioned above with populations 4.5 to 8 miles apart, but distances from the San Diego to the San Jacinto ranges and Santa Ana Mountains are 18 and 33 miles, respectively (Stephenson 1991). Historic records from the turn of the century documented spotted owls in riparian areas on the coastal lowlands, but their occurrence there today is unlikely because of the extensive loss of habitat to urbanization (Bloom pers. comm.).

Besides our concern that successful movement by owls among some of these relatively isolated islands of habitat may be declining or no longer possible, the southern California populations of owls may be isolated from the southern Sierra Nevada because of the nature of available connecting habitat. The Tehachapi Mountains, Liebre/Sawmill and Tecuya Mountain areas are critical for maintaining this linkage, if it still exists, and they are relatively distant from the nearest other known spotted owls in the San Gabriel Mountains and the southern Los Padres ranges.

Estimated owl sites, numbers of pairs, pair status, and distances from nearest neighboring populations of California spot-

ted owls for each of the 11 mountain areas are summarized in table 3H (Stephenson 1991).

Forest Service, Pacific Southwest Region (R5)

Most known spotted owl populations in southern California are on the Angeles, San Bernardino, Cleveland, and Los Padres NFs, with a total land base of 3,643,927 acres. The primary habitat types used are riparian/hardwood, live oak/bigcone Douglas-fir, and mixed-conifer (Chapter 5) (types described in Chapter 1), but in different proportions on the four NFs (table 3I). On the Angeles and San Bernardino, most spotted owls are found in live oak/bigcone Douglas fir at elevations of 2,000 to 5,000 feet and mixed-conifer (mostly Jeffrey pine) at elevations from 5,000 to 8,000 feet. These types cover 137,000 acres on the Angeles NF (20 percent of the landbase) and 308,000 acres on the San Bernardino NF (37 percent of the landbase). On the Cleveland NF most owls are found in similar habitats, including a total of 40,000 acres (9.6 percent of the landbase) but we believe that additional owls will be found in riparian/hardwood habitats when they are surveyed. These habitats make up 1-2 percent of the landbase on all four NFs (USDA, FS 1986a, 1987, 1988b, 1988d).

On coastal portions of the Monterey District of the Los Padres NF, large stands of redwoods on north slopes also provide owl habitat, but population surveys there are incomplete. Most owls on the Los Padres NF, especially in the southern block, are in narrow riparian corridors, where mixed hardwoods are closely flanked by chaparral.

Regional direction for the four NFs in southern California is to protect all known spotted owl sites and to manage the habitat based on local information about suitability and availability (USDA, FS 1984). FS surveys for occupancy and suitable habitat in southern California lags behind the Sierra Nevada Prov-

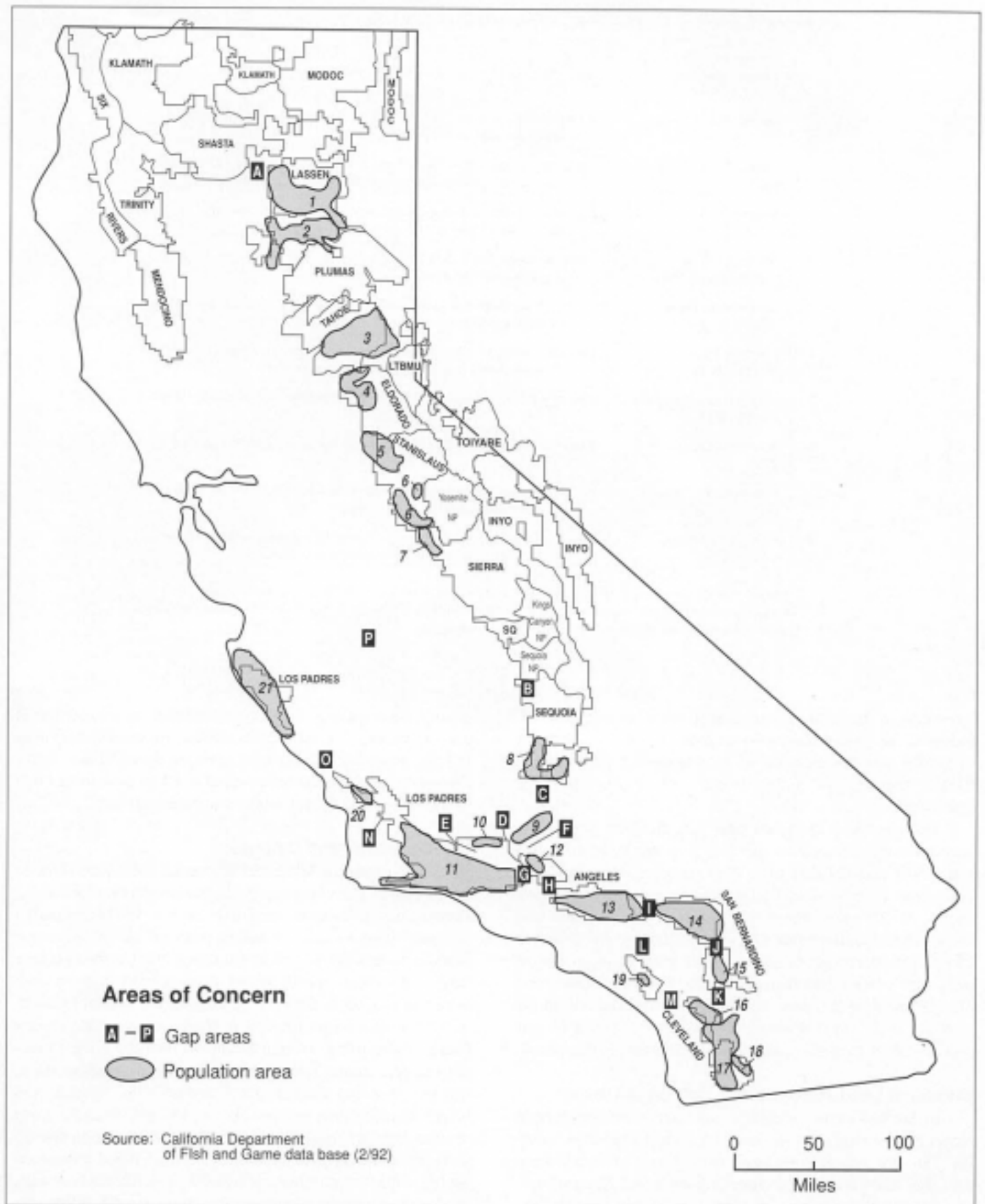


Figure 3A—Areas of current and potential concern for the California spotted owl. Gap areas delineate discontinuities in owl distribution; designated population areas have a variety of real or potential concerns, such as low population density, relatively fragmented habitat, or extensive loss of habitat from recent wildfires. Place names and reasons for concern are identified in tables 3G and 3K.

Table 3G—*Areas of concern for California spotted owls in the Sierra Nevada.*

Area ¹	General location (major ownership) ²	Reasons for concern
A	Eastern Shasta County (FS, IP)	A natural bottleneck between northern and California spotted owls; habitats are fragmented and owl densities low.
B	Central Tulare County (NPS)	Apparently a natural bottleneck in north-south distribution of owls because steep terrain provides only a narrow band of suitable habitat.
1	Lassen County (FS, NPS, IP)	Habitat in this area is discontinuous, naturally fragmented, and poor in quality due to drier conditions and lava-based soils.
2	Northern Plumas County (FS, IP, Pvt.)	A gap in known distribution, mainly on private lands, extends east-west in a band almost fully across the width of the owl's range.
3	Northeastern Tahoe NF (FS, IP, Pvt.)	An area of checkerboard lands; much dominated by granite outcrops and red fir forests; both features guarantee low owl densities.
4	Northern Eldorado NF (FS, IP, Pvt.)	Checkerboarded lands and large, private inholdings; owl densities unknown on some private lands and very low on others.
5	Northwestern Stanislaus NF (FS, IP, Pvt.)	Has large private inholdings; owl densities unknown on most private lands.
6	Southern Stanislaus NF (FS)	Burned in recent years; the little remaining habitat is highly fragmented.
7	Northwestern Sierra NF (FS)	Habitat naturally fragmented, due partly to low elevations and dry conditions; fragmentation accentuated by logging.
8	Northeastern Kern County (FS)	Only small, semi-isolated groups of owls in the few areas at elevations where habitat persists at the south end of the Sierra Nevada.

¹ Location codes correspond to letters (gaps and bottlenecks) and numbers (population areas) on figure 3A.

² Ownership codes: FS = USDA Forest Service; NPS = National Park Service; BLM = Bureau of Land Management; IP = Private industrial lands; Pvt. = multiple, small, private ownerships.

ince because threats to the population from management appeared to be less imminent in southern California. Southern California was not included in the monitoring phase of the RD&A Program, and funding for other survey efforts has been inadequate.

Three hundred seventeen sites with pairs or single owls have been documented on the four southern California NFs since 1970, and 294 sites since 1986 (table 3J). Over the last 5 years, pairs have been verified at 214 of these sites with reproduction at 107 sites. About 42 percent of known sites were located in the San Bernardino Mountains (LaHaye and Gutiérrez 1990). This probably reflects a higher relative abundance of owls over a larger area than elsewhere in southern California. The NFs estimate that approximately 190 additional sites might currently exist. The 294 sites identified since 1986 are 85 percent of all sites located in southern California during that period.

Bureau of Land Management, California Office

BLM lands are relatively few and scattered in the mountain ranges between the coast and inland deserts of southern California. They are located down-slope from, and in more arid areas than, NF lands and they include drainages and riparian/hardwood forests that may provide spotted owl habitat. In the California Desert District and the Caliente Resource Area, potential spotted owl habitats are managed for wildlife, riparian habitat

quality, water quality, and dispersed recreation. Total potential owl habitat, based on vegetation, in these two management units is 7,560 acres, but surveys have not been done (Saslaw 1991). One spotted owl site has been located on BLM lands in the last 5 years, the result of survey work on adjacent NF lands.

U.S. Department of Defense

Camp Pendleton Marine Base occupies about 125,000 acres on the coastal plain between the Santa Ana Mountains and the Pacific Coast in northern San Diego County. The higher part of the Base, with a small amount of potential habitat, abuts the Trabuco Ranger District of the Cleveland NF, but no owls have been found there recently (Buck pers. comm.). Spotted owls were observed about the turn of the century at several locations in riparian habitats on the coastal plain, including San Onofre Creek in what today is Camp Pendleton, but none is there today (Bloom pers. comm.). Santa Margarita Creek is another major drainage bisecting the Camp that probably had spotted owls historically, based on remnant bigcone Douglas-fir in the upper reaches, but the habitat has been too degraded by fire to support owls now (Bloom pers. comm.). The Base has a natural resource management program, including wildlife conservation, but long-term effects of training activities have degraded habitat for spotted owls to an extent that very little exists today (Buck pers. comm.).

Table 3H-Owl sites¹, number of pairs and status of pairs at those sites, pair status, and nearest-neighbor distances of California spotted owls in southern California²

Area	Owl sites (all years)	Pairs since 1987	Breeding since 1987	Potential population (no. sites)	Nearest neighbor distances ³
San Diego Ranges	37	18	6	76	18 -33 miles
Santa Ana Mountains	2	1	-	12	30 -40 miles
San Jacinto Ranges	20	16	9	29	11 -18 miles
San Bernardino Mountains	124	114	66	125	6 -11 miles
San Gabriel Mountains	54	22	5	95	6 -20 miles
Liebre/Sawmill Mountains	14	10	2	20	12 -20 miles
Tehachapi Mountains	4	0	-	12	unknown
Tecuya Mtn area	5	3	-	10	9 -12 miles
Los Padres	65	32	17	100	8 -12 miles
So. Santa Lucia Mountains	12	6	2	19	32 -45 miles
No. Santa Lucia Mountains	39	22	1	80	45 miles
Total	376	244	108	578	

¹ See definition of "owl site" in glossary (Appendix B).

² Based on Stephenson (1991) and California Department of Fish and Game database.

³ Where two distance values are shown (for example, 12-20 miles), they represent the distances to the two closest neighboring populations.

California State Parks

Five units of the SP system, totalling 58,182 acres, are in the vicinity of the Angeles, San Bernardino, and Cleveland NFs. Those with significant owl habitat are San Jacinto SP (about 12,500 acres of conifer and pine-oak forests), Cuyamaca Rancho SP (about 11,000 acres of conifer and hardwood forests), and Palomar Mountain SP (1,000 acres of conifer and hardwood forests) (Bakken pers. comm.). All three of these SPs have been surveyed for spotted owls in recent years. Based on research, existing habitat, and nine known sites, they could support 13 to 15 pairs of spotted owls (Stephenson pers. comm.).

Four additional SP units with a combined total of 300 acres of coastal conifer and hardwood habitats are on the central California coast and have potential for a limited number of spotted owls. These are Julia Pfeiffer Burns SP, Pfeiffer-Big Sur SP, Andrew Molera SP in Monterey County and Gaviota SP in Santa Barbara County (Bakken pers. comm.). Nojoqui Falls County Park is a 98-acre park which is part of the Santa Barbara County park system not far from Gaviota SP. It has had records of a spotted owl site since the early 1970s in riparian/hardwood habitat along Nojoqui Creek (Jimenez pers. comm.).

National Audubon Society

Starr Ranch, a 4,000-acre wildlife sanctuary owned and managed by the National Audubon Society, is located on upper Bell Canyon in Orange County, adjacent to the Trabuco Ranger District of the Cleveland NF (DeSimone pers. comm.). This area occasionally has nonbreeding spotted owls that move onto the property from NF lands, but they apparently do not nest there (Bloom pers. comm.).

Native American Tribal Lands

Several Native American Tribal Reservations are located in southern California; these have potential spotted owl habitat and a few documented sightings. The Pala, La Jolla, Santa Ysabel,

Mesa Grande, Los Coyotes, and Cuyapaipe Reservations all have potential habitat that has been identified by FS biologists from the Cleveland NF. Sightings indicate a population of at least four pairs, and known potential habitat could support a higher number. Activities and potential threats to spotted owls on these lands are unknown.

Other Private Lands

Major activities that threaten spotted owls on private lands in southern California are recreation, urbanization, fire, and water extraction from stream systems (Chapter 13). Both the San Bernardino and Cleveland NFs include significant areas of private land—about 145,000 and 120,000 acres, respectively (USDA, FS 1986a, 1988d). The San Bernardino NF surrounds the popular and rapidly growing mountain resorts of Big Bear Lake, Lake Arrowhead, Forest Falls, and Idyllwild. This is causing a loss of owl habitat, especially near Lake Arrowhead (Stephenson 1991). The situation on included lands on the Cleveland NF is not so severe, but expanding development and recreation on these lands pose long-term risks for the owl. Direct risks are caused by continual loss of suitable nesting habitat from these activities which fragments the already meager quantity of suitable habitat. An indirect risk is the decreasing ability of the FS to use prescribed burning to reduce fuel accumulations that can lead to stand-destroying fires, because of the potential risk of prescribed fires to residential areas as well as local air pollution regulations.

Urbanization and wildfires also affect owl habitat outside of and surrounding all four NFs. The Angeles and the Los Padres NFs do not have major problems with private inholdings, but they are experiencing residential development around their edges. Loss of habitat in these areas outside the forests reduce the quantity of suitable habitat around the edge of the isolated parcels of NF lands and occasional tracts of habitat on private lands. Additional impacts of urbanization are effects of fire management policies, recreation patterns, and diversions of wa-

Table 3I-Known California spotted owl sites, by habitat type, on and in the vicinity of National Forest lands in southern California, 1970-1991.

	National Forests				Total sites	Percent
	Angeles	San Bernardino	Cleveland	Los Padres		
Habitat types						
Riparian/hardwood		2	4	110	116	32
Live oak/bigcone	48	73	26		147	41
Douglas-fir						
Mixed-conifer	11	72	6	6	95	26
Redwood				2	2	>1
Total Sample¹	59	147	36	118	360	100
Reproductive sites						
Breeding pairs ²	10	82	7	8	107	

¹ Data provided by NFs for all sites with available information on habitats. Actual total counts of sites for southern California are given in Table 3J, based on CDFG's database.

² Data provided by NFs for sites where young were produced.

Table 3J-Estimated numbers of California spotted owl sites (pairs) in southern California.

Location	Total known sites (known pairs)				Sites in reserved areas		Estimated additional sites
	1970-1991		1987-1991		1970-1991	1987-1991	
Federal Lands National Forests Los Padres Angeles San Bernardino Cleveland Bureau of Land Management All lands Subtotal State and Local Lands State Parks Other State Local Parks Subtotal Private Lands Indian Nations Other (by county) Monterey San Luis Obispo Santa Barbara Ventura Kern Los Angeles San Bernardino Riverside Orange San Diego Subtotal Overall total							
	111	(62)	94	(61)	45 ¹	41	58-100
	59	(31)	56	(28)	9 ¹	7	40-80
	126	(114)	126	(114)	8	8	30-45
	21	(14)	18	(11)	3	3	14
	1	(0)	1	(0)			
	318	(221)	295	(214)	65	59	142-239
	7	(4)	7	(1)			13-15
	1	(0)	0				
	1	(1)	0				
	9	(5)	7	(1)			13-15
	4	(3)	4	(3)			
	2	(1)	1	(1)			
	2	(1)	0				
	3	(2)	2	(1)			
	0		0				
	5	(1)	4	(0)			
	3	(2)	3	(1)			
	16	(14)	16	(13)			
	7	(6)	7	(6)			
0		0					
7	(5)	4	(4)				
45	(32)	41	(29)				
376	(261)	343	(244)				

¹ Data from FS were augmented by information from CDFG's database for historical sightings only.

ter from streams for local residential use. These development; also accentuate the barriers separating owl populations. They also have the effect of reducing dispersal between blocks and the chance for population support from adjacent areas.

Over the last 5 years spotted owls have been found at 37 sites on private lands in all counties along the southern California coast except Ventura, Orange, and San Luis Obispo (table 3J). We expect these numbers to be low because most private lands are at elevations lower than "traditional" spotted owl habitat. Some surveys have been done in the gaps between NF lands and on NF lands with habitats similar to those found on private lands. Spotted owls have been located in local situations and at relatively low densities. We do not expect that further surveys will document additional, extensive populations that would dramatically change our current understanding of the species' distribution and density in southern California.

Areas of Concern: Southern California

Our concern for spotted owl populations in southern California is much greater than is the case for the Sierra Nevada, because processes are at work there that we believe will further isolate populations from one another and reduce the sizes of individual populations. These processes are likely to reduce the interchange of owls between populations (Chapter 9), lowering our estimates of the stability of the metapopulation in southern California. The likelihood of local extinction resulting from stochastic processes will increase if local populations are further isolated and suitable owl habitat declines.

Concern about the stability and persistence of the California spotted owl population in southern California centers on four factors: (1) Every population is separated from neighboring populations by unsuitable habitat; (2) even within mountain ranges, gaps occur in the known distribution of owls; (3) suitable habitat is highly fragmented; and (4) some areas have low crude densities of spotted owls. Whereas the Sierra Nevada contains one relatively contiguous population of spotted owls, southern California contains at least 11 populations separated from their nearest neighbors by at least 6 miles (figs. 3A, 9A; tables 3H and 3K). The gaps, in all but two cases, contain major highways, often urban development, and hotter, drier, lower elevations unsuitable for nesting, foraging, or dispersal.

The owl's habitat in the Sierra Nevada most often consists of relatively large areas with a fairly high proportion of suitable habitat. In southern California, even in areas with owls, the habitat is often restricted to narrow riparian strips separated from adjacent and similar habitat by open expanses of 1/2 mile or more of chaparral (Areas 10,11, 12, 15,17, 19, and 20 in fig. 3A, table 3K). The intervening areas are not amenable to changes that might result in their having suitable owl habitat.

Areas 9, 10, 11, 13, 17, 19, and 20 also have low crude densities, given the potential habitat that might be present. Estimates of low crude densities of owl pairs and individuals in many of these populations may be a result of insufficient survey work.

Conclusions

Diverse in character and geography, habitats of the California spotted owl are managed by several State and Federal agencies and various private landowners, most with different objectives and mandates. The FS has implemented policies to provide for conservation of the California spotted owl, but these policies have been challenged recently as a result of recommendations by the ISC for the northern spotted owl (see Thomas et al. 1990).

The extensive and nearly continuous nature of Federal land ownership in primary habitats of the California spotted owl over the length of the Sierra Nevada makes it feasible to implement a coordinated and effective conservation strategy there. We also believe that lands held by commercial timber companies and other private owners could make a substantive contribution to maintenance of the spotted owl population in the Sierra Nevada. Private timber companies differ in their land-management objectives and policies, however, and it is uncertain the extent to which future management of their lands will maintain suitable spotted owl habitat. The final form of expected new State forestry rules cannot be fully predicted except that, at a minimum, they will change logging practices on some private lands and probably benefit spotted owls as a net effect.

In contrast to the case in the Sierra Nevada, populations of spotted owls in southern California occur in relatively isolated blocks, primarily on mountain tops and in wooded ravines extending down the mountain sides, and most of these populations are small (Chapter 9). This island-like nature of owl distribution in southern California makes it especially challenging to contrive a conservation strategy for the bird, based solely on public lands. For a variety of reasons, southern California is losing spotted owl habitat for breeding, foraging, and dispersal. Among the primary reasons are residential developments in previously remote valleys and mountains, stand-destroying fires, increasing concentration of recreational activities in prime owl habitat, and the "mining" of water from streams within the range of the owl. These impacts will continue, leading to increased insularization of owls in the relatively small mountain ranges where they now occur. These are the primary risks facing continued spotted owl distribution in southern California. It will probably be impossible to maintain a viable population of spotted owls in southern California without stabilizing the amount and distribution of suitable habitat on public lands and without changes in land-use policies on private lands, especially those that adjoin public lands.

Table 3K-Areas of concern for California spotted owls in southern California.

Area ¹	General location (major ownership) ²	Reasons for concern
Gaps in known owl distribution		
C	East-central Kern County (Pvt., BLM)	A gap of 30 miles in the known owl distribution; believed to contain little or no suitable owl habitat.
D	Tejon Pass (Pvt., FS)	Includes Interstate 5 and has little suitable habitat; most is grasslands and chaparral.
E	Northern Ventura County (FS)	Has little suitable habitat; most is chaparral or pinyon-juniper woodlands.
F	Western Antelope Valley (Pvt.)	High desert with no suitable habitat.
G	Piru Gorge (FS, Pvt.)	Has little suitable habitat and bisected by Interstate 5; most of the area in chaparral.
H	Santa Clara River (FS, Pvt.)	Has little suitable habitat; includes State Highway 14 and associated developed areas; most of the area in chaparral and desert scrub.
I	Cajon Pass (FS, Pvt.)	Consists mainly of chaparral; bisected by Interstate 15.
J	Banning Pass (BLM, FS, Pvt.)	Mostly desert scrub and chaparral at higher elevations; has Interstate 10 and developments.
K	Anza area (BLM, FS, Pvt.)	Mostly chaparral; includes some grasslands, limited riparian woodlands, and semirural housing.
L	Los Angeles Basin (Pvt.)	No owl habitat; fully urban sprawl with some grasslands and residual chaparral areas.
M	Temecula area (BLM, Pvt.)	Mostly chaparral; includes Interstate 5; urbanization is increasing.
N	Cuyama River (FS, Pvt.)	Has little suitable habitat; contains chaparral and some semidesert scrub.
O	Northwestern San Luis Obispo Co. (Pvt.)	May contain some suitable hardwood and riparian habitat, but very poorly surveyed.
P	San Joaquin Valley (Pvt.)	Has little suitable owl habitat; most land in crops, grasslands, or residual desert scrub.
Population problems		
9	Tehachapi Mountains (Pvt.)	Habitat is fragmented and known owl density is low. This small population is isolated from the population to the south and probably from the population to the west.
10	Tecuya Mountain (FS)	Owl density is low and habitat occurs only in north-slope drainages. This small population is probably isolated from populations to the south and east.
11	Ventura/Santa Barbara (FS)	This is a large area with varying owl densities and distributions of habitat. Except for the San Rafael Wilderness Area, populations are scattered in suitable habitat, mostly in north-slope drainages. The population here is probably isolated from other populations to the northwest, northeast, and east.
12	Liebre/Sawmill (FS)	Area has a limited population in suitable habitat on the north sides of mountains; owls are isolated from the population to the southeast and probably from the ones to the north and west.
13	San Gabriel Mountains (FS)	Large area varying in habitat distribution and owl densities; much habitat is mixed-conifer or bigcone Douglas-fir/oak. This population is isolated from the population to the northwest and probably from the one to the east.
14	San Bernardino Mountains (FS)	Contains the largest population and most extensive owl habitat in southern California; at least partially isolated from the population to the west and maybe totally from the one to the south.
15	Mount San Jacinto (FS)	Most habitat here is bigcone Douglas-fir/oak on south and west sides of the mountain. The limited population is isolated from populations to the north and southwest.
16	Palomar Mountain (FS, IP)	The mountain-top habitat is mixed-conifer and bigcone Douglas-fir/oak. The owl population is isolated from populations to the northwest and northeast but is continuous with the population to the south.
17	Central San Diego County (FS, NATL, Pvt.)	This population is spread sparsely through the canyons at lower elevations south from Palomar almost to the Mexican border. It includes some smaller mountains and links Palomar with Area 18. Habitat is usually oak in canyons. Surveys here have been limited and local.
18	Cuyamaca/Laguna Mountains (FS, CA)	Area consists of two adjacent mountaintops, both with small, local populations. Habitat is mixed-conifer and oak-dominated canyons. This is southern-most population in California and only links to populations further north in San Diego County.
19	Santa Ana Mountains (FS)	This range contains the smallest known population (two sites), both in conifer/oak habitat at heads of canyons on the range's west slope. This population is isolated by the Los Angeles Basin from populations to the southeast and north-northeast.
20	Southern Santa Lucia Mountains (FS, Pvt.)	This limited population exists in canyons dominated mostly by oak habitats. It is probably isolated from populations to the southeast and northwest.
21	Coastal Monterey County (FS, Pvt.)	This is the northern-most population of the California Spotted Owl on the coast. It occurs in a variety of habitats including the southern-most groves of coast redwood. It is isolated from the northern spotted owl by 100 miles of mixed habitat, including the highly developed San Francisco area. It is isolated from California spotted owls in the Sierra Nevada by the San Joaquin Valley.

¹ Location codes correspond to letters (gaps and bottlenecks) and numbers (population areas) on figure 3A.

² Ownership codes: FS = USDA Forest Service; BLM = Bureau of Land Management; CA = State of California; NATL = Native American tribal lands; Pvt. = multiple, small, private ownerships.

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Chapter 4

The California Spotted Owl: General Biology and Ecological Relations

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Understanding a species' ecology and life history and its role in ecosystem functions is vital to successful management of that species. The extent to which this understanding is comprehensive and correct is also critical. This chapter emphasizes life history elements and ecological relations of the California spotted owl that bear directly on planning for its management. In that sense, this is not an extensive, detailed treatment of the owl's biology and ecology. Nor does it provide a thorough analysis of some of the primary factors that must be considered, such as habitat relations, home ranges, density, and demography. Instead, because these components are so critical to conservation planning, and each requires extensive analyses, other chapters treat them in considerable detail.

Description and Classification

The spotted owl is generally mottled in appearance, the back is brown with irregular white spots and the underparts distinctly lighter, with white spots and brown barring. The facial disk is pale brown with concentric rings of darker brown and bordered by a ring of dark brown feathers. Pale "eyebrows" and "whiskers" merge into a conspicuous, light-colored "X" between the eyes and above the beak. Unlike most other owl species, which have yellow eyes, the eyes of spotted owls are dark brown. The beak is pale yellowish. Wings and tail are rounded and all flight feathers are dark brown with light-brown crossbars. The legs and toes are fully covered with short, pale-buff feathers, and the claws are dark brown to black. Adult males and females cannot be distinguished by plumage (Forsman 1981), but they are readily identified by voice and size (Forsman et al. 1984, Blakesley et al. 1990). Barrows et al. (1982) indicated that sexes can be distinguished by the number of tail bars, but Blakesley et al. (1990) found this characteristic to be unreliable. Moen et al. (1991) noted that first-year and second-year adults can be distinguished by the shape of the tips of their tail feathers.

Only four of the 19 species of owls occurring in North America are larger than the spotted owl (Johnsgard 1988). Based on live weights from a sample of 46 adult male and 48 adult female California spotted owls captured in the Sierra National Forest (NF) and Sequoia National Park (NP) (Steger pers. comm.), females averaged 22.2 ounces-13.6 percent heavier than the

average of males at 19.6 ounces. Weights of individuals captured more than once differed markedly, which is not surprising considering that some common prey items of spotted owls (for example, woodrats) weigh as much as a third of an adult owl's weight. For comparison, live weights of 65 female northern spotted owls captured in northwestern California averaged 23.2 ounces; 68 males averaged 20.3 ounces (Blakesley et al. 1990).

The American Ornithologists' Union (1957) recognized three subspecies of the spotted owl-California spotted owl (*Strix occidentalis occidentalis*) (Xantus 1859), northern spotted owl (*Strix occidentalis caurina*) (Merriam 1898), and Mexican spotted owl (*Strix occidentalis lucida*) (Nelson 1903). The Mexican form, found from southern Utah and Colorado southward into Arizona, New Mexico, and Mexico, is geographically isolated from the California and northern subspecies. The California spotted owl is confined to the State of California (figs. 4A, 4B, and 4C), where its distribution in the southern Cascade Mountains adjoins a south-eastern extension of the range of the northern spotted owl. This contact zone is along the Pit River, east of Redding.

Barrowclough (pers. comm.) has observed north-south clinal variation (gradual change) in morphology of northern and California spotted owls. Barrowclough and Gutierrez (1990) found no electrophoretic differences between the northern and California subspecies, so their study shed no light on the question of a taxonomic distinction. As in other such studies, however, only a fraction of the total genetic information was compared. The American Ornithologists' Union has consistently recognized two subspecies of spotted owls in California; this position was recently reaffirmed (N. K. Johnson pers. comm.).

Questions about whether the northern and California spotted owls are valid subspecies, however, are essentially irrelevant to concerns about the status of the owls. Spotted owls certainly move back and forth across the Pit River, and interbreeding between northern and California forms undoubtedly occurs in that area. Subspecies, by definition, are not reproductively isolated from each other. The important management questions relate to conditions of populations and habitats in various parts of the spotted owl's overall range, not to details of its subspeciation. The owl may be doing well in some areas but not in others. Where it is not doing well, we need to consider options for improving its status. Generally, this will involve improving habitat conditions and increasing the crude densities of owls to increase the efficiency of dispersal (Chapters 8 and 9). Maintaining the continuity of spotted owl populations from the northern Sierra Nevada into the southern Cascades and northwestern California is an important part of assuring the overall viability of both subspecies (Dawson et al. 1987, Thomas et al. 1990).

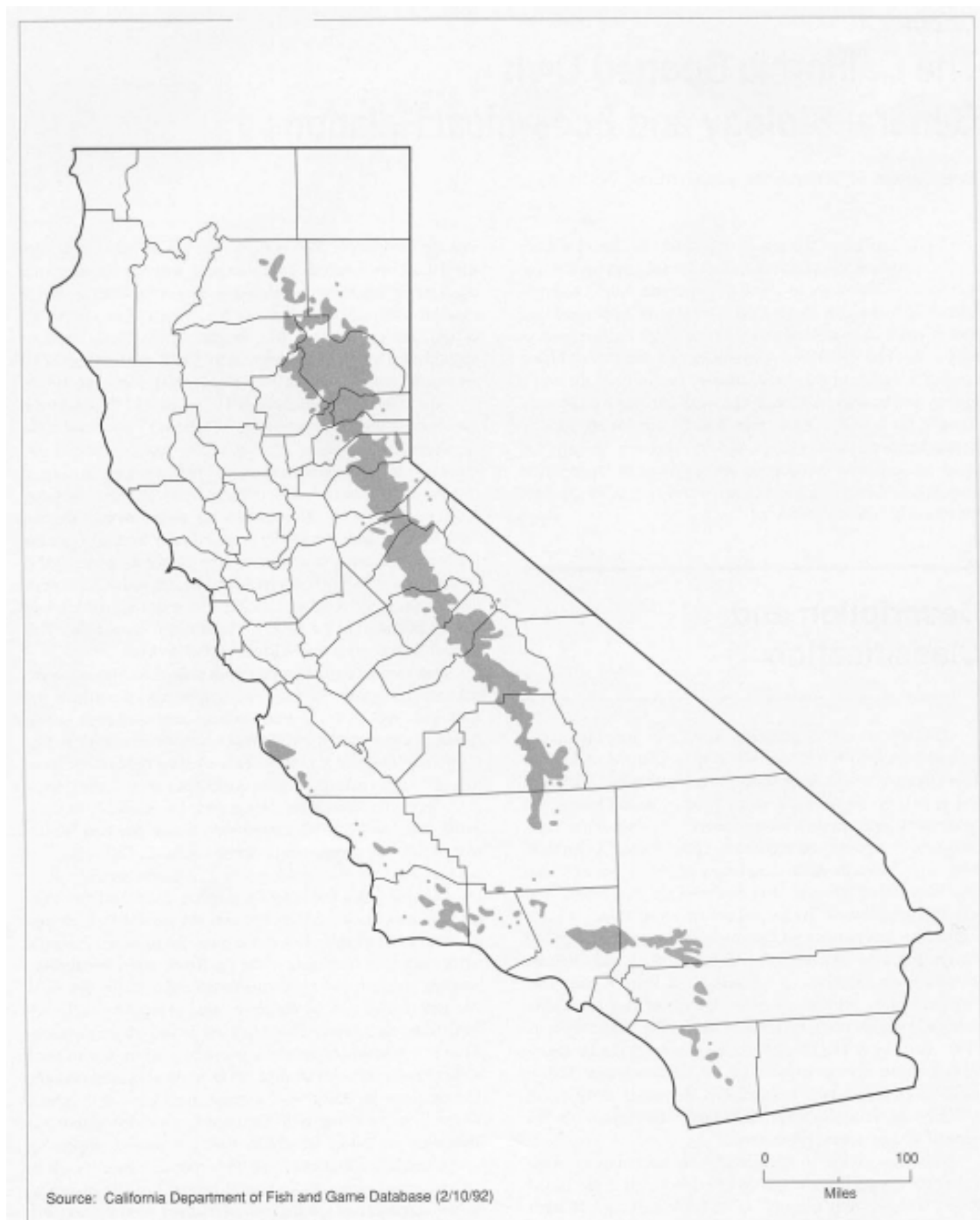


Figure 4A-Distribution of California spotted owls.

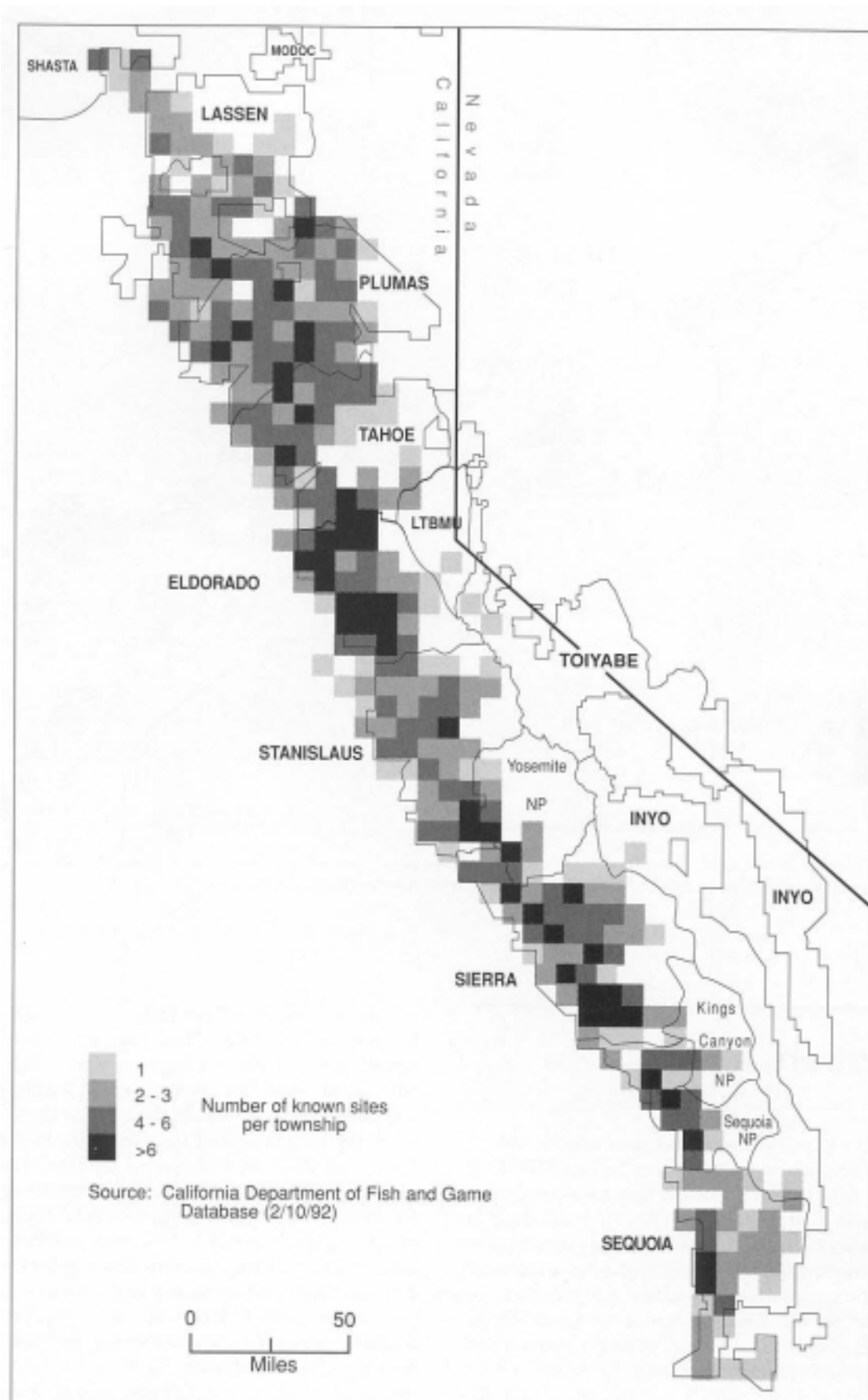


Figure 4B—Detail of the relative abundance of California spotted owls in the Sierra Nevada Province.

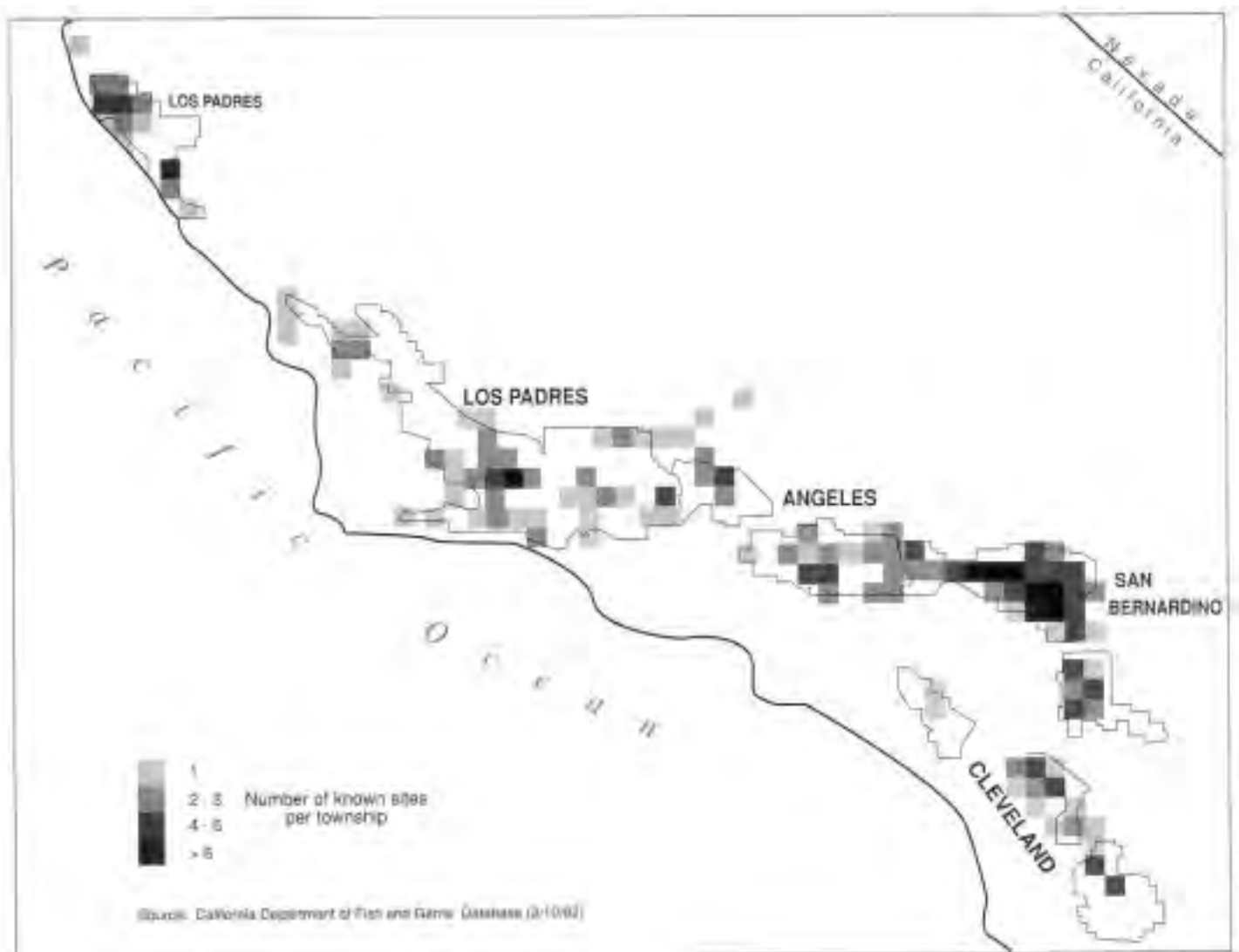


Figure 4C-Detail of the relative abundance of California spotted owls in the Southern California Province.

Distribution

The California spotted owl occurs in coniferous forests, mixtures of conifers and hardwoods, and in hardwood forests in the western Sierra Nevada; few locations have been documented east of the Sierran crest (figs. 4A and 4B). They also occur in conifer, conifer/hardwood, and hardwood stands in mountainous country of southern California, and in coastal mountains and foothills from the Santa Barbara area north at least into Monterey County (figs. 4A and 4C). Most owl pairs in the Sierra Nevada occur in the mixed-conifer forest type, but in the mountains of southern California they are almost equally represented in three major habitat types-mixed-conifer, live oak/bigcone Douglas-fir, and riparian/hardwood (tables 3A and 3I) (habitat types are described in Chapter 1 and Appendix B).

Areas in the coastal mountains north of Santa Cruz appear to have suitable habitats. These have not been inventoried adequately for owls, but they appear similar to others in the State where spotted owls are known to breed. Finally, spotted owls may also occur in denser stands of riparian/hardwood forests, especially in foothills bordering eastern portions of the Central Valley and along the south-central California coast (fig. 4D). The potential spotted owl habitat in lower-elevation hardwood forests depicted in figure 4D includes habitat within the ranges of both the northern and the California spotted owl. It encompasses about 5,000,000 acres, of which about 1,100,000 acres are rated "high" as potential owl habitat (Greenwood and Steger pers. comm.), with 625,000 acres of the high-potential habitat within the range of the California spotted owl. Essentially none of this has yet been surveyed for spotted owls, so we cannot estimate the number of pairs, if any, that may be located there. Obviously surveying these habitats, on a sample basis, is a priority need.



Figure 4D-Statewide distribution of potential California spotted owl habitat in lower-elevation hardwood forests.'

Habitat Associations

Quantitative details about habitat associations of California spotted owls are given in Chapters 5, 6, and 7. Generally, however, the birds occur only in habitats with substantial tree cover and especially with some larger, older trees present (see the set of color photos at the end of Chapter 5).

Nesting Habitat

Habitats used for nesting typically have greater than 70 percent total canopy cover (all canopy above 7 feet), except at very high elevations where canopy cover as low as 30-40 percent may occur (as in some red fir stands of the Sierra Nevada). Nest stands typically exhibit a mixture of tree sizes and usually at least two canopy layers, and some very large, old trees are usually present. Often these have large, natural cavities, broken tops, and/or dwarf mistletoe brooms. Nest stands in conifer forests usually have some large snags and an accumulation of fallen logs and limbs on the ground; downed woody debris is not a major component of nest sites in lower-elevation riparian/hardwood forests.

Spotted owls do not build their own nests but depend mainly on finding a suitable, naturally occurring site. Nest heights vary regionally-about 38 feet in riparian/hardwood forests at lower elevations; about 65 and 57 feet in conifer forests of the northern and southern Sierra Nevada, respectively; and about 58 feet in conifer forests in the San Bernardino Mountains (table 5K). In Sierran conifer forests, nests are usually in cavities or on broken-topped trees or snags. Less often they are on platforms associated with abandoned raptor nests, squirrel nests, dwarf mistletoe brooms, or debris accumulations in trees (Chapter 5). LaHaye (1988) found an increase from north to south in the proportion of platform nests used by northern spotted owls in a study in northwestern California. Similarly, cavity nests dominate nest types of California spotted owls in the Sierra Nevada, but platform nests predominate in the San Bernardino Mountains (table 5I). These trends probably reflect the distribution of stand ages rather than latitude.

Nest trees (details in Chapter 5) are typically large [mean diameter at breast height (d.b.h.) of about 45 inches for nest trees in Sierran conifer forests and 37 inches in the San Bernardino Mountains] and decadent. Among 124 nests found on NFs in the Sierra Nevada, 34 were in snags and 90 were in live trees. Eighty-two (66.1 percent) were in cavities and 19 (15.3 percent) were on broken tops of living or dead trees, or on dwarf mistletoe brooms. These conditions all tend to develop in older trees. Only 17 (13.7 percent) of the nests were on stick platforms built and used previously by other species (probably including goshawks, sharp-shinned hawks, ravens, and tree squirrels). Some owl pairs use the same nest cavity or platform repeatedly from year to year, some select new sites each year, and yet other alternate nest sites over time (Foreman et al. 1984, p. 31; R. J. Gutiérrez pers. observ.; LaHaye pers. comm.).

The species of nest trees used seems to depend on what is available, with 10 species of conifers and 7 species of hardwoods accounting for all nests in our database (table 5J). Locations of nest trees in the Sierran sample ranged in elevation from 1,000 to 7,740 feet, with 86 percent found from 3,000 to 7,000 feet in elevation. The highest elevation of nests increased from the northern to the southern Sierra Nevada (Lassen NF - 6,400, Plumas NF - 6,100, Tahoe NF - 7,000, Eldorado NF - 6,340, Stanislaus NF - 7,200, Sierra NF - 7,500, and Sequoia NF - 7,740 feet). The distribution of breeding spotted owls in the Sierra and Sequoia NFs extends down at least to 1,000 feet in elevation (Neal et al. 1989). The lower elevation of the study area with nests at 1,000 feet is bounded by a reservoir, so owls elsewhere may nest at even lower elevations. Few surveys have been done at these lower elevations. In southern California, nests ranged in elevation from 1,000 feet (Los Padres NF) to 8,400 feet (San Bernardino NF). The mean elevation of nest sites in the San Bernardino Mountains was about 6,000 feet.

Roosting Habitat

Stands used for roosting are similar to those used for nesting, with relatively high canopy cover, dominated by older trees with large diameters, and with at least two canopy layers. Studies of roosting northern spotted owls indicate that they respond to variation in temperature and exposure by moving higher or lower within the canopy, or around the roost tree, to access more comfortable microclimates (Barrows and Barrows 1978, Forsman 1980, Barrows 1981, Solis 1983, Forsman et al. 1984). The structure of multistoried stands characteristic of roost sites facilitates this movement. This observed response led Barrows and Barrows (1978) to propose that old-growth forests are necessary for spotted owls to avoid heat stress. Based on the following observations, however, we doubt that avoidance of heat stress is an essential benefit of old-growth forests: (1) California spotted owls are relatively common in riparian/hardwood forests in southern California and the Sierran foothills, where ambient temperatures are high during summer months. (2) A female nested in full sunlight on an abandoned Cooper's hawk nest platform in the Sierran foothills. While incubating, she was sometimes exposed to ambient temperatures exceeding 100 degrees Fahrenheit, and the developing young experienced like conditions (Steger pers. comm.). (3) Adult California spotted owls often roost in full sunlight or high in the canopy on hot days, which is not typical of northern spotted owls (R. J. Gutiérrez pers. observ.). We agree that the birds probably move about in a forest canopy to find a comfortable microclimate, but they seem to be able to tolerate relatively high ambient temperatures.

Foraging Habitat

Foraging habitats include suitable nesting and roosting sites, as well as more open stands, regularly down to 40-50 percent canopy cover, that are generally similar in structure and composition to nesting and roosting habitat. Typical conditions in conifer forests include:

1. A mixture of tree sizes, usually with some trees exceeding 2 feet in d.b.h., resulting in tree canopies at a wide range of heights in a stand but not necessarily in distinct layers. (Many sites depicted in the color photos at the end of Chapter 5 were taken in areas where spotted owls were known to forage.)
 2. Signs, of decadence-snags, overmature trees, downer woody debris (large logs are especially characteristic).
 3. The presence of hardwoods probably tends to enhance foraging habitat in conifer forests.
 4. Ample open flying space within and beneath the canopy
- Conditions in foraging habitat in hardwood stands in southern California, and at lower elevations in the Sierra Nevada, tend to have less downed woody debris than found in conifer forests and stands tend not to be multilayered. Because woodrats dominate the diets of owls in these hardwood habitats, we can infer that they provide good habitat for woodrats as well. Live oaks are common in the canopy and a variety of shrubs provide food (leaves, buds, flowers, and so on) for woodrats (Chapter 10).

Home Range and Territoriality

Spotted owls generally have large home ranges, defined by Thomas et al. (1990, p. 419) as "the area to which the activities of an animal are confined during a defined period of time." By contrast, an animal's "territory" is generally a defended area (Nice 1941) within its home range. Home ranges of radio-tagged, neighboring spotted owls overlap to varying degrees (reviews in Thomas et al. 1990, appendix I; Carey et al. 1992; Chapter 6). Observations by Forsman et al. (1984, p. 52-53) indicate that aggression between neighboring birds is infrequent, apparently confined to interactions between members of the same sex, and generally more pronounced when an intruder is well within the home range of another bird. These observations suggest a form of territoriality in which "...an individual or a pair may be dominant in the core area of its home range but not in the periphery. This tends to produce a regular dispersion by effectively excluding other individuals from breeding in the core without necessarily excluding their presence there as subordinates engaged in other activities" (Brown and Orians 1970, p. 244).

Median, combined home ranges of members of pairs of northern spotted owls, estimated from radio-tagged birds and using minimum convex polygons as the estimator, ranged from 1,411 acres in the South Umpqua River Valley in the Klamath Mountains of southwestern Oregon to 9,930 acres on the Olympic Peninsula in northwestern Washington (Thomas et al. 1990, p. 194). Home ranges were generally larger in Washington than in areas to the south. In Oregon, areas where median pair home ranges exceeded 5,000 acres were usually in heavily logged sites with a low percentage of the landscape covered by older forests

(Forsman et al. 1984, Carey 1985, Thraillkill and Meslow 1990). Home ranges of the California spotted owl exhibit similar variation in size, being measured in thousands of acres in higher-elevation conifer forests but only in hundreds of acres in foothill woodlands of the Sierra Nevada (Chapter 6). We strongly suspect that prey availability accounts for a major part of the variation in home-range size of the spotted owl (see discussion below in section entitled "Why Differences in Home-Range Size?").

As in other bird species, some spotted owls do not exhibit fidelity to an area, their movements indicating instead that they do not occupy a specific home range (Chapter 6). Juveniles often wander widely in search of a vacant home range, and similar behavior may occur among adults displaced for some reason from their former home range. They may move within or among the home ranges of other birds, where they await opportunities to join the breeding population when a territorial owl dies or deserts its territory. These birds are referred to as "floaters" by ornithologists (Smith 1978, 1984). Their role in avian population dynamics is believed to be critical (review in Thomas et al. 1990, p. 295; Franklin 1992), but less is known about them than any other subset of bird populations. This is true because floaters are typically quiet and secretive, avoiding contact with territorial birds and being less susceptible to detection by researchers. For these reasons, we have no quantitative information on the ratio of floaters to territorial birds in any population of spotted owls.

Vocalizations

Spotted owls communicate with a variety of hoots, "barks," and whistles (Forsman 1976, Forsman et al. 1984). The context of some of these calls is unknown, but researchers generally agree on the function of some of the more common calls. For example, the most common call is the four-note hoot, phonetically described as "hooo---hoo-hoo---hooooo." It advertizes the fact that an owl is on its territory and probably functions both to repel intruders and to attract potential mates. Given at a lower pitch and intensity, this same call is also used by the male to announce prey delivery to his mate, and in other sexual interactions. Owl biologists most often imitate this call when attempting to locate or attract spotted owls in the field.

Another common call is the multiple-note "series," which is a highly variable rendition of the basic four-note hoot (Fitton 1991). It is used by birds in an excited state. Spotted owls also produce whistles that usually serve to maintain contact between members of a pair (Forsman et al. 1984). The calls of females are higher-pitched than those of males, facilitating identification of sexes in the field. Calls of spotted owls also vary spatially and temporally (Ganey 1990, Fitton 1991).

Pair Bond

All available evidence indicates that spotted owls are monogamous. Forsman et al. (1984, p. 53) concluded that pair bonds are usually maintained from year to year primarily because (1) individuals of both sexes tend to remain within their home ranges, and (2) they tend to exclude other individuals of the same sex from their home ranges. Owls that remain throughout the year in the same home range generally maintain a solitary existence during the nonbreeding period, seldom even roosting near their mates. Mate constancy, therefore, may be "more a function of the attachment to a traditional home range than attachment to a particular mate." Observations of migrant spotted owls support this conclusion. Mates do not migrate or spend the winter months together. Survivors return to their former summer home ranges, where former pair bonds are renewed if both members of the pair survive (Verner et al. 1991).

Not all pair bonds last for as long as both members of the pair survive, however. "Divorces" have been observed in several demographic studies of spotted owls, but they are rare and reasons for them are unknown (R. J. Gutiérrez pers. observ., LaHaye pers. comm., Steger pers. comm.). When an owl of either sex loses its mate, it may desert its old home range and form a new pair bond elsewhere; it may remain on the old home range and acquire a new mate there; it may remain unmated for an extended period of time; or it may become a floater. Too few instances have been observed to identify a pattern, although LaHaye suspects that females that lost mates left their old home range more often than was the case for males in his study in the San Bernardino Mountains.

The Annual Cycle

Knowledge of the owl's annual cycle is essential for delineating any restrictions on projects and activities that might be planned within owl territories. The following account of the spotted owl's breeding chronology is drawn mainly from Forsman et al. (1984), who have provided the best quantitative information. Although it is based primarily on observations of pairs, nests, and broods of the northern subspecies in Oregon, we believe it is the same or similar for the California spotted owl. Estimated periods for the different stages of the cycle were based on unpublished information and summaries provided by National Forest biologists; by Blakesley (pers. comm.) and Steger (pers. comm.) for the Sierra Nevada; by LaHaye (pers. comm.) for the San Bernardino Mountains; and by Stephenson (pers. comm.) for owls at lower elevations in southern California.

Available evidence indicates that spotted owls are physiologically capable of first breeding at the age of 2 years (Barrows 1985, Miller et al. 1985), although rare cases of nesting by yearlings are known (LaHaye pers. comm., Steger pers. comm.). Determining the "usual" age at first breeding is complicated by the fact that nesting by the owls does not occur annually, even among older birds. As a result, a bird that has attained reproductive maturity may not nest for one or more years beyond that age, probably for ecological reasons.

Here and elsewhere in this assessment we recognize five stages of the breeding cycle—prelaying, laying, incubation, nestling, and fledgling. The timing of these stages (fig. 4E) is especially important information for management purposes. Because not all birds begin nesting at the same time, the duration of each stage for all owls in a region, such as the conifer forests of the Sierra Nevada, is considerably longer than it is for a single pair.

The breeding cycle of California spotted owls extends from about mid-February to mid- or late September or early October, when young are no longer cared for regularly by their parents (fig. 4E). The cycle apparently begins earlier in some places than in others in a given year. For example, Steger (pers. comm.) believes that spotted owls in the foothills of the Sierra Nevada initiate breeding about 2 weeks earlier than birds in the higher conifer forests at the same latitude. The various stages tend to begin about 4 days earlier in the San Bernardino Mountains than in the conifer zone of the Sierra Nevada (fig. 4E). As in the Sierra Nevada, timing at lower elevations in southern California apparently precedes that in the San Bernardino Mountains by about 2 weeks (Stephenson pers. comm.). Reasons for these differences may be related to local differences in peak periods of prey abundance for the owls. Before this can be determined, however, much more information is needed to refine details of the owl's breeding cycles and periods of prey abundance in all localities.

Prelaying Stage (duration variable) (see Forsman et al. 1984, p. 34)

Members of nonmigrating pairs generally do not roost together during the winter. By late winter, however, they increasingly roost together, engage in mutual preening, and occasionally copulate in the evening. For 2 weeks or so before the date of first laying, paired birds typically roost together every night and copulate once or twice each evening. Beginning about a week before laying, the female spends most of her time near the nest, receiving an increasing share of her food from the male. These activities probably do not last as long for birds that migrate, because members of migrant pairs spend the winter in different locations and do not return to their breeding territories until shortly before laying begins. Because the prelaying stage has no clearly definable beginning, we have arbitrarily designated the 3 weeks prior to laying of the first egg as the prelaying stage.

Laying Stage (1-6 days)

Data suggest that the peak laying period probably occurs from about 7 to 21 April in the San Bernardino Mountains and from about 11 to 25 April in conifer forests of the Sierra Nevada. When egg laying begins, a female spotted owl spends almost all



Figure 4E—Chronology of the breeding seasons of California spotted owls in conifer forests of the Sierra Nevada and the San Bernardino Mountains.

of her time in the nest, and her mate provides nearly all of her food. Copulation continues on a daily basis throughout the egg-laying stage and for up to about 4 days after incubation begins.

The clutch size of the spotted owl is one of the smallest among North American owls (Johnsgard 1988). Most clutches contain two eggs; three-egg clutches are infrequent and four-egg clutches are rare (only two records—Bendire 1892, Dunn 1901). The interval between laying of successive eggs is 72 ± 6 hours (Forsman et al. 1984, p. 33), so the laying period would be 1 day for a clutch of one egg, 3 days for a clutch of two, and 6 days for a clutch of three. (A rare clutch of four eggs would presumably stretch the laying period to 9 days.)

Incubation Stage (30 ± 2 days) (Forsman et al. 1984, p. 33)

Incubation begins shortly after laying of the first egg and is done solely by the female, who may leave the nest at night for periods up to 2 hours during the first 2 days of incubation. Thereafter, she only occasionally leaves the nest for periods of 10 to 20 minutes at night to regurgitate pellets, defecate, preen, or accept food from her mate. The female does not forage during the incubation period, receiving all her food from her mate. The male typically roosts within 650 feet of the nest during the daytime and begins to forage shortly after sunset (Forsman et al. 1984, p. 35).

Coincident with the laying of eggs, the female develops a brood patch—"a feather-free area with thickened skin and a rich supply of blood vessels to facilitate the transfer of heat from the body of the incubating bird to the eggs" (Pettingill 1970, p. 355). The presence of a well-developed brood patch is clear evidence that a female has been incubating.

Nestling Stage (normally 34-36 days) (Forsman et al. 1984, p. 37)

The peak hatching period probably occurs from about 3 to 17 May in the San Bernardino Mountains and from about 7 to 21 May in the conifer zone of the Sierra Nevada. The female broods the new hatchlings almost continuously for 8-10 days, still depending on her mate to provide food for herself, and now for the young. By the time her young are 2-3 weeks old, the female begins to forage for increasingly longer periods at night—typically 1-4 hours. The male continues to bring food to the nest, but the female then passes the food to the young. Apparently the male seldom, if ever, passes food directly to nestlings. Forsman et al. (1984, p. 35) reported that they never observed males feeding nestlings. If the male brings food to the nest while the female is away, he simply leaves it in the nest. The female continues to roost in the nest until 3-6 days before the young leave it.

Most young observed by Forsman et al. (1984) fledged (left the nest) when 34-36 days old, occasionally moving off the nest to perch on nearby limbs for a few days before leaving the nest permanently. Occasionally young leave their nest earlier than normal. Because such young are less developed physically, they may spend more time on the ground than young that remain in the nest for the full nestling period. This may increase their mortality rate compared to that of later-fledging young (Forsman et al. 1984, p. 36).

Fledgling Stage (80-120 days) (Forsman pers. comm.)

The fledgling stage covers the period after the young leave the nest until they become independent of their parents. The

peak period of fledging probably occurs from about 8 to 22 June in the San Bernardino Mountains and from about 12 to 26 June in conifer forests of the Sierra Nevada. New fledglings are weak fliers, often falling to the ground, where they may spend several hours to several days. Within about 3 days after fledging (assuming a normal nestling period of 34-36 days), most young can flutter or climb to elevated perches; usually in a week they can fly clumsily between trees. Within about 3 weeks after fledging, they can hold and tear meat from prey brought by their parents (Forsman et al. 1984, p. 37). Although adult males bring food for the fledglings at all ages, they generally do not give the food directly to the young until they have been out of the nest for at least 2 weeks (Forsman pers. comm.). Both parents regularly bring food to the fledglings and generally continue to do so until mid- to late September, apparently regardless of the age or capabilities of the young. Because of this, the fledgling stage may be relatively long or short, depending upon when a given nest was begun and on variations in the age of the young at fledging.

The Nonbreeding (Winter) Period

Activities of spotted owls during this period are primarily related to basic maintenance-capturing prey, securing protection from the elements, avoiding predators, preening; and so on.

The beginning of the nonbreeding period is technically the date when adults quit feeding their young, although this may not be well-defined because feeding may continue sporadically even well after the young can capture and kill prey for themselves. Three changes in owl status indicate that 1 October is a reasonable beginning of the nonbreeding period in the Sierra Nevada, at least for most birds: Young are generally independent of their parents by late September; juveniles begin dispersal as early as 1 October (Laymon 1988); and some adults begin fall migration early in October (Laymon 1988, Neal et al. 1989). The end of the winter period coincides with the beginning of activities characteristic of the prelaying stage. This is also a poorly defined date, partly because the initiation of prelaying behavior is not abrupt and partly because timing differs among pairs. Many pairs, however, have initiated prelaying activities at least by the end of February, and egg laying and incubation begin at some nests by the end of March. For planning purposes, therefore, we can reasonably set the end of the winter period at the end of February, at least for most birds.

Movements

Regular, long-distance movements of birds beyond home-range boundaries are of two types-migration and dispersal. Migration is an annual movement between breeding and nonbreeding home ranges. Natal dispersal is the movement of young birds from their natal territory to a site where they breed or at least establish a territory where breeding could occur (Green-

wood 1980). Sometimes adult birds are displaced from established territories by loss of habitat through fire, logging, or other major disturbances. Adults displaced by loss of habitat, or separating from a mate, may begin searching for new territories. Their movement to a new territory is referred to as breeding dispersal.

Migration

Migration is rare among northern spotted owls (Forsman et al. 1984), although a few individuals in the Washington Cascades have moved back and forth several miles between breeding and nonbreeding home ranges without an appreciable change in altitude, latitude, or habitat type (Brewer and Allen 1985). Some radio-tagged California spotted owls in the Sierra Nevada have migrated altitudinally, however, moving downslope for the winter period on the Eldorado NF (Laymon 1988) and the Sierra NF (Neal et al. 1988, 1989, 1990; Verner et al. 1991). At least 8 of 10 birds in Laymon's study left breeding home ranges in mixed-conifer forests (elevations 4,000-5,200 feet) to spend the winter in oak/pine woodlands (elevations 1,000-3,500 feet). The mean elevational displacement between breeding and nonbreeding areas was 2,450 feet; the straight-line distance between areas was 10 to 36 miles (mean = 20). The earliest migrant left its summer home range on 18 October, the latest on 18 November. Dates of return to breeding areas were not determined, because batteries in the radio transmitters failed during the winter. The owls were, however, back in their breeding territories by mid-April.

Six of 18 radio-tagged owls on the Sierra NF migrated from summer home ranges in mixed-conifer forest at 5,700-6,700 feet in elevation to winter home ranges in oak/pine woodlands at 1,100-2,050 feet in elevation. Departure dates ranged from 8 October to 17 December; one female departed her summer home range on 8 October 1987, 8 November 1988, and 20 November 1989. Vertical displacement ranged from 3,680 to 5,541 feet (mean = 4,628) and straight-line distances between areas were 9.6 to 15.3 miles (mean 12.3). Spring return dates ranged from 27 February to 28 March.

None of four owls radio-tagged by Call (1990) migrated during his study on the Tahoe NF (elevations from 2,200 to 5,200 feet), where he tracked from summer through early December in both 1986 and 1987. Call's tracking period in both years lasted well beyond the fall migration dates observed by Laymon, and >2 feet of snow had accumulated in his study area by December of 1986.

No members of any pair in either the Eldorado NF or the Sierra NF study migrated together or established winter home ranges in the same area. In both studies, at least one migrant moved back and forth between winter and summer home ranges once or twice during the winter. Six of the 18 owls in the Sierra NF study whose movements were well-documented were year-round residents, remaining within essentially the same home-range boundaries during summer and winter periods. Two simply enlarged their summer home ranges for the winter period, and five shifted their home range for the winter period but their summer and winter home ranges overlapped. Nine of the 18 were tracked through at least two annual cycles; none of these birds changed behavioral patterns from one year to the next (that

is, once a migrant always a migrant, and so on). The Sierra NF study included another 11 owls that remained as permanent residents in foothill riparian/hardwood forests, at elevations ranging from 1,000 to 4,000 feet. Home ranges of these birds were often shared in winter with migrants from higher elevations.

Data available from these studies thus show individual variation in migratory behavior of the California spotted owl. Collectively, the three studies tracked 32 birds with summer home ranges in the higher-elevation conifer forests long enough to determine whether they did or did not migrate; at least 14 (44 percent) were altitudinal migrants. Because the sample is small, however, we cannot sort out the reasons why some individuals migrated and others did not. Nor can we determine why all 10 owls in the Eldorado NF study migrated, none of the four in the Tahoe NF study migrated, and only about a fourth of the 18 birds in the Sierra NF study migrated. It does not appear to be the case that habitat quality was best in the Tahoe and poorest in the Eldorado study area. Only 35 percent of the Tahoe study area was in stands of large sawtimber (≥ 21 inches in d.b.h.). Because Call (1990) did not report the proportion of the large sawtimber that also had ≥ 40 percent total canopy cover, we assume that something less than 35 percent had both large sawtimber and

suitable canopy cover. The Sierra study area was only about 14 percent large sawtimber (table 6C). On the other hand, the Eldorado study area, with the highest proportion of migrants, was 39 percent in large sawtimber that also had ≥ 40 percent canopy cover (Bias 1989). Finally, in the Sierra study area, some owls left areas for the winter that were subsequently used during the winter by other owls (Steger pers. comm.), suggesting that the birds that left them did so for reasons other than food shortage.

Altitudinal migration may expose owls to added sources of mortality, some related to various human activities. They may cross roadways and be hit by a vehicle. In many lower sites, in foothills of the western Sierra Nevada, traditional wintering areas for the owls are being developed for home sites, even communities. And the development of residential properties, with resulting homes, lawns, driveways, and so on, will eliminate otherwise suitable habitat for woodrats—the staple winter diet of spotted owls in these oak/pine woodlands (table 4A). Finally, foothill woodlands are used extensively to graze cattle and to harvest firewood from oaks. Both of these activities can have negative impacts on woodrat populations and on the cover value of the habitat for owls.

Table 4A -A summary of California spotted owl diets, expressed as estimated percent biomass from different studies.

Diet	Sierra Nevada								Southern California	
									Mixed-evergreen forest	Riparian/mixed hardwood
	Sierran mixed-conifer forest				Riparian/hardwood woodland					
	Lassen National Forest	Eldorado National Forest	Sequoia/Kings Cyn. Nat. Prk.		Sierra National Forest				Riverside, San Diego, Orange cos.	Los Padres National Forest
	Spring/summer	Summer	Summer	Spring/summer	Spring/summer	Fall/winter	Spring/summer	Fall/winter	All seasons	Spring/summer
Woodrats ¹	10.1	35.0	37.5	4.0	8.3	0	73.8	88.0	79.3	93.9
Northern flying squirrel	61.1	24.5	31.3	60.0	50.1	76.6	9.6	0	0	0
Mice ²	1.1	3.0	1.2	1.8	1.5	1.5	1.4	2.6	6.0	1.2
Pocket gophers ³	6.2	1.3	8.1	26.9	20.4	14.7	11.6	5.6	6.0	2.5
Moles ⁴	1.6	4.2	2.0	3.4	3.0	2.1	0.6	0.2	0.2	0
Diurnal squirrels ⁵	4.4	16.5	6.8	4.0	1.9	0	0	0	0.2	0
Lagomorphs ⁶	6.1	0	0	0	0.8	0	0	0	1.0	0
Shrews and voles	2.1	2.4	0.7	0.2	1.2	0.5	1.1	0.6	0.2	0
Bats	<0.1	0.3	0	0.1	0.1	0	Trace	0	0	0.5
Birds	6.7	12.7	12.4	2.7	12.3	4.3	1.9	3.0	7.1	1.5
Insects	0.6	0.1	0.3	0.3	0.5	0.3	0.1	0.1	0.3	0.3
Number of prey items	1,008	1,232	139	162	531	71	234	556	296	30
Elevation (feet)	4,700-6,800	3,500-5,000	3,000-5,500	5,300-6,900	4,500-7,000	4,500-7,000	1,000-4,500	1,000-4,500	3,000-5,500	1,000-3,600
Source	Blakesley (pers. comm.)	Thrailkill Laymon (1988)	Roberts and Bias (1989)	(pers. comm.)	Steger and Eberlein (pers. comm.)				Barrows (1980)	Smith (pers. comm.)

¹ The Lassen sample included both bushy-tailed and dusky-footed woodrats; only dusky-footed woodrats occurred elsewhere.

² Most were white-footed mice (*Peromyscus* spp.), but some samples included minor percentage of pocket mice, jumping mice, or house mice.

³ As many as three species in some samples.

⁴ As many as two species in some samples.

⁵ Included ground squirrels, tree squirrels, and chipmunks.

⁶ The Lassen sample included one pika; all other lagomorphs identified at all sites were rabbits (*Sylvilagus* spp.)

Dispersal

Successful dispersal is essential for population viability. Without it, a population will slowly decline to extinction, because deceased individuals in the breeding population will not be replaced by recruits from dispersing juveniles or adults that have been displaced or have not yet secured a territory. As Miller (1989, p. 1-2) stated, "The distance between adjacent pairs or groups of breeding owls should be such that dispersal of juveniles can replace losses (deaths or emigrations) among existing pairs and provide for colonization of suitable, unoccupied habitats. An understanding of dispersal in juvenile spotted owls is thus basic to formulation of criteria for appropriate spacing of habitat to accommodate pairs of owls." We especially need data on the variability of dispersal distances, dispersal directions, and habitats used by dispersing birds. We also need quantitative information on the extent to which fragmentation of forest habitats impedes successful dispersal (Chapter 9).

Dispersal Among California Spotted Owls

Unfortunately, information on dispersing California spotted owls is nearly nonexistent. Four radio-tagged juveniles on the Eldorado NF (Laymon 1988) initiated dispersal from 1 to 24 October. One was never relocated, another moved 1 mile before it was found dead on 1 December; the others moved straight-line distances of 8.8 and 11.5 miles from their natal sites. This last bird crossed two major rivers and a major highway before settling in oak/pine woodlands near the town of Columbia, at an elevation of 1,300 feet. Two radio-tagged juveniles on the Sierra NF (Steger and Eberlein pers. comm.) moved straight-line distances of 6.1 miles (radio signal lost) and 12.7 miles from their natal areas. The latter bird moved from mixed-conifer forest into oak/pine woodlands. Three color-banded juveniles in the Sierra study dispersed 3.4, 3.5, and 4.1 miles from natal areas to their first territories; four adults banded as members of pairs later shifted territories, moving 2.1, 2.2, 2.4, and 4.4 miles. All of these banded birds were relocated because they stayed within the Sierra NF demographic study area (Steger and Eberlein pers. comm.).

A male color-banded as a fledgling, probably on the Eldorado NF, was found on the Stanislaus NF on 5 September 1990. It was paired and had raised at least one young. This bird was reared in mixed-conifer forest and later paired with a bird in the same forest type. The straight-line distance from its natal home range to its breeding territory was at least 68 miles.

Observations of Dispersing Juvenile Northern Spotted Owls

Because information on dispersal of California spotted owls is so meager, we rely here on studies of dispersal by northern spotted owls to establish quantitative information needed for this assessment. We believe this is a reasonable course of action, because the two subspecies are so closely related that we have no reason to expect dispersal behavior or capability to differ markedly between them.

Over a 4-year period in western Oregon, Miller (1989) fitted 48 juveniles with radio transmitters and monitored their movements regularly. Thirty-two survived to disperse from na-

tal areas (mean = 104 days after fledging). Twenty-seven (84 percent) initiated dispersal between mid-September and mid-October. Their initial movement was usually rapid, and "...most juveniles settled into well-defined areas for their first winter after the initial dispersal movements. Those...surviving their first winter often began moving again in late winter or early spring." From a subset of birds positively identified to sex, males dispersed an average of 16.2 miles (SD = 14.6; $n = 7$) and females an average of 20.4 miles (not significantly different--SD = 6.6; $n = 6$). Initial directions taken by dispersing juveniles did not differ from a random distribution, although six of nine juveniles in 1983 dispersed down the McKenzie River drainage from the H. J. Andrews Experimental Forest. Miller found no significant relation between forest fragmentation and either the final distance moved or the number of days survived by birds in his study. Dispersing juveniles used a wide variety of habitats, but 12 of 18 birds exhibited significant selection for old-growth and mature forests.

In a study of 23 dispersing juveniles in northwestern California (11 in 1983 and 12 in 1984), the birds departed from their natal areas from 22 September to 5 October (Gutiérrez et al. 1985). Dispersing juveniles in 1983 moved a mean of 5 miles per day (range 1 to 11), compared to 1.3 miles per day in 1984 (range 0.8 to 6.4). The difference was statistically significant. Directions taken by dispersing birds varied. They left their natal areas in random directions, with no relation between dispersal direction and the geographic orientation of drainages or ridges. During the first 80 days of dispersal, individuals moved total distances of 15.3 to 92.9 miles ($n = 11$) in 1983 and 0.7 to 62.8 miles ($n = 7$) in 1984. Total distance was the sum of all segments between successive locations as birds were followed during dispersal. Total distance is greater than the straight-line distance between beginning and ending points.

In addition to these more extensive radio-tracking studies of dispersing juveniles, we compiled results from all sources to estimate dispersal distances of radio-tagged juveniles after they left their natal areas (fig. 4F). Only one of the 54 juveniles whose dispersal distances are known was later found as a member of a mated pair, but apparently it never nested (R. J. Gutiérrez pers. observ.). All other birds either died (68 percent), their transmitters failed (27 percent), or they disappeared (5 percent). This raises a question about whether estimates of dispersal distance from radio-tagged birds were biased because the birds were wearing radios. Although radios may have affected their survivorship or their ability to form a pair bond, we found no evidence that distances moved by radio-tagged juveniles were affected by radio transmitters.

If juvenile spotted owls carrying transmitters tended to die sooner than normal, that is, before they dispersed as far as they would without a radio, their dispersal distances might be underestimated. Miller (1989) observed that dispersing juvenile northern spotted owls tended to move quickly from their natal area to a point where they settled for their first winter. Our data set on 54 dispersing juveniles includes a subset of 31 with data on the number of days they dispersed and the number of days they survived thereafter. The dispersal period was highly variable ($\bar{x} = 128.3$ days; SD = 168.5; range = 0-657 days; $n = 31$). The

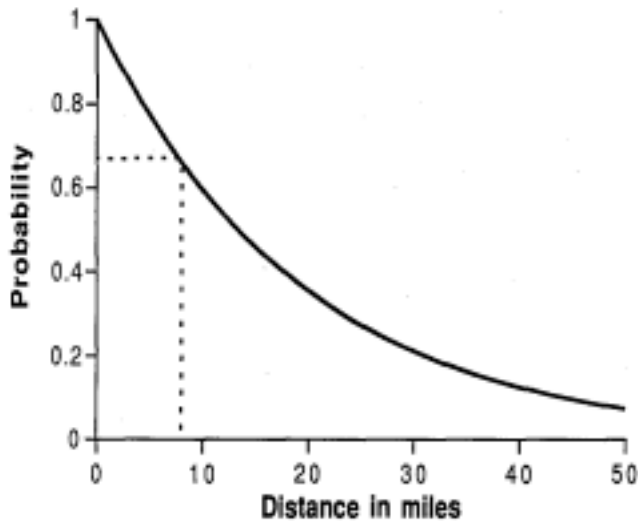


Figure 4F-Probability of dispersing juvenile spotted owls traveling various distances, based on observed dispersal distances of 56 radio-tagged northern spotted owls (Thomas et al. 1990, appendix P). For example, two-thirds of the juveniles would be expected to disperse at least 8 miles (Murphy and Noon 1992).

survival period following dispersal, however, was more consistent ($\bar{x}$ = 119.2 days; SD = 37.4; range = 88-156 days, with one outlier each at 45 days and 284 days). In this subset of 31 dispersers, 13 quit dispersing within 46 days after leaving their natal territory and 11 quit dispersing after at least 83 days (maximum of 657 days). The mean dispersal distances of these two groups were 22.4 miles (SD = 15.7) and 22.0 miles (SD = 8.1), respectively. The correlation coefficient (ρ) between maximum dispersal distance and the number of days dispersed was not significant (r = -0.03; P = 0.88; 95 percent confidence intervals were -0.38 and +0.33; n = 31). The power of the test was 0.37 for ρ = 0.30, 0.61 for ρ = 0.40, and 0.83 for ρ = 0.50. The power for any value of $\rho \geq 0.70$ was 1.0. Consequently, the likelihood of failing to detect a statistically significant correlation that might have had biological significance was slight, and the likelihood of failing to detect a significant ρ of at least 0.70, if one truly existed, was essentially nil.

These results suggest that dispersing juveniles quickly attained their maximum dispersal distance from their natal territory. If they continued to disperse thereafter, their movements tended to keep them within that earlier-attained, maximum dispersal distance.

We also computed the correlation coefficient between maximum dispersal distance and the number of days that juveniles carried radio tags (r = 0.02; 95 percent confidence intervals for the true correlation coefficient were -0.25 and +0.30). ρ was not statistically significant (P = 0.87). The power of the test was 0.60 for ρ = 0.30, 0.86 for ρ = 0.40, and 0.98 for ρ = 0.50. The power for any value of $\rho \geq 0.60$ was 1.0. Examination of scatterplots suggested no patterns that might be missed by just using a correlation coefficient. Additional analyses reported in Thomas et al. (1990, p. 306) corroborate the conclusion from the above results that radio transmitters did not bias estimates of dispersal distance. Lacking critical data from dispersing juvenile California spotted owls, we have therefore used the full data

set on northern spotted owls to estimate dispersal distances of radio-tagged, juvenile spotted owls. The function derived from these data (fig. 4F) was used to parameterize one model for assessing the sensitivity of the southern California metapopulation of spotted owls to various changes in its numbers and distribution (Chapter 9).

Mortality

Birds of most species die of undetermined causes, because they simply are not found in the inconspicuous places where they die. In addition, their bodies are often quickly consumed by other animals in the environment. Spotted owls are no exception. We have little information on their sources of mortality, certainly not enough to establish proportions or even to rank the causes of death. Many dead spotted owls have been examined carefully by veterinarians in an effort to determine the cause of death, but even those examinations are generally unable to pinpoint the exact cause. Instead, a variety of contributing factors is typically suggested. We do know, however, that spotted owls die from the usual variety of causes that befall most wild birds (D. H. Johnson pers. comm.).

Predation

Although spotted owls appear to have few predators, we know that great horned owls and goshawks occasionally capture and eat them: Forsman et al. (1984, p. 38) reported seeing a Cooper's hawk attempt to capture a recently fledged owlet and Forsman and Meslow (pers. comm.) reported one incident of predation by a red-tailed hawk. The great horned owl and the goshawk are both larger than the spotted owl, and all three species often occupy the same forested areas. Great horned owls tend to be more common in areas with lower tree densities than is the case for spotted owls, and the smaller size of spotted owls probably enables them to outmaneuver great horned owls in dense forest. Forsman (pers. comm.) suspects that great horned owls only opportunistically prey on spotted owls.

Goshawks kill both adult and juvenile owls (Gutiérrez et al. 1985, Miller 1989, D. H. Johnson pers. comm.), but spotted owls sometimes nest within goshawk territories and defend their young against attacks by goshawks (R. J. Gutiérrez, pers. observ.). We agree with Forsman et al. (1984, p. 38) that goshawks probably are not serious threats to spotted owls.

Accidents and Starvation

A few deaths from accidents (flying into obstacles, automobiles, and drowning) and starvation have been recorded among spotted owls (for example, Gutiérrez et al. 1985, Laymon 1988, Neal et al. 1988, 1989; R. J. Gutiérrez pers. obser., Forsman and

Meslow pers. comm.). Starvation may result from low abundance or availability of prey, or from lack of hunting experience. Death by starvation is more common among juveniles than adults (Gutiérrez et al. 1985, Miller 1989, Sisco 1990, D. H. Johnson pers. comm.).

Shooting

Shooting deaths have also been documented for spotted owls. For example, both members of a pair of birds that occupied riparian/hardwood habitat in the Switzer Picnic Area in the Angeles NF were shot and killed with "BB" guns by two young boys (Stephenson pers. comm.). This was apparently just a thoughtless act, not a malicious effort to destroy spotted owls, but it does raise a question about the safety of owls in heavily used recreation areas.

Diseases and Parasites

Little is known about diseases and parasites of spotted owls, and nothing is known about the extent to which they contribute to mortality, although Forsman and Meslow (pers. comm.) observed several instances of mortality that they attributed to diseases or parasites. Gutiérrez (1989) surveyed blood parasites in all three subspecies, finding an infection rate of 100 percent, exceeding that recorded in nearly all other bird species (Greiner et al. 1975). Spotted owls must be adapted to these high parasite loads, however, because their survival rates are high even where infection rates are high (Franklin et al. 1990). Hoberg et al. (1989) examined 20 northern spotted owls for helminth parasites and found eight species, representing round worms, flat worms, and spiny-headed worms. More than 80 percent of the birds were infected with at least one species, and multiple infections were common.

Young et al. (1992) reported two species of hippoboscids from northern spotted owls in northwestern California. One species was found only once among the 382 owls examined, but about 17 percent of the owls they examined had hippoboscids infestations of the other species. Fly densities on owls were higher in years with higher summer and fall temperatures and lower winter precipitation. Young et al. (1992) speculated that low temperatures may have depressed survival of fly pupae. In demographic studies in the Sierra NF and Sequoia/Kings Canyon NPs, hippoboscids were detected on 15 of 45 birds (33 percent), but searching for the flies was not an objective of field crews, and limited evidence indicated that the flies were more likely to crawl to the outer surface of an owl when it was handled longer (Steger pers. comm.).

Competition

The barred owl, probably the closest relative of the spotted owl, was historically restricted to eastern North America. Gradually it has extended its range westward through Canada, and finally southward from British Columbia into Washington, Oregon, and more recently into northern California, as far south as the Tahoe NF in the Sierra Nevada (G. I. Gould, Jr., pers. observ.; R. J. Gutiérrez pers. observ.). Barred owls are larger and more aggressive than spotted owls in interspecific territorial interactions, and they are more generalized in their selection of prey, the habitat types they use, and their nest site requirements (Hamer et al. 1989). Their recent invasion into the range of the spotted owl (Taylor and Forsman 1976) is a possible source of competition between these closely related species. Evidence available already indicates that barred owls have displaced spotted owls from some sites in Washington (Hamer et al. 1989). Because barred owls have now been reported from about 27 different sites in California, interactions between these species will bear further study. A few hybrids between spotted and barred owls have been observed recently. Such hybridization is not uncommon between closely related species of wild birds. The extent of hybridization between these two owl species is still very limited, however, and the eventual outcome of this hybridization will take many decades or even centuries to resolve.

Diets

Spotted owls are "perch and pounce" predators (Forsman 1976), selecting an elevated perch from which they locate potential prey, either by sight or sound. When an owl detects a prey, it drops from its perch and attempts to capture the prey in its talons (the "pounce"). Spotted owls are agile, capturing prey in shrubs, trees, and on the ground. If a potential prey is in an inaccessible location or at some distance from the owl's perch, the owl may move closer before initiating its pounce. Its silent flight allows it to approach prey without being detected. In addition, spotted owls are adept at "hawking" behavior—capturing flying prey, primarily birds and insects.

Spotted owls forage primarily at night. Forsman et al. (1984) rarely observed daytime foraging by northern spotted owls, concluding that it occurred only opportunistically. On the other hand, Laymon (1991) concluded that California spotted owls in his study on the Eldorado NF, in the western Sierra Nevada, foraged regularly during the daytime when they were raising young, but not otherwise. Neal et al. (1989) reported that they often observed spotted owls—even nonbreeders—foraging for insects in the Sierra NF, taking them from bark surfaces, from

the ground, and even catching them in the air. These observations were usually in the late afternoon or early evening (Steger pers. comm.).

Marshall (1942) was the first to report on diets of the California spotted owl, based on stomach contents of two specimens and 23 regurgitated pellets gathered beneath roost trees at Whitaker Forest, Tulare County, in Sierran mixed-conifer forest with giant sequoias, at an elevation of about 5,500 feet in the western Sierra Nevada. The stomachs contained limb bones of frogs or toads, four bats (genus *Myotis*), one deer mouse, and four crickets ("probably *Gryllus*"). The pellets contained remains of 11 flying squirrels, two deer mice, and single individuals of four other mammal species, six bird species, and one June beetle. The relatively high proportions of flying squirrels and birds in this small sample are in line with several recent, more extensive studies of spotted owl diets in conifer forests of the Sierra Nevada (table 4A).

California spotted owls eat a variety of prey. For example, three samples from Sierran mixed-conifer forests produced a combined list of at least 78 different species—at least 1 amphibian, 1 lizard, 24 birds, at least 34 mammals, and at least 18 insects from a combined total of 2,716 prey items (Marshall 1942–63 prey items; Laymon 1988–1,275 prey items; Steger and Eberlein pers. comm.—1,405 prey items). In spite of this diversity, only one to five species or species-groups comprised at least 5 percent, by weight, of the owls' diets in the eight samples shown in table 4A, and at least 85 percent of the total biomass in each sample consisted of only one to four species or species-groups. Either northern flying squirrels or dusky-footed woodrats, or both, dominated prey biomass in all samples. Preliminary results from an analysis of the spotted owl's diet in the San Bernardino Mountains agree—about 80 percent of the biomass was dusky-footed woodrats, and about 10 percent consisted of medium-sized mammals like northern flying squirrels and gophers (Smith pers. comm.). The general pattern suggests a prey specialist with a search emphasis on just a few species, but which will capture and eat a wide variety of species and sizes of prey as they are encountered.

Four patterns in the results of these studies may be important: (1) Spotted owls in conifer forests of the Sierra Nevada, particularly above mid-elevation mixed-conifer forests (about 4,000–5,000 feet, depending on latitude), prey mainly on flying squirrels. (2) Owls in the mid- to lower elevations of the mixed-conifer zone and the upper part of the ponderosa pine/hardwood belt prey heavily on both flying squirrels and woodrats. (3) Both of these sets of owls consume a relatively high proportion of diurnal squirrels and/or birds, suggesting more daylight foraging than is the case for spotted owls elsewhere. And (4) spotted owls in the Sierran foothills and throughout southern California, even at high elevations, obtain 79 to 97 percent of their energy needs from woodrats. A dichotomy between flying squirrel and woodrat dominance of the diet is known for the northern spotted owl as well (review in Thomas et al. 1990, p. appendix J; Carey et al. 1992). Given the California spotted owl's diet, therefore, we need to consider ways to manage for habitats that will maintain thriving populations of flying squirrels in Sierran conifer forests and woodrats everywhere else.

Although woodrats dominate owl diets in Sierran foothill riparian/hardwoods and throughout the owl's range in southern California, only about 25 percent of all California spotted owl sites are in habitats where woodrats are abundant (table 1B). The remaining 75 percent occur in Sierran conifer forests where flying squirrels are the primary prey species.

Ecological Relations

Owls and Their Prey

Common sense tells us that no animal species can survive or reproduce in areas without sufficient food, but documenting these relations by direct field studies is usually very expensive and time-consuming. For owls in general, the time needed for such studies is typically several years, or even decades, depending on the life span of the owl species studied and the kinds of prey they eat. For example, owls with diets consisting mainly of small mammals whose populations exhibit regular, cyclic "booms" and "busts" in numbers, will require longer studies to cover at least two cycles of the prey. In spite of the high demands on time and resources to complete such studies, many have been reported in the literature on owls of the world. They portray a general picture of a marked dependency of owls on the availability of their key prey species—a fact widely recognized among raptor biologists in general and owl specialists in particular.

Relations between owls and prey are manifested in a variety of ways; some species of owls are affected in several ways. A moderately extensive (but not exhaustive) search of the world's literature on owls revealed at least five common, major effects of prey availability on owl biology (table 4B): Owl reproductive rates are often positively related to prey availability. Some species of owls nest earlier when and where prey are more abundant and available. Some owl pairs do not even attempt to nest when prey are scarce. The density of breeding owls is commonly higher when and where prey species are more abundant and available. And some species of owls exhibit major movements (whole populations may shift) when prey become scarce in the area occupied.

Several studies linking prey and spotted owls have been undertaken (Thomas et al. 1990), but little evidence has been found of relations between prey abundance and the biology of spotted owls. In a study in northwestern California, Ward (1990) found that prey abundance (mainly woodrats) was low and that it varied over the landscape. The owls did not necessarily forage in stands where woodrats were most abundant, but they hunted instead in areas where the availability of prey was more predictable. The strategy suggests one of optimizing search effort. Only the study of northern spotted owls in Washington and Oregon by Carey et al. (1992) has been intensive and extensive enough to suggest relations between the owls and their prey. Owls in

Table 4B—Review of ecological relations between owls and the relative availability of their prey. Researchers report a variety of relations, grouped here into five categories, from owl species in North America, Europe, and northern Asia.

Species	Observed ecological relations				
	Reproductive rate positively related to prey abundance	Earlier nesting when prey are abundant	Some pairs do not nest when prey are scarce	Breeding density higher when prey are abundant	Exhibit major movements when prey are scarce
Common barn owl	Otteni et al. 1972 Baudvin 1975, 1976 Kaus 1977 Bunn et al. 1982 Colvin & Hegdal 1985				Bunn et al. 1982
Eagle owl			Olsson 1979		
Great horned owl	Houston 1971, 1975 Adameik et al. 1978 Rusch et al. 1972	Adameik et al. 1978	Houston 1971, 1975 Rusch et al. 1972	Rusch et al. 1972	
Snowy owl	Portenko 1972 Bunn et al. 1982 Mikkola 1983		Bunn et al. 1982	Bent 1938 Pitelka et al. 1955 Watson 1957 Parker 1974 Wiklund & Stigh 1986	Gross 1947 Mikkola 1983
Northern hawk owl	Mikkola 1983			Mikkola 1983 Cramp 1985	Mikkola 1983 Cramp 1985
Eurasian pygmy owl	Sonerud et al. 1972 Jussila & Mikkola 1973 Kellomäki 1977 Solheim 1984				Mikkola 1983 Cramp 1985
Great gray owl	Mikkola 1983		Mikkola 1981, 1983		Groot 1969 Nero 1980 Mikkola 1983
Tawny owl	Linkola & Myllymäki 1969 Southern 1970 Petty 1987		Southern 1970 Petty 1987	Mikkola 1983 Hirons 1985	
Ural owl	Lundberg 1976, 1981 Lundberg & Westman 1984 Pietäinen et al. 1986 Pietäinen 1988, 1989	Linkola & Myllymäki 1969 Lundberg 1981 Lundberg & Westman 1984 Pietäinen et al. 1986 Pietäinen 1988, 1989	Lundberg 1981 Lundberg & Westman 1984 Pietäinen 1988, 1989		
Long-eared owl	Hagen 1965 Linkola & Myllymäki 1969 Ziesemer 1973 Nord 1978 Mikkola 1983 Village 1985	Village 1985	Mikkola 1983 Cramp 1985	Mikkola 1983 Cramp 1985 Village 1985	Mikkola 1983
Short-eared owl	Rendall 1925 Mikkola 1983 Cramp 1985 Lockie 1955			Lockie 1955 Pitelka et al. 1955 Holzinger et al. 1973 Clark 1975 Mikkola 1983	
Boreal owl (Tengmalm's)	Linkola & Myllymäki 1969 Mikkola 1983	Mikkola 1983 Korpimäki 1987		Mikkola 1983	Mysterud 1970 Mikkola 1983 Korpimäki 1986

western hemlock forests on the Olympic Peninsula of Washington used about 4,200 acres of old forest annually; those in Douglas-fir forests in southwestern Oregon used about 2,000 acres of old forest annually; and owls in mixed-conifer forests in southwestern Oregon used about 1,120 acres of old forest annually. Estimates of the combined biomass of primary prey species taken by the owls were 5.3, 21.3, and 29.4 ounces/acre in the three forest types, respectively. Carey et al. (1992, p. 241) concluded that "Geographic variation in the areas traversed and amounts of old forest used by spotted owls reflected similar variation in the abundance and diversity of the medium-sized mammals that are the preferred prey of the owl."

Understanding Spotted Owl Habitats Through Ecological Linkages

A full understanding of why California spotted owls occur where they do, and why they do or do not reproduce well enough to maintain their populations, depends ultimately on comprehending how various components and functions within forest and woodland ecosystems relate to the owl's ecology. Here we have attempted to interpret some of those relations in terms of the owl's key prey species, typical nest sites, and the general dynamics of forest and woodland ecosystems where California owls are known to occur and reproduce. A general graphic representation of these relations helps to envision how all the

pieces fit together (fig. 4G). Assuming that presence and nesting by California spotted owls depends on the availability of a sufficient prey source, we believe that much of what is known about the owl's habitat associations can be better understood in relation to the ecology of its primary prey, especially northern flying squirrels and dusky-footed woodrats. Other key linkages relate to assuring an abundance of suitable nest sites. How does all of this relate to what we judge to be important attributes of suitable owl habitat?

Why Big, Old Trees?

Large, old trees are preferentially selected for nest sites by spotted owls (Chapter 5). For example, nest trees averaged larger than 40 inches in d.b.h.—much larger than the mean diameter of trees generally available. About one fifth of all nests found were in snags (dead trees) and about four fifths were in live trees. Two thirds of the nests were in large, natural cavities formed by decay at sites where branches broke off or tore out of the trunk of the tree, and another 20 percent were on broken tops of living or dead trees, or on dwarf mistletoe brooms. These conditions typically develop only after a tree is relatively old. In addition, larger trees are needed to provide large snags and longer-lasting components of dead, decaying wood on the ground, especially in the form of large logs but also in fallen limbs of various sizes.

Why Downed Woody Debris?

Functional linkages among spotted owls, their major prey species, the prey's food, and the general forest or woodland/shrub community where these linkages occur can be traced in figure 4G. Some major linkages are highlighted by broader arrows. For example, northern flying squirrels feed extensively on hypogeous (underground) fungi, especially during periods when the ground is not covered by snow. They may even cache some of these fungi to be eaten after snowfall. At least two California studies (McKeever 1960, Hall 1991) and one Oregon study (Maser et al. 1985) found that flying squirrels eat primarily fungi and lichens. Hypogeous fungi comprised the bulk of the summer diet, and the winter diet was largely arboreal lichens. The density of flying squirrels in red fir/white fir stands in the Lassen NF was strongly associated with the abundance of truffles (fruiting bodies of hypogeous fungi), and truffle abundance was strongly associated with the presence of a well-developed soil organic layer and a large volume of decaying logs (Waters and Zabel 1992). These data suggest that management practices that decrease the soil organic layer and the number of large, decaying logs will reduce the capability of a habitat to support flying squirrels, and possibly spotted owls as well.

Hypogeous fungi probably also comprise a major food source for white-footed mice (Maser et al. 1978a), an important prey species of the California spotted owl. Spores of the fungi pass unharmed through the digestive tract of these and other small mammals that consume them and are thus spread in fecal pellets over the forest floor. All hypogeous fungi are also mycorrhizal: "Mycorrhiza literally means 'fungus-root' and denotes a symbiotic relationship between certain fungi and plant roots" (Maser et al. 1978b, p. 79). Trees depend on mycorrhizae for an

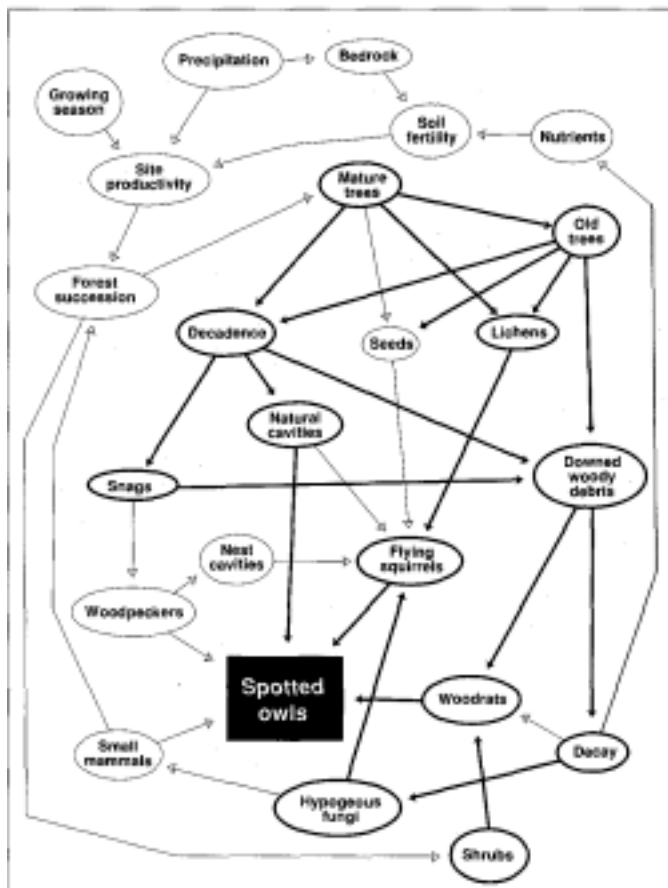


Figure 4G—Simplified, schematic representation of some important ecological linkages associated with California spotted owls.

adequate uptake of various nutrients, and the fungi benefit by obtaining carbohydrates produced by the trees. Interestingly, the spores of hypogeous fungi are spread by the small mammals that eat them, thus completing a loop of interdependencies in forest ecosystems (fig. 4G).

As important as large, decaying logs are to functional ecosystems where spotted owls seem to thrive, logs that are positioned perpendicular to the slope of the land are most valuable. This is because they are best situated to intercept soil and water moving downslope and, as a result, to become a substantial water reservoir as they reach an advanced state of decay. Even more important is the fact that very large logs can make a vital contribution to the forest ecosystem for a longer period than they did as standing, live trees (Maser 1989). These log reservoirs provide refuges for many animal species during hot, dry parts of the year, just as they provide water to trees whose roots, aided by the symbiotic fungal mycorrhizae, have penetrated them. To ignore the role of logs in our forest ecosystems may be to lose those ecosystems in the long run.

Why Snags?

Spotted owls occasionally select snags for nest sites, either on their broken top or in natural cavities in the snags, cavities that either carried over from the live tree or were created by decay after the tree died. Among the 263 nests reported in our sample from conifer forests (table 5I), 17 percent were in snags. Snags provide the primary nesting substrate for many other cavity-nesting birds as well. Woodpeckers, which are occasionally captured and eaten by spotted owls (table 4A), excavate nesting and roosting cavities, and a variety of nonexcavating species later use the same cavities for nests or roosts. Of particular significance in the ecology of spotted owls, flying squirrels often use old woodpecker cavities for den sites. Finally, snags eventually fall and contribute to the accumulation of decaying wood on the ground. Therefore, the snag component benefits the owls both directly and indirectly in a variety of ways (trace arrows in fig. 4G).

Why Multiple Canopy Layers?

A possible ecological explanation for the prevalence of multi-layered canopies in habitats frequented by spotted owls is not clear. The structural diversity associated with these "layers" may contribute to a greater diversity of prey species. Perhaps, as Barrows and Barrows (1978) have hypothesized, the different layers provide opportunities for the owls to move up and down within the overall canopy to find the most comfortable microclimate for roosting. Or they may be important in allowing foraging owls to use perches at a variety of heights as they search for prey. On the other hand, multiple layers may be simply a covariate of some other component of the owl's habitat that is vital, such as the owl's prey.

Why Dense Canopies?

Among the most consistent habitat relations found for spotted owls is their greater use than expected of stands having 40 percent or greater (foraging) and 70 percent or greater (nesting and roosting) total canopy cover (Chapters 5 and 6). Like the owl's association with multiple canopy layers, however, possible reasons for this are not readily apparent. It may relate to one

or more of the following: (1) Denser stands tend to be cooler and, as proposed by Barrows (1981), they would allow the owls a wider range of choices for locating thermally comfortable roosts. (2) Denser stands provide more concealing cover, where the owls may be able to nest and roost with less chance of discovery by potential predators. It may be no coincidence that their plumage is speckled, as this pattern would tend to camouflage them during the daytime in a forest full of sunflecks. (3) In conifer forests, where flying squirrels dominate the owls' diet, prey may be more abundant and available in denser forest stands (see Chapter 10). This would not necessarily account for the same observed relation between canopy cover and owl habitat use in areas where woodrats dominate the diet, however, because woodrats tend to be most abundant in relatively dense stands of shrubs. To benefit owls, these must be intermingled with, or adjacent to, the hardwood stands where the owls roost and nest.

Why Differences in Home-Range Size?

In general, the largest home ranges of California spotted owls occur where flying squirrels comprise the majority of the owl's diet and the smallest home ranges occur where woodrats dominate. Home ranges of spotted owls in conifer forests of the Sierra NF are several times larger than home ranges <10 airline miles away, in foothill riparian/hardwood forests (Neat et al. 1990). Owls in the conifer forest prey mainly on flying squirrels, but those in the low-elevation hardwood stands prey almost exclusively on woodrats (table 4A).

The importance of these prey to the ecology of spotted owls has been emphasized by the bolder connecting links in figure 4G. Although only one study of spotted owls has shown a clear connection between prey abundance and areas used by the owls (Carey et al. 1992), we strongly suspect that the approximately 10-fold difference in observed home-range sizes of California spotted owls results primarily from regional differences in diet. Apart from common sense and the study by Carey et al., our strongest scientific support for this contention is the degree to which densities and reproductive activities of owl species throughout the world—at least those that have been studied well enough to establish the relations—are influenced by the availability of their prey (table 4B). Not only are woodrat populations denser than flying squirrel populations, often by at least 10-fold (Chapter 10), but also woodrats weigh nearly twice as much as flying squirrels.

Why Do Most Pairs of Owls Not Nest Every Year?

Spotted owls exhibit marked yearly variation in the proportion of pairs that nest. This has ranged from essentially no pairs to nearly all pairs nesting. For example, from as low as 11 percent to as high as 70 percent of owl pairs in the Eldorado demographic study have nested in different years (R. J. Gutiérrez, pers. observ.). On the other hand, Franklin et al. (1990) reported little variation in the proportions of pairs nesting during a 6-year study in northwestern California. Much annual variation has also been observed in nesting success (proportion of pairs nesting that also fledge young) from year to year and from region to region, ranging from as low as 0 to as high as 100 percent (Forsman et al. 1984, Gutiérrez et al. 1984, Thomas et al. 1990, Lutz 1992, LaHaye et al. 1992).

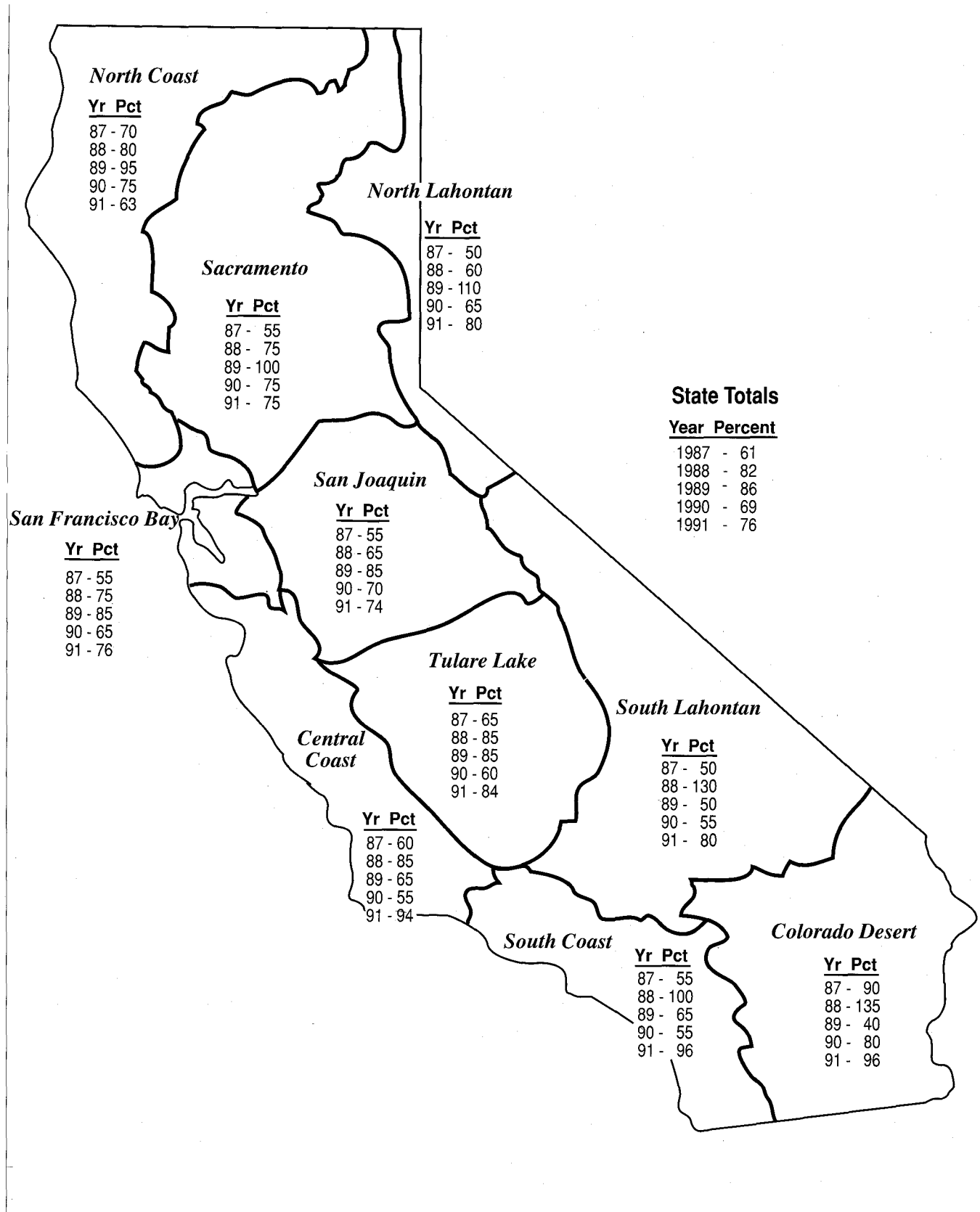


Figure 4H-Percentages of mean annual precipitation in California from 1987 through 1991, by water year (1 October through 30 September) and hydrologic region (California Department of Water Resources 1991).

Surveys of California spotted owls have been used to determine distribution, density, and other measures of "status" (see tables 3A, 3B, 3F, and 3H-J). These counts overestimate the functional owl population, however, because pairs do not occupy all sites in all years, occupied sites do not always support pairs, and each pair does not breed every year. A compilation of results from sites occupied for 4 consecutive years, adjusted to represent 50 known sites where owls defended a territory in any one of the 4 years (G. I. Gould, Jr., pers. observ.), suggests that only about 41 sites would be occupied in a given year, 34 would be occupied by pairs, and only 11 of those would produce young. Over the 4-year period, owls at 20 sites, usually the most consistently occupied, would produce 90 percent of the young.

For many owl species, failure to breed in some years has been shown to result from low prey availability (table 4B). As for home-range size, even lacking definitive studies of spotted owls, we strongly suspect that the local prey base largely determines whether a given pair of owls attempts to nest in a given year, and whether it succeeds if it does make an attempt. Drought may be a corollary here. Nearly all of the detailed studies of the California spotted owl, upon which this report is based, have been done during an ongoing drought that began in 1987 (fig. 4H). A variety of scenarios might occur. For example, drought has been observed to depress woodrat populations or not to affect them (Chapter 10), so the drought may or may not have lowered reproduction among the owls. Mild winters accompanying the drought may have increased the survival rates of the owls or the flying squirrels, or both. We cannot reach conclusions about these or other options. All we can do is acknowledge the attendant uncertainty.

Conclusions

California spotted owls share many attributes of their natural history with the northern spotted owl. Yet our knowledge of the California spotted owl's biology is meager relative to its more famous northern relative. For example, we are not yet able to set clear bounds on the range of habitats that are capable of supporting self-sustaining populations of the California subspecies (Chapter 8). And we are not likely to be able to do this until the owls have been studied thoroughly during both wet and dry climatic cycles. Our only good estimate of juvenile survival rate for the subspecies is based on the population in the San Bernardino Mountains (Chapter 8), although we estimate that about 75 percent of all California spotted owl pairs occur in the Sierra Nevada, where habitat change (by logging) is of greatest concern. Similarly, with the exception of the San Bernardino Mountain study, estimates of age-class survival and fecundity schedules are lacking or are imprecise. No studies are available that relate California spotted owl populations to populations of their prey species. Finally, we know little about the factors important

in the biology of the owl's primary prey species. The work of Waters and Zabel (1992) on flying squirrels in the Lassen NF is exemplary in that regard. Their work needs to be replicated elsewhere, and equally comprehensive studies of woodrat ecology need to be undertaken.

The general lack of information about nearly all phases of the California spotted owl's biology and ecological relations leads to high uncertainty about its present status. Because of this uncertainty, we recommend continuation of basic ecological studies and prudent forest management-following practices that will maintain future options.

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Chapter 5

Habitat Relations of the California Spotted Owl

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The California spotted owl's distribution spans a latitudinal range similar in extent to that of the northern spotted owl (Johnsgard 1988). It occurs at higher elevations than the northern subspecies, however, and portions of the overall population exist in "island" subpopulations on isolated mountain ranges in southern California (Gutiérrez and Pritchard 1990). It also occurs within sight of the Los Angeles Basin, with one of the largest human populations in North America. Grinnell and Miller (1944) first recognized that California spotted owls occupy a variety of forest types. The extent of this variety has been documented by Laymon (1988), Bias (1989), Neal et al. (1989), Call (1990), Call et al. (1991), LaHaye et al. (1992a), and Bias and Gutiérrez (1992). In this chapter we summarize the patterns of habitat variation and habitat use across most of the range of the California spotted owl.

Study Areas and Methods

Sierra Nevada

Six major studies have described habitat relations of California spotted owls in four general areas spanning the length of the Sierra Nevada (fig. 5A). From north to south, these four study areas were: (1) The Lassen Study Area (Zabel pers. comm.), which included primarily high-elevation (5,500-7,200 feet) forests of red fir and white fir (Rundel et al. 1977) and secondarily some lower-elevation habitats dominated by pines and Sierran mixed-conifer forests (see color photos 5-1 and 5-4 at the end of this chapter). The area was a mosaic of selectively logged, clearcut, and uncut stands (old-growth). (2) The Tahoe Study Area (Call 1990) was primarily in mid-elevation mixed-conifer forest (Rundel et al. 1977) at 2,200-5,200 feet. The past history of logging there resulted in a diverse patchwork of different stand ages, types, and densities. (3) The Eldorado Study Area (Laymon 1988, Bias 1989, Lutz 1992) extended from low- and mid-elevation mixed-conifer forest to higher-elevation fir forest (1,000-7,400 feet) (color photos 5-11, 5-12, and 5-18). Logging history has varied there because of the pattern of land ownership-about 40 percent of the land was in private industrial forests that occupied alternate sections in a "checkerboard" pattern with federal lands (Bias and Gutiérrez 1992). Laymon's study included winter observations of migrant owls that moved from their higher-elevation nesting habitats to foothill riparian/hardwood forests as low as 1,100 feet. These latter sites should not be construed as representative of owl sites

in the Sierran conifer zone. (4) The Sierra Study Area, in the Sierra National Forest (NF) (Verner et al. 1991), included two distinct habitat types-one dominated by mixed-conifer forest at elevations ranging from about 4,500 to 7,500 feet, the other dominated by hardwoods in oak-pine woodlands and relatively dense riparian/hardwood forests at elevations from about 1,000 to 3,500 feet. Only this study area included breeding populations both in high-elevation conifer forests and riparian/hardwood forests at low elevations (color photos 5-21 and 5-22).

Southern California

Several habitat studies have been done on isolated mountain ranges in southern California (fig. 5A). Here we discuss only one major study area-the San Bernardino, which encompassed almost the entire owl population in the San Bernardino Mountains (LaHaye et al. 1992b). It was the largest of the isolated "island" populations of spotted owls in California. The San Bernardino Study Area included numerous habitat types (see Thorne 1977) because it ranged in elevation from 2,500 to about 9,000 feet (color photos 5-34 to 5-37).

The habitat of two isolated populations studied by Gutiérrez and Pritchard (1990), on Mount San Jacinto and Palomar Mountain (fig. 5A) (color photos 5-39 to 5-42, and 5-44), had lower diversity than the San Bernardino Study Area and involved much smaller owl populations. Barrows (1980) reported observations at five roost sites of pairs or individuals on four mountains in southern California. In addition to these investigations, qualitative assessments of habitat have been made by U.S. Department of Agriculture, Forest Service (FS) biologists from the various NFs in southern California, but especially from the Los Padres NF (Sandburg and Winter 1989) (color photos 5-29 to 5-32, and 5-38). Observations of owls by forest biologists were part of their normal duties, and did not include designation of specific study area boundaries.

Photo Series

A set of color photographs of California spotted owl habitat from throughout the subspecies' range augments our text descriptions of habitats. These photographs, presented as a set at the end of this chapter, were taken from June to September 1991 during field trips by the Technical Assessment Team. The purpose of the trips was to become directly familiar with the full range of variation in the habitat occupied by this owl.

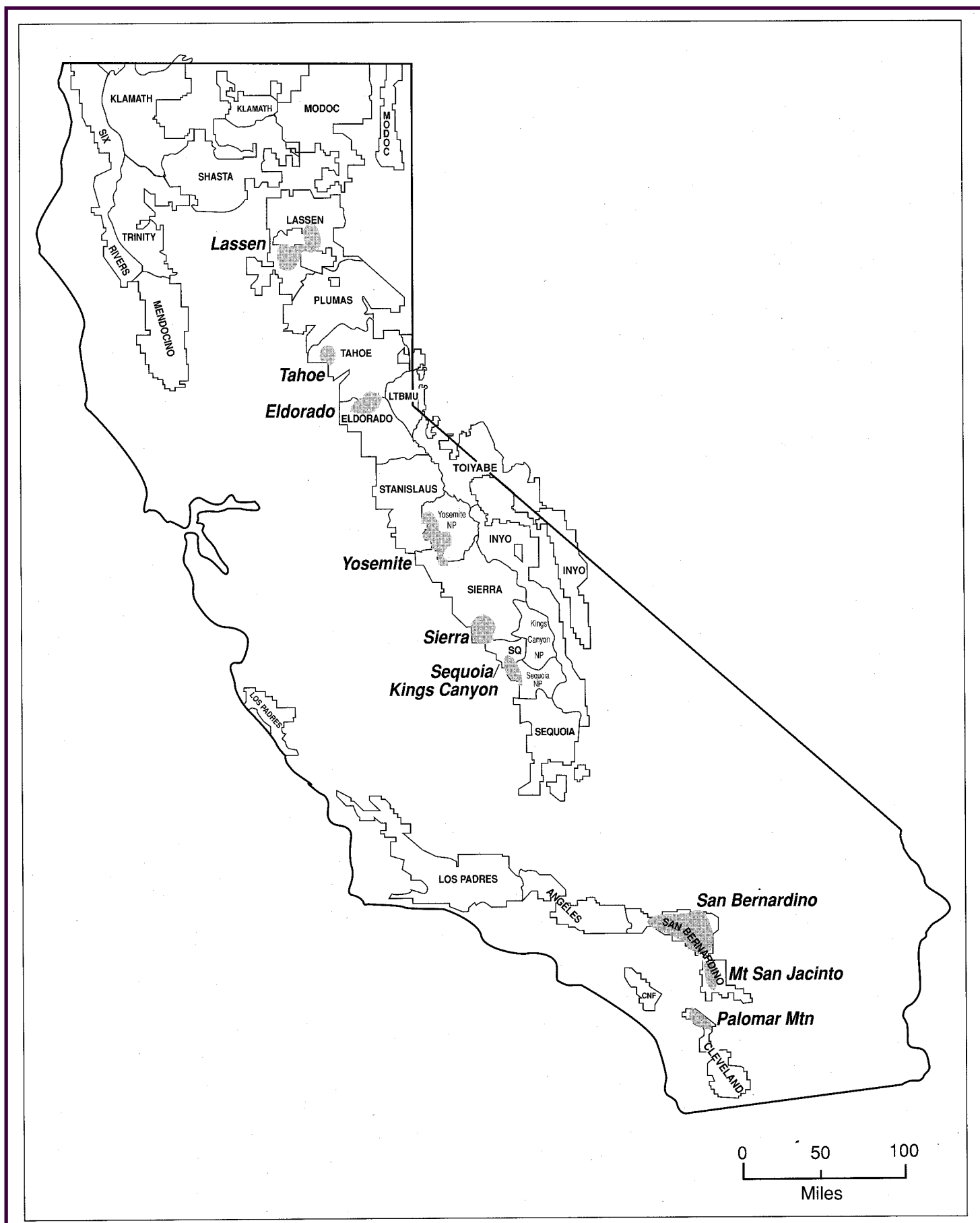


Figure 5A-Locations of radio-tracking and demographic study areas for California spotted owls.

Conifer Forests of the Sierra Nevada and Southern California

Patterns of Habitat Use at a Landscape Scale

California spotted owls use forested habitats almost exclusively (color photos 5-1 to 5-48). Only one record is available of a pair nesting in a tree not closely surrounded by a stand of other trees. That pair nested in a residual snag in a clearcut on the Sierra NF, although relatively dense stands of oaks were within 160 feet of the nest and the young moved there shortly after they left the nest (Yamanaka pers. comm.). Spotted owls have occasionally foraged in relatively open areas, such as shrubfields, meadows, or plantations, but this is exceptional. Call (1990), for example, found such habitats to be used significantly less than expected, based on availability in the Tahoe Study Area. We included these observations only to illustrate that California spotted owls occasionally occur in habitats that do not meet all their life history requirements (that is, they are unsuitable). It is important to note that one cannot infer suitability from the occasional presence of owls in a habitat.

Data at a Landscape Scale

Each of the seven Sierra Nevada NFs provided the following information on detected owl nests ($n = 148$): (1) timber

type and size of the stand in which the nest was located, based on verified database mapping in their Land Management Plans (LMPs); (2) the same information as in (1) for each stand polygon that bordered the nest stand and was in a timber type used for foraging, roosting, or nesting; and (3) a map of the nest and adjacent stands. Stands bordering nest stands were primarily M2G, M3N, M4N, M3G, M4G, R3N, R4N, R3G, and R4G (codes for timber strata are defined in table 1C and in Appendix B). The estimated number of acres in habitat types listed in table 5A were based on the most recent FS inventory data (Fiske, pers. comm.).

Selective Use of Forest Types

Based only on those habitat types in which nests had been observed and verified, we found a significant difference between habitats selected for nesting stands and the overall distribution of available habitats in Sierran NFs (table 5A, fig. 5B). A 95-percent Bonferroni interval test (see Neu et al. 1974, Byers and Steinhorst 1984) on the forest types contributing to this difference (table 5A) showed that, based on availability of different forest stand types, spotted owls in the Sierra Nevada nested more than expected in mixed-conifer stands with medium- to large-sized trees [24 to 36+ inches in diameter at breast height (d.b.h.)], stands with a wide range of tree sizes overall (5 to 60+ inches in d.b.h.), and medium (40-69 percent) (stand type M4N) to high (70-100 percent) total canopy cover (stand type M4G). Forty-five percent of all nest stands in Sierran conifer forests, however, were in the M4N and M4G habitat types. All other habitat types that we evaluated were used equal to or less than their proportional availability (table 5A).

Table 5A—Distribution of California spotted owl nest habitat types compared with proportions of available habitats in the Sierra Nevada.

Habitat Type ¹	Sample size	95 percent Bonferroni interval			Available	Result
		Lower	Point estimate	Upper		
M2G ²	2	0	0.0135	0.0390	0.0209	U = A ³
M3P	10	0.0121	0.0676	0.1231	0.2369	U < A
M3N,G	44	0.1962	0.2973	0.3984	0.2501	U = A
M4P	10	0.0121	0.0676	0.1231	0.1418	U < A
M4N,G	67	0.3426	0.4527	0.5628	0.2005	U > A
R3P	2	0	0.0135	0.0390	0.0448	U < A
R3N,G	3	0	0.0203	0.0514	0.0522	U < A
R4N,G	10	0.0121	0.0676	0.1231	0.0464	U = A
Total	148					

¹ See figure 5B for distribution of habitat types that were significantly different ($\chi^2 = 79.9$, $df = 7$, $P < 0.05$) between used and available types.

² Habitat codes correspond to FS timber strata labels: M = mixed-conifer, R = red fir; 2 = pole-sized trees (<12 inches in d.b.h.), 3 = small sawtimber (trees 12-24 inches in d.b.h.), 4 = medium and large sawtimber (24-40 and >40 inches in d.b.h.); G = 70+ percent canopy cover, N = 40-69 percent canopy cover; P = 0-39 percent canopy cover.

³ U = A; current evidence does not indicate a difference between use and availability.

U < A; used less than expected.

U > A; used greater than expected.

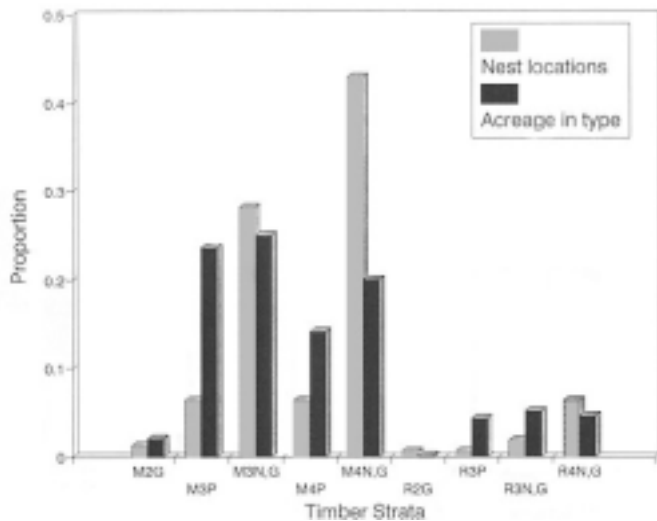


Figure 5B—Nest locations ($n = 148$) and proportional availability of different timber strata (see Appendix B or table 5A for definitions of strata codes).

In addition to the strata listed in table 5A and figure 5B, four nests were in pure stands of ponderosa pine (one each in P3N, P4P, P3G, and P4G) and eight nests in hardwood types. Because of a lack of consistency among NFs in typing these timber strata, we could not develop reliable estimates of their acreages available, or of their associated nests. Consequently, these nests were omitted from the analysis of use-versus-availability presented in table 5A. Ponderosa pine types commonly include hardwood components, but these are not considered in timber inventories. As a result, a site with ponderosa pines in the overstory and an understory of hardwoods would be judged by its stratum label to be unsuitable for nesting (and possibly even for foraging) by the owls, even though that may not be the case. Although we lack the needed data to perform rigorous statistical tests, it is our firm biological understanding that pine stands with high canopy closure and a significant hardwood component are excellent owl habitat. Not only do they have all of the necessary structural components, but also they are in an elevational zone where the distributions of woodrats and flying squirrels overlap. The presence of a rich and diverse prey base, proper structural characteristics, and relatively mild climatic conditions may well make these sites among the highest quality owl habitat in the Sierra Nevada. We believe, therefore, that at least the P4G strata is selected for nesting by owls, in excess of its availability.

Bias and Gutiérrez (1992) found that nesting and roosting owls on the Eldorado Study Area almost exclusively used mixed-conifer stands with medium (M3G) to large (M4G) timber and at least 70 percent canopy cover (color photos 5-11 and 5-18). The M4G stands were more abundant on public than on private land in the study area, and the owls used public lands for nesting and roosting significantly more than they used private lands. Gutiérrez and Pritchard (1990) found that spotted owls on Mount San Jacinto used conifer and riparian/hardwood forests (color photos 5-41 and 5-42) significantly more than expected, based on their availability, and that owls on Palomar Mountain used primarily conifer or mixed forests of conifers and hardwoods (color photos 5-39 and 5-40).

Density of Owl Sites in Relation to Amount of Suitable Habitat

Based on intensive surveys for owls by NF personnel and others, owl densities in U.S. Geological Survey quadrangles (1:24,000; $n = 49$) in the zone of mid-elevation, Sierran mixed-conifer forests were significantly, but weakly, correlated with the percentage of forests having medium-sized and larger trees and high canopy closure ($R^2 = 0.38$, $P < 0.05$; fig. 5C). We interpreted these relations cautiously, however, because survey effort was not uniform among the survey units and error exists in the type mapping of mixed-conifer habitat by the FS (Call 1990, Bias and Gutiérrez 1992, G. N. Steger pers. observ.). Nevertheless, this analysis suggested that, as with nest stands, owl densities were higher in areas with a higher proportion of dense stands and large trees.

Patterns of Habitat Use at a Home-Range Scale

Here we report results of various studies that have compared attributes of sites used for nesting, roosting, and foraging with the same attributes measured at sites randomly selected from the surrounding forest. Only results of studies done in conifer forests of the Sierra Nevada and San Bernardino Mountains are reported here. Methods used to measure habitat attributes varied among the studies. Although direct statistical comparisons could not be made across all studies, we believe all methods provided objective, quantitative estimates of the attributes in local owl habitats.

All workers except Laymon (1988) used consistent methods within their studies, and workers from three study areas (Tahoe--Call 1990, Eldorado-Bias 1989, and San Bernardino--LaHaye et al. 1992a) used consistent methods among the studies. Workers from these latter three studies used a variable circular-plot design, using basal area prisms that resulted in an increasing plot size with increasing diameters of trees, an estimation procedure commonly used by foresters for estimating

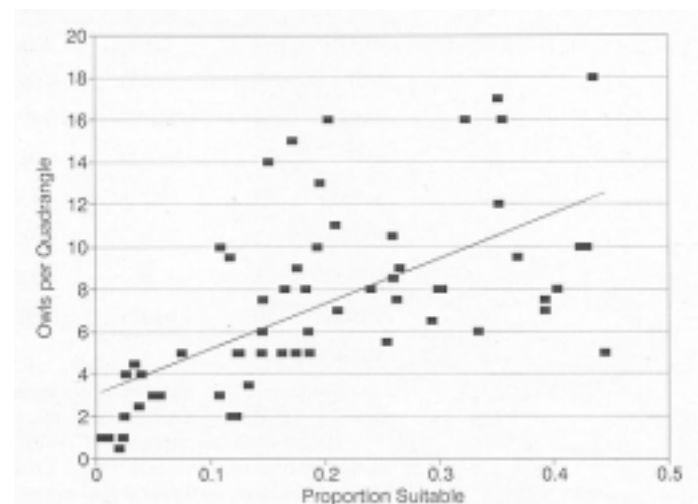


Figure 5C—Density of owl sites in the Sierra Nevada ($n = 49$) in relation to the proportion of habitat considered to be suitable for spotted owls in U.S. Geological Survey quadrangles (1:24,000).

Although our conclusions from studies in the Tahoe Study Area were basically the same as those reported by Call (1990) and Call et al. (1991), some details of our results differed slightly because we eliminated from Call's sample of random points all locations with <40 square feet per acre in basal area of softwoods. Eliminating recent clearcuts and shrubfields allowed more meaningful biological comparisons with foraging sites. In addition, we subsampled the sample of foraging sites by eliminating, at random, all but one location from each owl, or owl pair, in a given day.

In addition to studies that compared habitat attributes between random sites and sites used by owls, B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.) sampled nest stands in the Lassen Study Area and the Sierra Study Area, respectively, but not in comparison with random sites. In these studies, vegetation at nest sites was sampled using strip transects arranged perpendicular to one another and centered on the nest tree. Beginning 32.8 feet from the center of the nest tree, the long axes of four strip transects (32.8 by 113.7 feet-total area sampled = 0.30 acre) radiated on four sides of the nest tree along perpendicular lines through the nest tree. No vegetation data were collected within the 32.8 by 32.8 foot square centered on the nest tree.

Finally, Steger and Eberlein (pers. comm.) sampled habitats, by canopy-cover class (0-39 percent, 40-69 percent, and 70+ percent), throughout the radio-tracking portion of the Sierra Study Area, based on stratified random samples of habitat polygons in both the foothill riparian/hardwood and mixed-conifer portions of the study area. Their method used four sets of nested plots randomly located in each polygon. Plots were 16.4 by 328 feet for all trees and snags, 32.8 by 328 feet for trees >35.4 inches in d.b.h., and 65.6 by 328 feet for snags >15.7 inches in d.b.h.

Differences Among Methods

Laymon (1988), Bias (1989), and LaHaye et al. (1992a) all used tree-centered plots for the evaluation of the nest sites, but they did not center random plots on trees. This method introduced a potential bias in the comparisons between nest/roost sites and random locations. It also had the potential to bias the inferences drawn concerning stand attributes based on nest locations. Data from Call (1990), B. B. Bingham (pers. observ.), and Steger and Eberlein (pers. comm.) did not have this bias.

The magnitude of any bias introduced by centering on a large tree is related to the density of similar trees in the surrounding stand and the size of the sample plot. One way to envision the bias is to ask how likely it is that a random plot (of identical size and shape) in the same stand would sample either the nest tree or another tree having similar size and condition. We would expect samples centered on nest trees to be more strongly biased than roost locations-roosts are often in small trees in dense stands, whereas nest trees are generally larger than trees in the surrounding stand (for example, tables 5B-5D).

Based on plot size, Laymon's (1988) data may be the most biased. He used small (0.17-acre), fixed plots and all of his owl-use plots, including foraging locations, were tree-centered. Bias (1989) and LaHaye et al. (1992a) both used variable-plot meth-

ods with a basal area factor (BAF) of 20. This sampling technique has the advantage that plot size increases with the size of the nest tree. For a tree 40 inches in d.b.h., the plot size is 0.44 acres; it is nearly an acre for a 60-inch tree.

Estimating the Bias-We could not repeat these studies or obtain all the raw data for re-analysis. We could, however, estimate the probable magnitude of the statistical bias due to tree-centering and determine the extent to which it changed the inferences drawn from these analyses. For Bias (1989) and LaHaye et al. (1992a), we corrected for total basal area simply by removing the nest/roost tree. When prism sampling, overall basal area can be determined simply by counting the number of "count trees" in the plot. Each counted tree represents a certain basal area per acre, as determined by the BAF. With a BAF of 20, for instance, each tree represents 20 square feet basal area per acre (BA/acre). At nest and roost sites, Bias obtained an average of 251 and 294 square feet BA/acre, respectively (table 5B), and LaHaye et al. reported 223 and 267 square feet BA/acre for nest and roost sites, respectively (table 5C). On average, Bias and LaHaye et al. were "counting" between 11 and 15 trees in each sample plot. Removing the nest tree from the basal area calculation would remove only one tree from each plot, a reduction of 20 square feet BA/acre. This suggests a range from 203 to 274 square feet BA/acre in their nest and roost stands.

While this decrease is not large, we believe it probably exceeds the potential bias of including the nest or roost tree in the sample. For example, if the nest tree were not within the plot, most likely other trees would be. The basal area of these trees would, in part, compensate for the removal of the nest tree. To obtain better estimates of the true bias, we analyzed nest site data from B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.). These data were taken in the vicinity of the nest tree but did not include the nest tree. We added the nest tree and recomputed live tree and snag basal area. For Bingham's data, live tree basal area was increased by about 7 square feet BA/acre and was not significantly different from the original estimate ($P = 0.18$). Basal area for the largest diameter-class, however, was shifted by 16.4 square feet BA/acre ($P = 0.002$). Similarly, snag basal area was significantly overestimated by including the nest snag in the sample. For Steger's and Eberlein's data, live tree basal area was increased about 4 square feet/acre, not significantly different from the original estimate ($P = 0.17$). Snag basal area was increased 5 square feet/acre, not significantly different from the original estimate ($P = 0.36$).

B. B. Bingham (pers. observ.) and Steger and Eberlein (pers. comm.) used fixed plots of 0.3 acres. These plots were smaller than the plots associated with large d.b.h. classes using a BAF of 20, but not greatly so. We believe these data can be used to make reasonable inferences concerning the magnitude of bias in the results of Bias (1989) and LaHaye et al. (1992a). Laymon's (1988) plots were about half the size of those used by Bingham and by Steger and Eberlein, so the potential for bias is therefore greater.

Conclusions-Given their sampling methods, results from Bias (1989) and LaHaye et al. (1992a) should be interpreted with a number of cautions. The overall basal area figures and basal area for all trees >16 inches in d.b.h. would not be significantly

Table 5B-Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl nest (n =11) and roostsites (n = 29), and random sites (public land, n =328) in the Eldorado Study Area, central Sierra Nevada (Bias 1989).

	Nest sites		Roost sites		Random sites	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes						
Percent slope	26.1	46.8	30.1	58.3	32.3	61.2
Elevation (feet)	4,900.0	18.6	4,561.0	14.6	4,728.3	18.1
Structural attributes						
Percent cover	89.3	16.1	95.6 ^a	3.9	79.2	32.0
Basal area (square feet per acre)						
Hardwoods	38.3	69.1	43.6	60.9	61.3	138.1
Softwoods	234.4	43.8	268.4 ^a	44.0	151.6	80.2
Total live	251.0	25.1	293.7^a	37.0	173.4	70.5
Snag	52.7 ^a	45.8	52.7 ^a	72.8	37.0	134.2
Basal area (square feet per acre, by d.b.h. class) ^{1, 2}						
3.9-4.8	5.5	-	7.4	-	3.9	-
4.9-10.7	14.5	-	24.4	-	44.7	-
10.8-20.6	89.9	-	90.3	-	61.9	-
20.7-35.5	91.0	-	82.7	-	52.4	-
>35.5	110.9	-	95.1	-	42.6	-
Downed woody debris (percent cover, by diameter class in inches)						
1-11.8 inches	12.1	57.8	10.2	69.0	11.2	122.6
>11.8 inches	2.7	87.0	2.6	187.8	3.9	244.6

^a Significantly different from the corresponding random sample, at the 0.001 level of significance (1-way ANOVA, using Scheffe test for multiple comparisons).

¹ Diameter at breast height, in inches.

² CVS could not be computed for these data.

Table 5C-Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl nest (n = 131) and roost sites (n = 43), and random sites (n = 296) in the San Bernardino Study Area, southern California (LaHaye et al. 1992a).

	Nest sites		Roost sites		Random sites	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes						
Percent slope	51.2 ^a	50.8	54.7 ^a	44.6	32.3	68.8
Elevation (feet)	6,052.0 ^a	20.9	6,299.2 ^a	18.5	6,942.3	14.7
Structural attributes						
Percent cover	76.9 ^a	21.3	83.6 ^a	15.3	52.2	50.5
Basal area (in square feet per acre)						
Total live	222.7^a	41.7	266.7^a	35.2	124.2	68.8
Snag	21.4 ^a	120.9	20.9 ^a	123.3	7.8	217.3
Dead-topped trees	12.2	143.3	15.7	99.1	7.0	224.6
Hardwoods (by d.b.h. class) ¹						
0-5.9	5.2	263.0	10.5	182.8	14.8	245.2
6.0-11.8	13.1	207.1	32.7	182.3	14.8	230.3
11.9-17.7	14.4	224.6	25.7	163.9	3.5	356.0
>17.7	19.6	151.0	28.8	162.5	3.1	391.6
Total	52.31	129.5	97.61	119.5	36.2	169.0
Softwoods (by d.b.h. class)						
0-9.8	12.2	178.1	16.6	160.5	13.1	207.1
9.9-19.7	27.0	123.8	41.4	128.4	24.8	135.7
19.8-29.5	46.2	100.3	43.6	117.4	21.8	127.8
>29.5	85.4	77.1	67.1	67.7	29.2	124.1
Total	170.4^a	58.9	168.6^a	68.5	88.0	85.1

^a Significantly different from the corresponding random sample, at the 0.001 level of significance (Mann-Whitney U test).

¹ Diameter at breast height, in inches.

Table 5D-Habitat characteristics of California spotted owl roost sites in summer (n =120), fall (n = 78), and winter (n = 61), and at random sites throughout summer/fall (n = 120) and winter (n = 66) in the Eldorado Study Area, central Sierra Nevada (Laymon 1988). Note that all winter data were obtained in low-elevation, oak-pine forests, where the birds migrated for the winter (see Chapter 4).

	Roost sites				Random sites		Roost sites in winter		Random sites in winter	
	Summer		Fall		Summer/fall					
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes										
Percent slope	18.1 ^a	36.3	21.1 ^a	35.6	23.4	46.8	26.8 ^a	36.4	19.9	30.6
Structural attributes										
Percent cover	85.8 ^a	6.4	75.2	9.4	67.9	29.0	63.5 ^b	12.9	29.7	32.8
Basal area (square feet per acre)										
Hardwoods	20.9	79.8	12.6 ^a	106.5	26.1	146.0	18.7 ^b	56.7	7.0	126.9
Softwoods	330.7 ^a	21.6	259.7 ^a	25.9	163.8	62.6	57.1 ^b	65.1	29.2	78.8
Total live¹	351.6	-	272.3	-	189.9	-	75.8	-	36.2	-
Snags	41.4 ^a	57.6	47.5 ^a	60.8	17.4	246.4	35.7 ^b	168.3	19.6	63.2
Downed woody debris (tons per acre, by log diameter class) ²										
0-3 inches	0.82	0.30	0.90	0.32	0.82	0.74	0.23 ^b	0.78	0.18	0.50
>3 inches	12.16 ^a	0.59	10.53	0.72	9.36	1.39	1.56 ^b	1.55	0.62	1.44

^a Significantly different from corresponding random sites in summer/fall, at the 0.05 level of significance (Student's *t* test).

^b Significantly different from corresponding random sites in winter, at the 0.05 level of significance (Student's *t* test).

¹ The sum of softwood and hardwood basal areas. Data were not available to compute a percent Coefficient of Variation for this variable.

² Assumes a specific gravity of 0.4 for downed woody debris.

biased. Basal area in the largest diameter-class would, however, be overestimated, by perhaps as much as 20 square feet BA/acre. Similarly, snag basal area would be overestimated by perhaps 10 square feet BA/acre. Laymon's (1988) basal area data should be viewed with caution. For all of these studies, we have no reason to believe that estimates of canopy closure were affected by tree-centering (for example, see table 5B).

No important changes in inferences made from results of these studies were associated with these biases, although it is possible that the statistical significance of certain test results could be altered. It is important to note that in Bias (1989) and LaHaye et al. (1992a) the statistically significant basal area differences from random samples were associated most strongly with sites of roost trees, where we do not expect tree-centering to have as much impact as at nest tree sites. It is also worth noting that the statistical results presented by Call (1990), B. B. Bingham (pers. observ.), and Steger and Eberlein (pers. comm.) were not based on tree-centered plots.

Nest and Roost Sites

Physiographic Attributes-Mean elevation at nest sites in conifer forests increased -from about 5,300 feet in the northern Sierra Nevada to 6,000 feet in southern California-about coincident with low- to mid-elevation mixed-conifer zones. Nests at the highest elevations were in red fir forests in the Sierra Nevada and white fir forests in the San Bernardino Mountains. No nests have been located in subalpine forests anywhere in California.

Blakesley et al. (1992) reported that nest sites of northern spotted owls in northwestern California tended to be on steeper slopes and in the lower third of canyons. This pattern was true for the California spotted owl only in the San Bernardino Study Area (table 5C). Based on statistical methods for analyzing data from circular distributions (Zar 1984, p. 422-469), the mean

aspects of nesting, roosting, and random sites were not significantly different in the San Bernardino Mountains (LaHaye et al. 1992-). Assuming equal availability of aspects, significantly more nest sites in the Sierra Nevada were located on north aspects and fewer on southwest aspects than expected (*n* = 148; *P* < 0.001; fig. 5D). These results should be viewed with caution, however, as we cannot evaluate the validity of the assumption that all aspects were equally available.

Roost sites used by California spotted owls were similar in structure and composition to those used for nesting, although we know less about owl roosting habitat than nesting habitat. Some spotted owls have repeatedly used the same roost sites, suggesting that they have narrow selection patterns for roosting (Barrows and Barrows 1978, Barrows 1980, Steger and Eberlein pers. comm.) or that they tend to return to familiar or favorable roosts.

Within study areas, roost and nest sites were similar in elevation and slope (tables 5B and 5C), probably because the owls often roosted near a nest site (LaHaye et al. 1992a). All of the roosting California spotted owls found by Barrows (1980) were on north-facing slopes. Studies in the Sierra Nevada (Laymon 1988, Bias 1989) and in the San Bernardino Mountains (W. S. LaHaye pers. observ.), however, did not reveal a significant

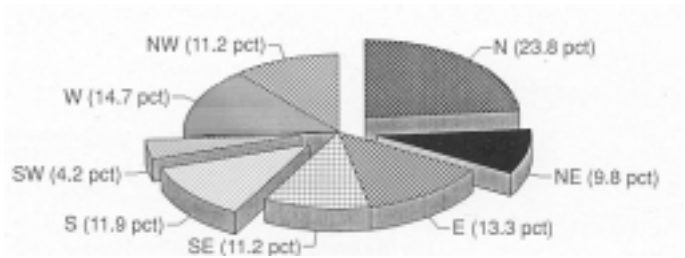


Figure 5D-Proportions of nest sites on slopes facing different directions from all nest sites located on National Forests within the range of the California spotted owl (*n* = 143).

difference in mean aspect between roost sites and random locations. The owls studied by Barrows (1980) were in habitats at low elevation, where the dense-canopied stands selected by the owls would be found most often on north-facing slopes.

Structural Attributes-Mean canopy cover at nest and roost sites, for the three studies that measured these variables (tables 5B-5D), was consistently higher than the canopy cover at random samples-on average, about 20 percent higher. Canopy closure at nest sites was not significantly higher than at random locations in the central Sierra Nevada (table 5B), but it was significantly higher in the San Bernardino Mountains (table 5C). Roost sites had significantly ($P = 0.001$) higher canopy closure than random sites in all three studies.

Mean softwood basal area was also consistently higher at nest and roost sites in all three studies. Total live tree BA/acre averaged 127 square feet greater in nest and roost stands than at

random sites. As with canopy closure, measures of basal area were more often significantly different between roost sites and random sites than between nest sites and random sites (tables 5B-5D). In all cases allowing a statistical comparison, roost sites had significantly more total live tree basal area and basal area of softwoods than random locations. At nest sites, total live tree basal area and softwood basal area were consistently higher than at random sites in both studies reporting these results (tables 5B and 5C), significantly so for both attributes in the San Bernardino Study Area (table 5C).

Tree size-class data were available for nesting and roosting sites in the Eldorado NF (table 5B) and the San Bernardino NF (table 5C) and for nest sites in the Sierra and Lassen NFs (table 5E). In the Eldorado NF, nest sites averaged 111 square feet BA/acre in trees >35.5 inches in d.b.h. Nest sites in the San Bernardino NF had, on average, >85 square feet BA/acre in trees >29.5

Table 5E-Habitat characteristics (mean and percent Coefficient of Variation) of spotted owl nest sites in the Lassen Study Area ($n = 24$), southern Cascade region of northern California (B. B. Bingham pers. observ.), and the Sierra Study Area ($n = 11$), southern Sierra Nevada (Steger and Eberlein pers. comm.).

	Lassen Study Area		Sierra Study Area	
	Mean	Percent CV	Mean	Percent CV
Physiographic attributes				
Percent slope	25.8	51.6	7.9	66.2
Elevation (feet)	5,599.6	8.0	4,840.0	7.9
Structural attributes				
Percent cover	85.2	9.8	85.6	13.8
Live trees ¹				
Basal area (square feet per acre)				
Total	243.8	36.7	185.8	73.3
Stems per acre (d.b.h. class in inches) ²				
5-10	93.2	72.0	96.3	73.3
11-20	60.3	50.8	35.9	43.7
21-35	17.1	73.8	16.6	57.0
>35	8.0	86.7	5.2	88.7
Stems per acre (height class in feet)				
13-25	14.8	251.7	99.0	101.9
26-39	44.3	87.1	35.0	60.1
40-53	34.2	84.4	25.1	65.3
54-79	42.4	83.4	35.0	62.3
80-105	20.8	92.3	10.4	90.9
106-131	13.2	70.6	9.2	135.3
132-157	6.7	160.1	6.4	215.2
158-183	1.8	172.0	2.1	145.2
>183	0.4	358.7	0.6	222.5
Snags				
Basal area (square feet per acre)				
Total ³	47.5	85.0	33.0	167.2
Large ⁴	21.3	119.1	19.5	131.8
Stems per acre (d.b.h class in inches)				
5-10	8.8	171.4	20.2	146.5
11-20	7.7	185.8	5.8	109.9
21-35	5.9	79.5	2.5	151.8
>35	2.8	130.8	1.2	222.0
Downed woody debris (tons per acre, by log diameter-class) ⁵				
11-20 inches	3.2	103.2	2.5	78.6
21-35 inches	7.7	94.4	5.1	131.
>35 inches	11.4	100.7	13.5	128.5

¹ Only live trees with d.b.h. >4 inches.

² Diameter at breast height, in inches.

³ Snags >4 inches in d.b.h., and ≥4.6 feet tall (Lassen Study Area) or ≥6.6 feet tall (Sierra Study Area).

⁴ Snags ≥15 inches in d.b.h. and ≥20 feet tall.

⁵ Only logs >10 inches in diameter at the large end. Assumes a specific gravity of 0.4 for downed woody debris.

inches in d.b.h. Nest sites in the Sierra and Lassen NFs averaged five and eight stems per acre >35 inches in d.b.h., respectively. These data, when combined with the analysis of nest-site preferences based on timber strata (table 5A, fig. 5B), demonstrate that a significant large-tree component is present in most owl nest stands.

At nest sites, basal areas were highest in the large-tree classes (>24 inches in d.b.h.) and decreased through each of the smaller size-classes (tables 5B and 5C). This often resulted in multi-storied nest stands dominated by larger trees with a well-developed understory (for example, color photo 5-27). The vertical stratification in these stands was not as extensive as that observed in nest stands of the northern spotted owl in northwestern California (LaHaye 1988, Solis and Gutiérrez 1990, B. B. Bingham pers. observ.).

Percent canopy cover, total live tree basal area, softwood basal area, hardwood basal area, and snag basal area were generally greater at owl roost sites than at random locations (tables 5B-5D). As at nest sites, the basal area of trees at roost sites was concentrated in the large size-classes, but with trees of all sizes resulting in multi-storied canopies.

Many of these parameters exhibited a large degree of variability, and the differences between habitat used by spotted owls and random locations may or may not have been statistically significant within a given study. The data were, however, consistent and mutually supportive among all studies. California spotted owls in these various studies chose to nest and roost in stands that were denser than average and that contained a large-tree component. Most nest sites were selected in dense mixed-conifer stands with average quadratic mean diameters of canopy trees >24 inches in d.b.h. We know of no data that contradict these findings.

Size of Activity Centers

Activity centers are areas within which owls find suitable nesting sites and several suitable roosts, and in which they do a substantial amount of their foraging. Using the sample of nest trees from conifer forests in the Sierra Nevada ($n = 148$), we estimated the sizes of stands containing the nest trees and the cumulative size of each nest stand plus all adjoining stands that were of a timber type used equal to or greater than its availability (table 5A). These adjoining stands may make important contributions to activity centers, because the owls have direct access to them. In some instances, nesting pairs may even spend more time in one or more of the adjoining stands than they do within the stand containing their nest.

The mean size of nest stands was 99.9 acres (SD = 114.9 acres) and the median was about 65 acres. The mean size of the nest stand plus adjacent stands was 306.7 acres (SD = 386.6 acres) and the median was about 265 acres. Numerous roosts would be available in the nesting and adjoining stands. Cumulative distribution functions for these two variables provide two important insights (fig. 5E). The majority of nest stands were smaller than 100 acres, but, in contrast, the majority of nest-plus-adjacent stands exceeded 200 acres.

Based on results of radio-tracking studies, the latter variable provides a better estimate of the size of activity centers. An

estimate of the area used for foraging in an activity center may be approximated by the area that includes half of the nighttime (foraging) locations of owls during the breeding period, as estimated by the adaptive kernel method (Worton 1989). In the radio-tracking study in the Sierra NF (G. N. Steger pers. observ.), this averaged 317 acres (SD = 202; $n = 9$) in 1987, 296 acres (SD = 110; $n = 7$) in 1988, and 310 acres (SD = 127; $n = 9$) in 1989. These estimates were not independent from year to year, because some of the same individuals' home ranges were included in 2 or 3 of the years. In the radio-tracking study in the Lassen NF (Zabel pers. comm.), the average was 788 acres (SD = 347; $n = 10$) in 1989-90. In all cases, only birds with at least 20 nighttime locations were used for these estimates.

Nest Sites on Private Timberlands

Hofmann and Taylor (1992) reported general habitat conditions at 18 nest sites on industrial forest lands in the northern ($n = 4$), central ($n = 5$), and southern ($n = 9$) Sierra Nevada. Fourteen of the pairs nested successfully, but the report did not indicate the proportion of all owls found on private lands that nested or the proportion that fledged young. The owls nested in a variety of forest stands, ranging from sparse (5 percent) to high (86 percent) cover by multi-storied stands with large-diameter trees. Reported values of site attributes were within ranges given above for nest sites in NFs. Overall, 60-65 percent of the area within a radius of 1,000 feet of nests had "dense" canopy cover. No other structural habitat features were reported.

Taylor (1992) provided additional information on the habitat associations of owls nesting on industrial forest lands in the Sierra Nevada. Based on a sample of 28 nests, Taylor found "...a clear pattern of dominance of nest sites by medium and large d.b.h. stands..." and the data to clearly indicate "...that owls nest in areas with moderate-to-dense canopy closure" (Taylor 1992, p. 9). These results are consistent with those reported in tables 5B-5D.

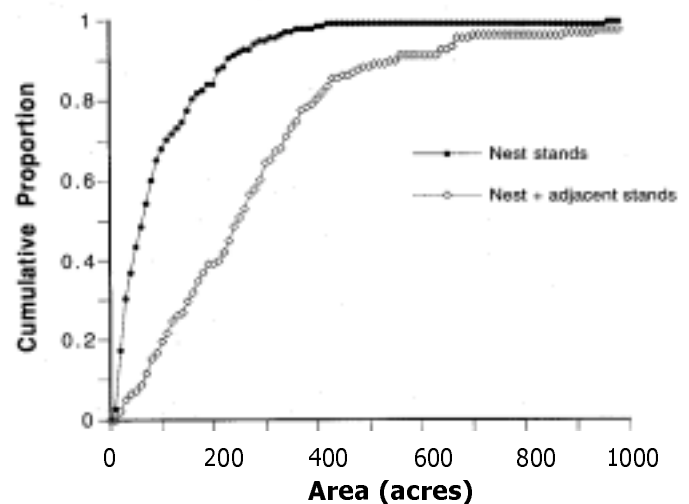


Figure 5E—Cumulative distribution of nest stands, and nest stands plus adjacent stands, arranged by size. Adjacent stands were restricted to those timber types used equal to, or greater than, their availability ($n = 138$).

Foraging Sites

Attributes of foraging habitats used by California spotted owls have been estimated in only two studies (Laymon 1988, Call 1990). In both studies, the range of habitat structures used by the owls was greater in foraging habitats than in nesting and roosting habitats. Laymon (1988, p. 100) concluded that the majority of spotted owl foraging locations in his Eldorado study were on sites with medium to large trees (in Laymon's classification, these were trees >24 inches in d.b.h.) and dense canopy closure (60 to 100 percent). They significantly selected for stands with trees >24 inches in d.b.h. and canopy cover of 40 to 59 percent, based on availability. On the other hand, they used stands significantly less than expected that had (1) trees in the 11- to 24-inch d.b.h. group and 60 to 100 percent cover, and (2) trees >24 inches in d.b.h. and canopy cover of 10 to 39 percent. Laymon (1988, p. 115) also reported that the owls in his study selected "foraging sites with more and larger snags."

Call (1990, p. 30) concluded that the owls in his Tahoe NF study area used clearcuts, shrubfields, and plantations significantly less than expected ($P = 0.01$), based on availability. They used medium timber (11-20 inches in d.b.h.) in proportion to availability ($P = 0.51$), and they used large timber (20-35 inches

in d.b.h.) significantly more than expected ($P = 0.01$). In addition, the probability of an owl's using large timber was significantly greater than of its using medium timber ($P = 0.003$). Based on vegetation sampled at foraging locations by Call (1990, p. iv), a "discriminant function analysis indicated that the owls selected habitats with late-successional stand characteristics including mature and old-growth timber [>35 inches in d.b.h.], multiple vegetation strata, and high live timber basal area." The combined results from Laymon's and Call's studies suggest that spotted owls in these Sierran conifer forests tended to forage in stands of intermediate to older ages.

Based on three canopy-closure classes (see table 5F), owls in the Sierra Study Area used stands with 70+ percent canopy closure significantly more and stands with 0-30 percent canopy closure significantly less than expected (Verner et al. 1991; also see Chapter 6).

Physiographic Attributes-Laymon (1988) found that random sites were significantly steeper than foraging sites during both summer and fall in the Eldorado Study Area (table 5G), but Call (1990) found no difference in the Tahoe Study Area (table 5H).

Table 5F-Structural attributes of habitats (mean and percent Coefficient of Variation, by canopy cover class) used by California spotted owls during radio-tracking studies in the mixed-conifer zone of the Sierra Study Area, southern Sierra Nevada (Steger and Eberlein, pers. comm.).

	0-39 percent canopy cover (n = 64)		40-69 percent canopy cover (n = 35)		70+ percent canopy cover (n = 21)	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Percent canopy cover						
By densiometer	26.5 ^a	67.6	60.0 ^b	23.9	73.7 ^c	14.0
By aerial photo	21.0 ^a	49.9	52.9 ^b	16.7	74.8 ^c	6.8
Basal area (square feet per acre)						
Green trees	61.4 ^a	84.2	172.2 ^b	41.3	211.3 ^c	20.7
Snags	4.7 ^a	137.0	12.1 ^b	76.3	13.9 ^b	64.1
Hardwoods (by d.b.h. class) ¹						
0-4.7 inches	0.1 ^a	300.0	0.3	200.0	0.6 ^b	269.2
4.8-10.6 inches	0.7 ^a	280.0	1.5 ^b	144.1	2.0 ^b	104.1
10.7-20.5 inches	1.1 ^a	250.0	2.0	188.9	1.6 ^b	141.0
20.6-35.4 inches	0.6	323.1	1.3	313.8	2.0	233.3
>35.5 inches	0.1	800.0	0.6	442.9	0.0	0.0
Total	2.6^a	193.3	5.6^b	160.9	6.2^b	109.4
Softwoods (by d.b.h. class) ¹						
0-4.7 inches	1.7 ^a	137.5	3.7 ^b	107.1	4.4 ^b	72.4
4.8-10.6 inches	7.2 ^a	107.8	13.9 ^b	70.8	21.2 ^c	46.6
10.7-20.5 inches	15.4 ^a	99.2	39.5 ^b	45.3	54.5 ^c	38.2
20.6-35.4 inches	22.6 ^a	107.9	63.2 ^b	60.8	74.0 ^b	60.0
>35.5 inches	12.0 ^a	148.0	46.3 ^b	79.4	51.0 ^b	75.7
Total	59.0^a	84.2	166.5^b	43.9	205.2^c	21.1
Shrubs per acre	3.7 ^a	325.5	18.0 ^b	293.7	8.4	250.9
Downed woody debris (tons/acre, by log diameter-class) ²						
11-20 inches	2.1 ^a	88.9	3.2 ^b	75.5	3.1 ^b	74.2
21-35 inches	4.0 ^a	102.1	4.7 ^b	100.7	6.9 ^b	83.7
>35 inches	3.3 ^a	213.3	9.3 ^b	144.7	8.2 ^b	106.1

^{a,b,c} Values in the same row with different alpha superscripts are different at the 0.05 level of significance (one-way ANOVA).

¹ Diameter at breast height, in inches.

² Assumes a specific gravity of 0.4 for downed woody debris.

Structural Attributes-Percent canopy cover, softwood basal area, total live tree basal area, snag basal area, and the amount of large, downed woody debris were generally greater at foraging than at random sites (tables 5G and 5H). Stand measurements reported for the Sierra Study Area were not related to specific foraging locations of spotted owls, so they could not be used to compare attributes at foraging locations with those at random locations. Total basal areas reported in the Sierra Study Area (table 5F) in stands with 40-69 percent and 70+ percent canopy cover were comparable to those at foraging sites reported by Call (1990) for the Tahoe Study Area and by Laymon (1988) for the Eldorado Study Area. That was not the case, however, for stands with 0-39 percent canopy cover in the Sierra Study Area. Conifers were the dominant component of basal area in all locations studied (tables 5F-5H). Point estimates for softwood, hardwood, and snag basal areas also were generally less in foraging than at roost and nest sites.

Selection Patterns of Radio-tagged Birds

Where significant patterns of habitat selection were observed among radio-tagged owls, results were consistent with those from the studies reported here. In the Lassen and Sierra Study Areas, some radio-tagged owls used denser stands and were associated with larger trees more than expected on the basis of availability. Only one bird used stands in the lowest canopy-cover class more than expected, and none did so for small tree classes (Chapter 6).

Results of Call's (1990) and Laymon's (1988) studies, reported earlier in this chapter, tend to show stronger selection for

habitat attributes by foraging owls than suggested by studies reported in Chapter 6. We believe this resulted from differences between studies in their scale of measurements. Call and Laymon sampled habitats at or very near actual locations where owls foraged. Studies reported in Chapter 6, on the other hand, characterized the entire stand in which a given owl foraged, thus lacking the localized scale used by Call and Laymon.

Patterns of Habitat Use at a Stand Scale

Nest Types

All recently located nests of California spotted owls have been in trees, but some early records exist of nests found in other locations. For example, records obtained from the Western Foundation of Vertebrate Zoology (Kiff pers. comm.) included notes on 14 nests located between 1889 and 1947. Five were on cliff ledges, one was in a pigeon coop, and eight were in hardwood trees. The pigeon coop nest was composed of "manure," hay, and feathers in a deserted coop under a roof supported by four posts. This nest contained four eggs-only one of two clutches of that size ever reported for spotted owls (see Johnsgard 1988).

Quantitative information on nest trees and nest sites were provided by each of the seven NFs in the western Sierra Nevada and the four southern California NFs. This database was supplemented with identical information from four of the major study areas (Lassen--Blakesley pers. comm.; Eldorado-Moen pers. comm.; Sierra and Sequoia/Kings Canyon--G. N. Steger pers. observ.; and San Bernardino--W. S. LaHaye pers. observ.).

Table 5G--Habitat characteristics (mean and percent Coefficient of Variation) of California spotted owl foraging locations in summer (n = 120) and fall (n = 79), and at random locations throughout summer/fall (n = 120) in the Eldorado Study Area, central Sierra Nevada (Gaymon 1988).

	Foraging sites				Random sites in summer and fall	
	Summer		Fall			
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Physiographic attributes						
Percent slope	19.4 ^a	90.3	17.9 ^a	86.9	23.4	46.8
Structural attributes						
Percent cover	66.8	32.0	61.6	45.5	67.9	29.0
Basal area (square feet per acre)						
Hardwoods	16.6 ^a	172.9	9.2 ^a	275.2	26.1	146.0
Softwoods	200.4 ^a	69.0	196.1	74.1	163.8	62.6
Total live¹	217.0	-	205.3	-	189.9	-
Snags	23.1	216.9	28.8	208.8	17.4	246.4
Downed woody debris (tons per acre, by log diameter-class) ²						
0-3 inches	0.80	0.75	0.83	0.82	0.82	0.74
>3 inches	11.84	1.67	13.76 ^a	1.43	9.36	1.39

^a Significantly different from the corresponding random sites, at the 0.05 level of significance (Student's *t*-test).

¹ The sum of softwood and hardwood basal areas. Data were not available to compute a percent Coefficient of Variation for this variable.

² Assumes a specific gravity of 0.4 for downed woody debris.

Table 5H *Habitat characteristics (mean and percent Coefficient of Variation) of foraging (n = 158) and random sites (n= 256) from six California spotted owl home ranges in the Tahoe Study Area, central Sierra Nevada (Call 1990).*

	Foraging sites		Random sites	
	Mean	Percent CV	Mean	Percent CV
Physiographic attributes				
Percent slope	28.4	58.1	27.4	63.0
Elevation (feet)	3,852.0	12.5	3,888.0	13.9
Structural attributes				
Percent canopy cover	91.8 ^a	12.4	85.2	47.1
Basal area (square feet per acre)				
Hardwoods	23.9	161.0	20.2	153.5
Softwoods	154.9 ^a	52.7	129.8	52.3
Total live	178.7^a	43.7	150.6	44.1
Snags	15.3 ^a	154.6	10.1	169.6
Basal area (square feet per acre, by d.b.h. class) ¹				
3.9-4.8 inches	1.6	374.5	2.2	379.2
4.9-10.7 inches	25.5	119.9	27.6	116.9
10.8-20.6 inches	52.8	79.7	51.8	86.2
20.7-35.5 inches	67.1 ^a	81.1	49.5	94.7
>35.5 inches	32.1 ^a	104.9	19.7	149.14
Downed woody debris (percent cover, by diameter class)				
1-11.8 inches	5.86	82.1	4.5	103.3
>11.8 inches	3.26	184.8	1.7	195.9

^a Significantly different from the corresponding random sites, at the 0.005 level of significance (Student's *t*-test).

^b Significantly different from the corresponding random sites, at the 0.001 level of significance (Mann-Whitney *U* test).

¹ Diameter at breast height.

Based on nest locations in trees, we recognize five nest types that are used regularly by spotted owls in the Sierra Nevada and southern California (table 5I). (1) Cavity nests (color photo 5-3) are placed in natural cavities resulting from decay, usually in the heartwood of a large, old tree. Cavities large enough for owl nests can form where large branches tear out of the trunk of the tree (side cavities). (2) Broken-topped trees and snags (color photo 5-8) may develop depressions via decay, or they may persist without much decay but still provide a broad enough surface for the owls to lay their eggs. (3) Platform nests (color photo 5-14) are those placed on remnant platforms built by other species (for example, goshawks, ravens, or tree squirrels), or on debris accumulations in densely branching structures of trees. (4) Dwarf mistletoe brooms are often dense enough that they form a suitable nest substrate. (5) "Undefined" nest types are those that do not clearly fall into types 1-4 or for which we lack data. In spite of the variety of nest types used by these owls, the nest trees are still generally larger than other trees within the same stand (see below, table 5K). The large trees most often selected for nest sites by California spotted owls also exhibited signs of old age. Forty-three percent of the nests were in large decay cavities, and another 16 percent were on broken-topped trees or snags (for example, color photo 5-8). Many other nests were placed on limb deformities that supported debris platforms.

Among 276 nests located recently, most of them in NFs in the Sierra Nevada and southern California, nest type varied

markedly in different parts of the owl's range (table 5I). In particular, cavity nests dominated nest types in both northern and southern Sierran conifer forests, but platforms were most common in conifer forests of southern California, perhaps as a result of differences in the availability of nesting substrates (see LaHaye 1988). Patterns on industrial forest lands in the Sierra Nevada were similar, but with a greater proportion of platform nests. Based on a sample of 16 nests, half were cavity and half were platform type (Taylor 1992). Northern spotted owls in Oregon nested primarily in tree deformities (Forsman et al. 1984). A similar pattern was found among northern spotted owls in northwestern California (LaHaye 1988), but platform nests were more frequent in the southern part of that study area.

Forsman et al. (1984) reported that young northern spotted owls from several platform nests in Oregon left their nests several days earlier than young from cavity nests. Because they were younger and less able to climb, they spent longer on the ground than young from cavity nests. Forsman et al. speculated that, as a result, these young may have experienced higher predation while on the ground than young from cavity nests. LaHaye et al. (1992a), however, found no differences in overall nesting success among broods produced in cavity nests, broken-topped nests, or platform nests in the San Bernardino Mountains.

Table 5I-Characteristics of nest trees used by California spotted owls, by major habitat type, based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.

General habitat type	Number of nests	Tree condition		Nest type ¹					Nest tree	
		Alive	Snag	CA	BT	PL	MI	UN	Conifer	Hardwood
Northern Sierran Conifer	83	61	22	55	9	15	4	0	79	4
Southern Sierran Conifer	41	29	12	27	4	2	2	4	29	12
Southern California Conifer	139	128	11	33	28	78	0	0	109	30
Riparian/hardwood forests	13	13	0	5	3	5	0	0	0	13

¹CA = cavity, BT = broken-top, PL = platform, MI = dwarf mistletoe, UN = undefined.

Table 5J-Tree species used as nest sites by the California spotted owl, based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.

General habitat type	White fir	Red fir	Douglas- fir	Bigcone Doug-fir	Incense- cedar	Sugar pine	Jeffrey pine	Ponderosa pine	Black oak	Live oak	White alder	Other ¹
Northern Sierran Conifer	22	9	21	0	7	16	2	8	3	0	0	1
Southern Sierran Conifer	12	5	1	0	1	2	2	5	12	0	0	1
Southern California Conifer	45	0	0	21	15	10	17	0	5	22	3	1
Riparian/hardwood forests	0	0	0	0	0	0	0	0	3	5	2	3

¹One nest each was in giant sequoia, Coulter pine, blue oak, tanoak, cottonwood, and California sycamore.

Table 5K-Nest stand and nest tree characteristics of California spotted owls, by general habitat type (mean $\pm$ SD), based on data from all study areas except the Tahoe, and from all relevant National Forest files, 1986-1991.

General habitat type	Elevation (feet)	Total canopy cover (percent)	Nest tree d.b.h. ¹ (inches)	Nest tree height (feet)	Nest height (feet)
Northern Sierran conifer	5,284 $\pm$ 922 <i>n</i> = 65	75.4 $\pm$ 17.2 <i>n</i> = 28	43.5 $\pm$ 14.7 <i>n</i> = 81	96.8 $\pm$ 36.7 <i>n</i> = 75	64.9 $\pm$ 25.7 <i>n</i> = 75
Southern Sierran conifer	5,750 $\pm$ 1355 <i>n</i> = 41	75.5 $\pm$ 27.4 <i>n</i> = 17	46.7 $\pm$ 19.6 <i>n</i> = 41	95.0 $\pm$ 52.7 <i>n</i> = 40	57.5 $\pm$ 31.0 <i>n</i> = 40
Southern California conifer	6,002 $\pm$ 1270 <i>n</i> = 137	79.3 $\pm$ 17.7 <i>n</i> = 131	37.0 $\pm$ 13.9 <i>n</i> = 139	87.5 $\pm$ 33.3 <i>n</i> = 139	56.5 $\pm$ 23.2 <i>n</i> = 139
Riparian/hardwood forests	2,618 $\pm$ 1271 <i>n</i> = 13	89.3 $\pm$ 10.6 <i>n</i> = 6	29.5 $\pm$ 16.6 <i>n</i> = 13	55.0 $\pm$ 23.5 <i>n</i> = 13	38.4 $\pm$ 14.0 <i>n</i> = 13

¹Diameter at breast height.

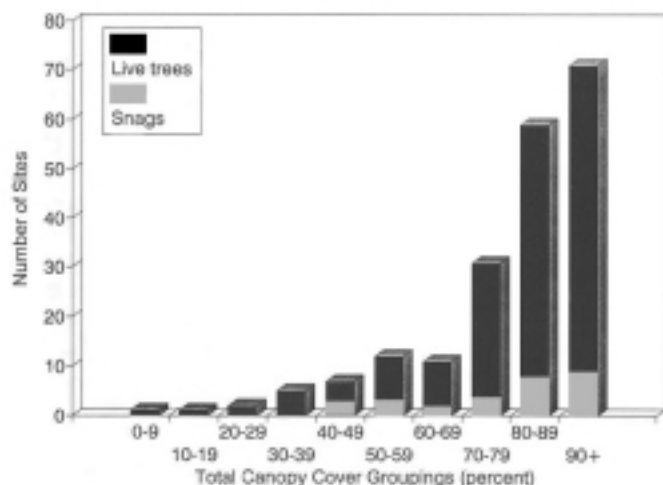


Figure 5F—Number of nest sites, by canopy-cover class; nests in snags and live trees are differentiated ($n = 201$).

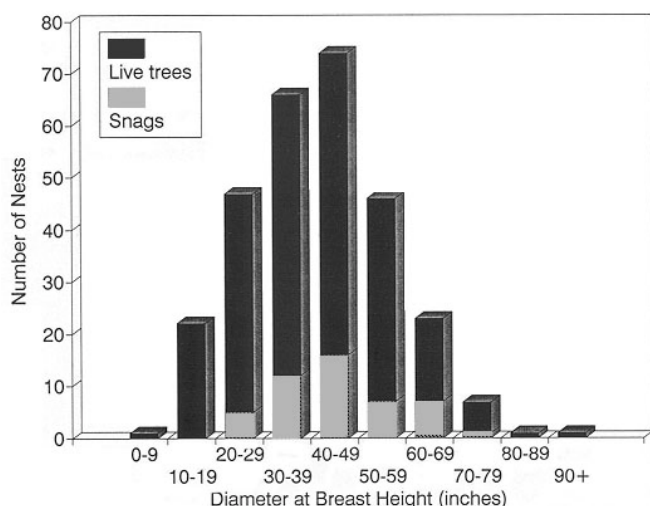


Figure 5G—Number of live trees and snags, by stem diameter-class, used for nest sites by California spotted owls ($n = 288$).

Nest Trees

Ten species of conifers and seven species of hardwoods accounted for all recent nest sites reported for California spotted owls (table 5J). Nest trees were typically in stands with high canopy cover—75.4 percent in Sierran conifer and 79.3 percent in southern California conifer forests (table 5K; see fig. 5F). These estimates compared favorably with those reported above for nest stands (tables 5B and 5C). Eighty-three percent of all nests in the conifer forests were in living trees (fig. 5G) and 82 percent were in conifers. These trees were very large, averaging about 90 feet tall (range 25–262 feet) and 41 inches in d.b.h. (range 9–81 inches), with means slightly higher in Sierran than in southern California conifer forests (table 5K). More than 75 percent of all nest trees were larger than 30 inches in d.b.h. (fig. 5H). Results from surveys of nest sites on industrial forest lands also showed that owls nested in large trees. Based on a sample of 17 nests from the Sierra Nevada conifer zone, nest tree d.b.h. averaged 41.8 inches (Taylor 1992).

The d.b.h. of nest trees in our current sample was significantly greater than that of conifers in general in the Sierra Nevada *even in 1900* ($\chi^2 = 167$, $df = 6$, $P < 0.001$; fig. 5I), based on trees on plots measured by Sudworth (1900) prior to extensive logging. Interestingly, the diameter distribution of white fir trees used as nest sites by owls was not significantly different ($\chi^2 = 7.469$, $df = 5$, $P > 0.10$; fig. 5J) from that of white firs measured by Sudworth. The white fir comparison is appropriate because that was the most common nest tree species used by California spotted owls (table 5J). Comparison of the sample of nest trees from Sierran conifer forests to the current diameter distribution in the M4G timber strata on the Tahoe NF also shows extensive selection for large-diameter trees (fig. 5K). To the extent that the Tahoe NF sample is representative of this timber strata in the Sierra Nevada, selection for large trees for nesting is clearly evident.

The significant inference from these results is that California spotted owls in conifer forests today are selecting nest trees from among the few remaining trees that are as large as or larger than average trees in 1900, before extensive logging began to remove the largest trees from the forest. When this pattern is coupled with the past and projected future trends of large trees in the Sierra Nevada (Chapter 13), it is reasonable to hypothesize large-diameter trees as a current or potentially limiting factor sometime in the future. That is, even if large trees are not currently limiting, we have reason to be concerned that they could soon be limiting if specific constraints on their removal are not invoked in the near-term.

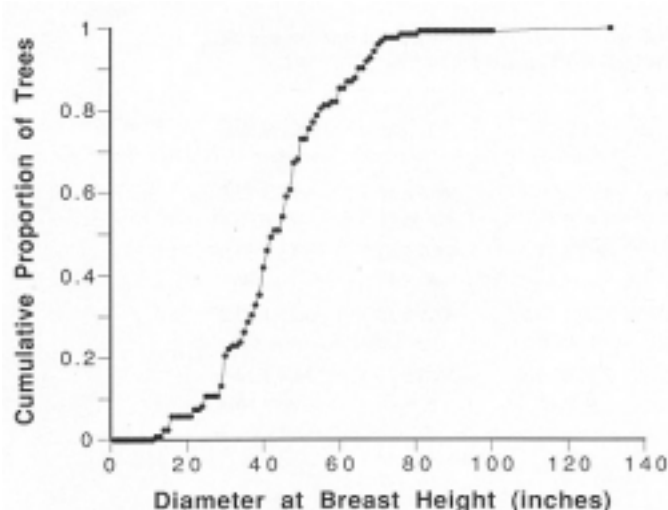


Figure 5H—Cumulative distribution of nest trees in the Sierra Nevada conifer zone, arranged by diameter at breast height ($n = 122$).

Foothill Riparian/Hardwood Forests

Measurements of winter foraging sites and foraging stand attributes in foothill riparian/hardwood forests were available for the Eldorado Study Area (Laymon 1988) and the Sierra Study Area (Steger and Eberlein pers. comm.) (tables 5D and 5L). Because sample sizes were small, these analyses should be considered as preliminary at this time. Point estimates suggest about the same range of values for percent canopy cover as observed in the conifer forests at higher elevations (compare tables 5D, 5F, and 5L). Basal areas of green trees and snags were considerably less, and shrub density was much higher in the hardwood type than in the conifer forest. Based on Laymon (1988), and a comparison of tables 5F and 5L, together with considerable on-site experience with these habitats, we found that riparian/hardwood forests dominated by oaks tended to have less canopy layering than most sites in the Sierran mixed-conifer and ponderosa pine/hardwood types (color photos 5-23 and 5-25). Multiple layers were present, however, in the mixed-hardwood forests in southern California, where spotted owls occur in narrow riparian corridors in steep-sided canyons, as in the Los Padres NF (color photo 5-28). Tables 5D and 5L also suggest less downed woody debris in the low-elevation hardwood type, compared to conifer forests.

Nest sites in riparian/hardwood forests averaged about 2,600 feet in elevation. No pattern was evident in the types of nests found in these forests (table 5I), but the sample size was too small to establish a pattern if one existed. All of the nests located were in hardwoods that averaged 55 feet tall (range 16-98 feet) and 30 inches in d.b.h. (range 13-72 inches) (table 5K).

Collectively, these data indicate that owl habitat in the foothill/riparian forests was characterized by both lower live tree basal area and lower canopy cover than higher-elevation sites in the conifer zone. The high closure measured at nest sites in the foothill zone (table 5K) may represent a highly localized phenomenon—one uncharacteristic of stands in this area in general. Furthermore, in the foothill habitats, the average nest-tree d.b.h. was smaller (table 5K) and platform nests were more common (table 5I) than in the conifer zone. Given these contrasts, the structure of owl habitats in foothill riparian/hardwood forests appeared to be substantially different from that in mixed-conifer forests. We caution that no data exist that suggest that stand basal areas, cover classes, and nest-tree sizes used in the foothill/riparian zone would, if created in the conifer zone, provide suitable owl habitat. Indeed, owls that migrated to low-elevation sites for the winter moved back upslope and chose dense stands with large trees in the mixed-conifer forest as summer habitat (table 5D).

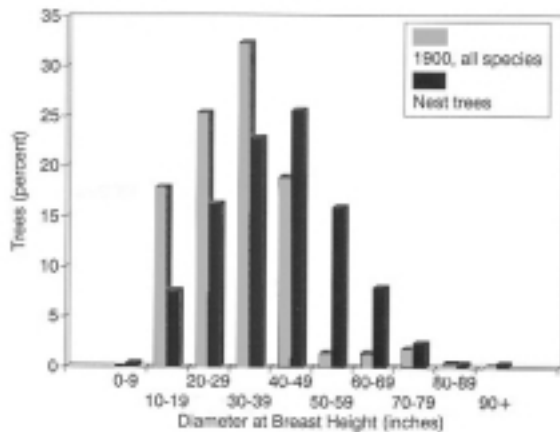


Figure 5I—Proportions of nest trees (recent) and trees available in stands in 1900 (Sudworth 1900), by stem diameter-class.

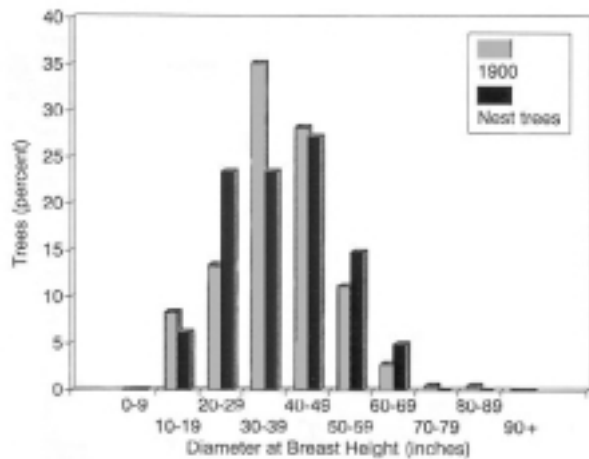


Figure 5J—Proportions of nest trees (recent) that were white firs, and white firs available in stands in 1900 (Sudworth 1900), by stem diameter-class.

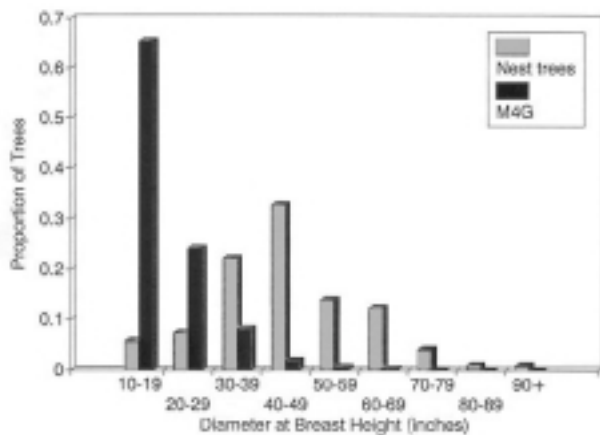


Figure 5K—Proportion of nest trees (recent) in Sierran conifer forests ($n=122$) and trees currently available in M4G stands on the Tahoe NF, by stem diameter-class.

Table 5L-Structural attributes of habitats (mean and percent Coefficient of Variation, by canopy cover class) used by California spotted owls during radio-tracking studies in the riparian/hardwood zone of the Sierra Study Area, southern Sierra Nevada (Steger and Eberlein pers. comm.).

Structural Attributes	0-39 percent canopy cover (n = 7)		40-69 percent canopy cover (n = 5)		70+ percent canopy cover (n = 8)	
	Mean	Percent CV	Mean	Percent CV	Mean	Percent CV
Percent canopy cover						
By densiometer	36.3 ^a	39.4	67.26	11.8	74.3 ^b	16.3
By aerial photos	15.9 ^a	66.8	59.06	11.6	80.0 ^c	5.8
Basal area (square feet per acre)						
Green trees	20.0 ^a	80.0	50.1 ^b	51.5	65.6 ^b	67.1
Snags	0.9 ^a	175.0	4.1	87.2	5.0 ^b	80.7
Hardwoods (by d.b.h. class) ¹						
0-4.7 inches	1.4 ^a	124.2	4.6 ^b	48.1	6.5 ^b	91.9
4.8-10.6 inches	6.7	115.0	18.8	37.4	19.0	30.7
10.7-20.5 inches	5.9	97.8	12.9	61.5	20.0	113.7
20.6-35.4 inches	5.1	125.0	8.5	80.9	12.0	129.1
>35.5 inches	1.0	262.5	5.4	150.0	1.3	279.3
Total	20.0^a	79.4	50.2^b	51.4	58.7^b	65.3
Softwoods (by d.b.h. class) ¹						
0-4.7 inches	0	0	0	0	0.1	200.0
4.8-10.6 inches	0	0	0	0	0.3	300.0
10.7-20.5 inches	0	0	0	0	2.3	219.2
20.6-35.4 inches	0	0	0	0	4.4	281.0
>35.5 inches	0	0	0	0	0	0
Total	0	0	0	0	7.0	258.1
Shrubs per acre	105.0	198.8	69.0	62.5	127.0	144.4
Downed woody debris (tons per acre, by log diameter-class) ²						
11-20 inches	0.09	264.4	0.10	223.5	0.68	164.1
21-35 inches	0		0.41	223.7	0.45	187.5
>35 inches	0		0		0	

^{a,b,c} Values in the same row with different alpha superscripts are different at the 0.05 level of significance (one-way ANOVA).

¹ Diameter at breast height, in inches.

² Assumes a specific gravity of 0.4 for downed woody debris.

Discussion

General Patterns of Habitat Use

The first specimen of the spotted owl was collected by Xantus (1859) in the Tehachapi Mountains of southern California. This bird was likely found in the closed-canopied, riparian/hardwood forests common to the Fort Tejon region. Following this first documented sighting by Europeans, many reports of California spotted owls appeared in the literature over the next 80 years (see Grinnell and Miller 1944, Gould 1974). These reports and several nest records at the Western Foundation of Vertebrate Zoology (Kiff pers. comm.) indicated that California spotted owls in past decades used both conifer and hardwood habitats, and were found consistently in densely forested areas.

More recent observations and studies document the habitat associations of this bird throughout its range and in a quantitative fashion. These results suggest some general patterns about

habitat use by California spotted owls. First, they use a broader array of habitats than used by the northern spotted owl. Second, within the general habitat types selected, they use forest patches that are complex in structure relative to what is available (for example, many trees in different diameter-classes and high canopy closure). Third, California spotted owls appear to select remnants of the older Sierran and San Bernardino conifer forests that have managed to survive 200-400 years to the present time (see table 5M). Especially for nesting and roosting, present data from several different sources suggest that most California spotted owls select dense stands with very large, presumably old trees. Fourth, although habitat attributes associated with California spotted owls at their nest and roost sites parallel those associated with northern spotted owls, foraging habitat used by the California subspecies appears to be much more variable than for its northern relative. Indeed, the considerable range in variation found in habitats used by California spotted owls is well-illustrated by the photos at the end of this chapter. In spite of this variation, however, results of studies reported in this chapter firmly establish that these owls use their forested environment in a nonrandom fashion.

Table 5M-Core data (mean $\pm$ SD) and ages of nest trees used by California spotted owls in the San Bernardino Mountains; sample sizes are in parentheses beneath means and SDs.

Trees	D.b.h. ¹	Tree height ²	Nest height ²	Core age in years	Mean percent of total radius cored
All trees	41 $\pm$ 13.0 (30)	103 $\pm$ 32.9 (30)	65 $\pm$ 4.3 (30)	230 $\pm$ 93.8 (29)	69 $\pm$ 26.4 (29)
White fir	41 $\pm$ 11.7 (14)	91 $\pm$ 25.1 (14)	65 $\pm$ 19.2 (14)	238 $\pm$ 68.2 (14)	70 $\pm$ 20.1 (14)
Sugar pine	37 $\pm$ 17.6 (3)	90 $\pm$ 31.2 (3)	53 $\pm$ 22.0 (3)	217 $\pm$ 43.1 (3)	46 $\pm$ 48.2 (3)
Jeffrey pine	40 $\pm$ 14.8 (8)	116 $\pm$ 37.9 (8)	68 $\pm$ 27.8 (8)	223 $\pm$ 143.1 (8)	78 $\pm$ 26.3 (8)
Incense-cedar	46 $\pm$ 15.8 (3)	131 $\pm$ 29.0 (3)	83 $\pm$ 27.5 (3)	193 $\pm$ 111.0 (3)	64 $\pm$ 31.4 (3)
Bigcone Douglas-fir	48 $\pm$ 16.1 (2)	115 $\pm$ 54.5 (2)	42 $\pm$ 28.3 (2)	320 $\pm$ 0.0 (1)	48 $\pm$ 0.0 (1)

¹ Diameter at breast height, in inches.

² Height in feet.

The association between the variable habitats used by California spotted owls and their population effects is not well understood. For example, we do not know if the birds survive and reproduce equally well in each of the many habitat types where they are found. We strongly suspect, however, that populations in some of those habitats are "sources" (reproduction exceeds replacement needs within the population, so surplus young are produced which emigrate to other areas) and populations in others are "sinks" (where reproduction is generally insufficient to replace local losses, so maintenance of the population requires immigration from other areas). We also do not know if spotted owls in the Sierra Nevada evolved in a more heterogeneous environment than was the case for northern spotted owls. Spotted owls evolving in different environments may exhibit different adaptive responses (for example, see Gutiérrez and Pritchard 1990). Although we do not yet know the answers to some of these critical questions, we infer that human-induced habitat changes (for example, from logging) may adversely affect the owls and lead to population declines.

California spotted owls in conifer forests exhibited significant overuse of M4G stands at the landscape scale. These are dense (70+ percent canopy cover) mixed-conifer forests with canopy trees averaging ≥ 24 inches in d.b.h. This pattern of selectivity was corroborated by comparisons with random locations of stands used for nesting, roosting, and foraging in the conifer forest. The vast majority of birds used sites with greater canopy cover, total live tree basal area, basal area of softwoods and hardwoods, and snag basal area than found at random sites. These are attributes that we would expect to find in M4G stands. Finally, selection of nest sites and nest trees by the owls further corroborates the findings from analyses at other scales of resolution. A high proportion of nest sites, especially in Sierran conifer forests, were in natural cavities or in broken-topped trees or snags. Trees used for nest sites were significantly larger and probably older than available in the general forest matrix, even in M4G stands. This pattern suggests that, currently, most nest trees are surviving remnants from forests of past centuries.

Is the Owl A Habitat Specialist?

In spite of the fact that the owl used a range of habitat conditions, we believe it should be characterized as a specialist. For example, we observed that 80 percent of all nest trees were located in stands with canopy cover of at least 70 percent. The average (and median, and modal) d.b.h. of nest trees in the Sierra Nevada was about 45 inches, but only 2 percent of all trees greater than 10 inches in d.b.h. in M4G stands on the Tahoe NF were in the 40-49 inch d.b.h. group. By specialist we mean an animal that shows a clear selection for certain habitats or habitat attributes. Two assumptions we invoked in our analyses were (1) the pattern of habitat usage we observed was not constrained by any other species, and (2) the use of a habitat type significantly in excess of its availability reflects selection. The degree to which these assumptions were met is unknown. It is possible, for example, that the California spotted owl's pattern of habitat use was influenced by competition with another raptor species. Also, the methods we used can be misleading if, for example, the preferred habitat is also the most common habitat. Regarding these two possibilities, we have no data that suggest direct competitive interactions with other raptor species, and the habitat used most commonly for nesting (M4G) is uncommon (about 20 percent, based on FS inventory data) in the Sierran landscape.

We do not claim dependence by the spotted owl upon any given habitat type or attribute. Further, we do not contend that our data, at this time, indicate that any given habitat type or attribute is "required," in the sense that its absence would lead to the owl's extinction. But we do believe that the habitat distribution patterns of the majority of owls, given the constraints of availability and possible biotic interactions, currently reflect optimal choices. If better choices were available, natural selection would act to remove those individuals making the wrong choice.

Based on our definition of a specialist and the operational manner in which we identified selection, we believe we have made the best use of the available data to craft a set of recommendations intended to secure future options for managing the

species. We have based our inferences on what the majority of the owls selected from among choices in their habitats, and assumed that these choices reflected the most important attributes to retain in future landscapes.

Recommendations

Translating all the habitat association patterns into a general characterization of nesting, roosting, and foraging stands that should be suitable for spotted owls in conifer forests is difficult. It is also risky! All too often, suggestions offered tentatively are misconstrued to be the last and definitive word on the matter. Even with these misgivings, however, we offer here some tentative estimates of stand attributes, based mainly on tables 5B-5H. Given these caveats, the tabulation below may be a fair, initial representation of the range of mean values of some attributes in suitable habitat for spotted owls in Sierran mixed-conifer forests. Most values in the tabulation generally reflect the range of means from the various studies reported in this chapter. We have combined values for nesting and roosting stands, because (1) they tend to be very similar, (2) spotted owls commonly roost within the stands that include their nests, and (3) we believe that a stand suitable for nesting would also provide conditions satisfying the roosting needs of the owls.

	Nesting and roosting stands	Foraging stands
Percent canopy cover ¹	70-95	50-90
Total live tree basal area ²	185-350	180-220
Total snag basal area	30-55	15-30
Basal area of large snags ³	20-30	7-17
Downed woody debris ⁴	10-15	10-15

¹ Mostly in canopy ≥ 30 feet high, including hardwoods.

² Square feet per acre.

³ Dead trees ≥ 15 inches in d.b.h. and ≥ 20 feet tall.

⁴ Tons per acre.

The values for total snag basal area are high and reflect sampling of all, or nearly all, dead trees by various workers. We believe, however, that relatively small snags have little value in terms of spotted owl habitat. Snags need to be large enough to accommodate nest sites for medium to large cavity-nesting birds and den sites for flying squirrels. In addition, larger snags take longer than small snags to decompose after they have fallen. We consider snags that are at least 15 inches in d.b.h. and 20 feet tall to be near the smaller end of suitability for owl habitat. In two comparisons of total snag basal area with the basal area of "large" snags (≥ 15 inches in d.b.h. and ≥ 20 feet tall (table 5E), large snags comprised 45 percent and 59 percent of the total. Snag values in the above tabulation could be adjusted accordingly to estimate the basal area of large snags in owl habitats. This limited analysis suggests that owl nest and roost sites have from about 19 to 31 square feet basal area of large snags, and foraging sites have from 7 to 17. Because we recommended an interim approach to management for spotted owls in the Sierra Nevada (Chapter 1), one based on the concept of preserving all options for future management of spotted owls, we recommend maintaining at least 20 square feet basal area of large snags

wherever possible in owl habitat. Based on current information, this standard appears to be appropriate for maintenance of suitable nesting and roosting sites. It is at the lower end of estimates for nesting and roosting sites and slightly above the upper end of estimates for foraging sites.

Estimates of the mass of downed wood in owl nesting, roosting, and foraging sites ranged from 10.5 to 24.7 tons per acre, with a mean of 17.4 and a standard deviation of 5.3. (Based on values in tables 5D-5G, and on approximations of tons/acre from values given in tables 5B and 5H.) Most of this was in pieces at least 11 inches in diameter. We believe that much of this has managed to accumulate because of effective fire suppression in Sierran conifer forests during the past 80-90 years, so these quantities probably exceed what was present during presettlement times. Fuels management specialists from R5 and from NFs in the Sierra Nevada have assured us that the fuel loads indicated by the average in owl habitats represent a significant hazard vis-à-vis the intensity of fires and the likelihood of stand-destroying fires. Consequently, we believe that a compromise is needed between fire threats and what the data indicate to be typical quantities of large logs in owl habitats. We suggest a range of 10-15 tons per acre, in the largest logs available, and believe it is inadvisable to retain logs smaller than 11 inches in diameter to attain this level. This range is at the low end of the values observed in owl habitats.

Research Considerations

Despite the considerable amount of study already done in an effort to estimate habitat-use patterns by spotted owls, we still have limited knowledge about this critical aspect of the bird's ecology. This is particularly true relative to the relations between habitat and demographic variation. This is the case largely for three reasons. First, research on this subspecies was slow in getting started, because most of the early concern was directed at the northern spotted owl. Funds available for research on the California spotted owl have not been sufficient to allow studies of their prey, or even to complete a full inventory of all habitats where the owl is likely to occur. Second, most definitive studies of the California spotted owl were initiated in 1986 or later. Coincidentally, this was when the current drought began (fig. 4H), making it impossible to determine whether observed results from owl studies should be interpreted primarily in relation to changing habitat conditions, to the drought, or both. Third, knowledge about different gradations in habitat suitability must be based on habitat-specific studies of the owl's demography--whether or not they reproduce well enough in a given habitat to equal or exceed annual mortality rates.

Demographic information on owl populations in a variety of different habitats will take many years to obtain and will depend on monitoring demographic trends through both wet and dry climatic periods. We should continue to build on existing demographic studies to attain some of the information needed, because they already have an accumulating database. We also need to consider a range of options for adding other demographic studies. In particular, we see great potential for demo-

graphic studies on lands of some of the major commercial timber companies whose forest practices differ in important ways. These are ad hoc experiments (Bias and Gutiérrez 1992) on the effects of different management regimes on the owls.

Every effort should be made to establish consistent methods, attributes to be measured, data forms, and analytical procedures to be used by all researchers on California spotted owls. Failing adoption of standard methods and so on, quantitative relations among different techniques should be developed to ease interpretation of data from different studies. Finally the efficiency and utility of different techniques should be explored to encourage adoption of a uniform protocol for basic information collection in the field.

The "Achilles heel" of wildlife management is separating correlation and causation. All analyses of habitat described in this paper are based on correlational studies. That is, we observe a particular variable, such as canopy closure, to be consistently high at owl sites relative to available sites, but we do not know if that variable is the reason why owls are present at the site. They may be there because canopy closure is usually associated with a different stand attribute, one that we have not measured and one that may be too subtle to quantify. Hence, we do not know if changes in canopy closure will consistently result in a functional response by owls inhabiting a site. The fact that we have not demonstrated cause-and-effect relations, however, does not dilute the power of these documented trends. Rather, it tempers our recommendations about managing for functional owl habitat.

Controlled experiments, in which one or more attributes are changed and subsequent functional responses of the owls are documented, are the best way to identify cause-and-effect relations. Experimentation in certain fields of science is the rule (for example, see Platt 1964). Experiments in natural ecosystems, however, are generally orders of magnitude more complicated and less controllable than experiments in fields like chemistry, physics, or molecular biology. Nevertheless, the widespread logging of forests for commodity production provides a possibility of undertaking ecological experiments on owl responses to changes in habitat. Experiments can occur at two spatial scales--the landscape (that is, a collection of owl home ranges) and the site (within a forest patch occupied by an owl or pair of owls). The critical question to be asked is: Do the changes in spatial arrangement or the structure and composition of habitats affect the owl's ability to survive and reproduce? Formulation of specific experiments should be based on empirical information generated from natural history studies (see above) and the creative application of results from modeling habitat conditions observed in natural history studies. The success of experiments in discerning alternative outcomes will determine their potential for applying a management system to a larger landscape.

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Chapter 6

Home-Range Size and Habitat-Use Patterns of California Spotted Owls in the Sierra Nevada

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Home range is an "area utilized by an individual during its normal activities such as food gathering, mating, and caring for young" (Burt 1943), as distinguished from its territory, which is typically defended against intrusion by other individuals of the same species, except a mate or a potential mate (Nice 1941). Home ranges of neighboring individuals commonly overlap, but territories are usually more exclusive. Studies of home ranges often require attachment of radio transmitters on animals, so their movements can be monitored. Many such studies have been done on spotted owls (recent review in Thomas et al. 1990, appendix I). In this chapter we report results of two radio-tracking studies in three different study areas, one in the northern and two in the central Sierra Nevada. These data provide estimates of home-range sizes of individual males and females, and of pairs, during different periods of the annual cycle. In addition, we have compared patterns of habitat use in home ranges in relation to the different habitats available to the birds. In that sense, habitat-use information given here augments that presented in Chapter 5.

A fundamental difference exists, however, between the scales of habitat use reported here and those reported in Chapter 5. Studies in Chapter 5 examined habitat selection by owls at three scales—landscape, home-range, and stand. Stand-scale studies measured habitat attributes very near the point of an owl's activity—nesting, roosting, or foraging—and compared them with similar measurements at random locations in the surrounding forests. This was a fine-grained scale of analysis that addressed habitat attributes closely associated with an activity. Studies reported in Chapter 6 were done at a scale intermediate between the home-range and stand scales. Here we examined habitat selection at the scale of a habitat polygon (stand), a patch in the overall forest landscape that was similar enough within itself to be set apart from adjoining patches. The minimum patch size we recognized was 5 acres. For example, a meadow would be one polygon type, and an adjoining patch of forest with fairly uniform canopy closure and tree size-class would be another type. But a forest polygon could still be heterogeneous—and typically it is, with smaller subgroups of trees within it having higher canopy closure and/or larger trees than the polygon as a whole. If an owl were selecting for attributes at a scale less than the polygon size, the stand-level analyses reported in Chapter 5

would be much more likely to detect that selection than would be the results reported in this chapter. We can differentiate habitat selection only at the level of the entire polygon. Consequently, evidence of habitat selection given in this chapter is likely to be less conclusive than that given in Chapter 5.

Study Areas

Results presented here came from two study areas, one in the Sierra National Forest (NF) near the southern end of the Sierra Nevada, and the other east of Lassen National Park (NP) in the Lassen NF, at the northern end of the Sierra Nevada and the extreme southern end of the Cascade Mountains. The study area in the Sierra NF had one division in mixed-conifer forest in the Huntington quadrangle (hereafter the S-CON site) and another in foothill riparian/hardwood forests and adjoining oak-pine woodlands in the Patterson quadrangle (the S-OAK site). These were situated about 45 miles northeast of Fresno, in watersheds of the San Joaquin River and the North Fork of the Kings River. Vegetation in the S-CON site was dominated by mixed-conifer forests of white fir, Jeffrey pine, ponderosa pine, sugar pine, incense-cedar, and red fir. Elevations ranged from 5,000 to 8,000 feet. Much of the area was selectively logged from 1880 to the present, with most of the old-growth conifer trees removed. Logging within the NF and on small parcels of private land within NF boundaries is now concentrated on second-growth timber and the few remaining stands of old-growth. The S-OAK site, at elevations from 1,000 to 3,000 feet, was dominated by blue oak, interior live oak, digger pine, and various chaparral species. The Lassen NF study area (the L-CON site) was dominated by red and white fir at high elevations (5,800 to 6,600 feet) and Jeffrey, ponderosa, sugar, and lodgepole pines at lower elevations (5,000 to 5,800 feet). Selective logging has been the predominant silvicultural method used there.

Methods

Field Operations

Owls were captured with noose poles, mist nets, or fish-landing nets and fitted with backpack-mounted radio tags weighing 0.6-0.8 ounces. We attached the radio tags with cross-chest harnesses (Forsman 1983). Radio tags (AVM Instrument Co., Livermore, Calif.) had 12-inch antennae and life expectancies of 12 months. Owls tracked >1 year were recaptured and fitted with new radio tags. Owls were located by radio triangulation using the loudest-signal method (Springer 1979). At least three compass bearings were taken from known points for each owl location and plotted on 1:24,000 topographic maps. Error polygons (the area enclosed by the intersection of three or more compass bearings) at L-CON were classified as <50, <20, <5, or <2.5 acres. We attempted to obtain error polygons of <2.5 acres for all observations. At S-CON and S-OAK, we obtained additional bearings on all birds until error polygons of <2.5 acres were attained. The geometric center of each error polygon was assumed to be the owl's location. We attempted to obtain one nighttime location, by radio tracking, on each of four nights per week and one daytime location per week by direct visual observation. All nighttime observations were considered foraging locations and all daytime observations were classed as roosting locations.

Vegetation Classification

Stands of relatively homogeneous vegetation were mapped at each study site and grouped into habitat types that could be cross-classified to U.S. Department of Agriculture, Forest Service (FS) timber stand types. Black-and-white aerial photos, U.S. Geologic Survey topographic maps, large-scale color aerial photos, and 1:24,000 FS black-and-white orthophotoquads were used to define vegetation boundaries. Stands were classified according to compositional (vegetation type) and structural (diameter size-class of dominant trees and canopy-closure classes) features that could be estimated from aerial photos (table 6A). Structural classes at S-OAK differed from those at S-CON and L-CON, because most trees there were oaks with relatively small diameters at breast height (d.b.h.) when compared to conifers. We assigned each stand to two canopy-closure classes: cover by all vegetation above 7 feet (total canopy closure) and cover by only the dominant trees in the canopy (dominant canopy closure). About 70 percent of the mapped stands (polygons) in each study area were field-verified for classification accuracy. Vegetation maps were subsequently digitized, stored in a Geographic Information System (GIS), and analyzed using ARC/INFO software.

Table 6A—Vegetation classifications used in Chi-square tests of habitat selection.

Classes	Characteristics
Tree size-classes	
Open grassland	No trees
Sapling	D.b.h. <5 inches ¹
Pole	D.b.h. 5-10 inches
Small sawtimber	D.b.h. 11-20 inches
Medium sawtimber	D.b.h. 21-35 inches
Large sawtimber	D.b.h. >35 inches
Canopy-closure classes	
Open	10 percent closure ²
Sparse	10-19 percent
Poor	20-39 percent
Normal	40-69 percent
Good	<69 percent
Suitability as owl habitat	
Suitable	Medium or large sawtimber, canopy closure class poor or better, and total closure >69 percent
Unsuitable	All other lands

¹ Diameter at breast height of the dominant size-class, according to basal area

² Canopy closure based on the dominant tree size-class.

Statistical Analysis

By definition, home-range estimators assume repeated use of an area, and a random flight path does not constitute a home range. For this reason, we determined whether individual owls exhibited site fidelity prior to calculating home-range size (Spencer et al. 1990). The mean-squared distance from the center of activity (MSD) (Calhoun and Casby 1958) was used to measure site fidelity. A bird displayed site fidelity if its flight path was less than the MSD for 975 of 1,000 simulated paths. (See Spencer et al. 1990 for simulation techniques.)

Home-range size was computed using two estimators, the 100-percent minimum convex polygon (MCP) (Mohr 1947 Hayne 1949) and the 95-percent adaptive kernel (AK) (Worton 1989, Baldwin pers. comm.). Because convex polygon areas are sensitive to sample size (Jennrich and Turner 1969), we used the 95-percent AK estimates for all comparisons and statistical tests. We report 100-percent MCP estimates of home-range size to allow comparisons with other studies reported in the literature and elsewhere. The correlation coefficient between AK and MCP estimates was significant ($r = 0.93$, d.f. = 52, $P < 0.0001$). Telemetry data were partitioned into a breeding period (1 March-31 August) and a nonbreeding period (1 September-28 February). Foraging (nighttime) locations were used to estimate home ranges.

The Chi-square goodness-of-fit test was used to test the hypothesis that owls used habitat types *within* their home ranges in proportion to availability (Neu et al. 1974). When this hypothesis was rejected, we used Bonferroni confidence intervals (at the $P < 0.05$ level) to determine which habitat types were used more or less than expected (Byers et al. 1984). Mapped polygons were classified by diameter size-class of the dominant

trees, total canopy closure, and dominant canopy closure. Chi-square analyses were performed for each of the three types of classification. In addition, the analyses were repeated after reclassifying polygons as suitable or unsuitable, based on current FS, Region 5 (R5), definitions of suitable spotted owl habitat. Suitable stands were those in which the diameter size-class of dominant trees was ≥ 21 inches in d.b.h., canopy closure of dominant trees was ≥ 20 percent, and total canopy closure was ≥ 70 percent.

Results

Home-Range Size

Eleven females and 10 males were radio-tracked between 26 April 1987 and 28 February 1990 at S-CON; and six females and six males were radio-tracked between 28 February 1989 and 28 February 1990 at S-OAK. Nine females and eight males were tracked between 25 May 1989 and 5 April 1990 at L-CON. Owls were monitored over periods ranging from 56 to 794 days. sampling intervals varied among owls because transmitters failed, individuals died, or owls permanently left the study areas.

Eighteen of 21 owls at S-CON, 12 of 12 at S-OAK, and 13 of 17 at L-CON passed the site-fidelity test. Owls that failed to exhibit site fidelity had few radio locations or made long movements during the breeding or nonbreeding seasons. All three birds at S-CON that failed the test were migrants that exhibited long movements (see Chapter 4).

To compare home-range sizes among sites and between seasons, we excluded owls that were tracked over a period of less than 5 months during the 6-month nonbreeding season. Our sampling frequency varied among individual owls, and 5 months was as close to complete coverage as we could achieve because of irregular sampling intervals. Estimates of home-range sizes for the nonbreeding period were calculated for 13 owls at S-CON, 5 at S-OAK, and 7 at L-CON that passed the site fidelity test and were tracked for a period of at least 150 days. The number of radio locations per season among these owls ranged from 21 to 91 ($\bar{x} = 58.6 \pm 17.0$). Home-range sizes of owls that passed the site-fidelity test and that were tracked over a period of at least 150 days were not significantly correlated with the number of radio locations. We relaxed the criteria for breeding-season estimates. Requiring a tracking period of at least 150 days, only seven owls had sufficient data to estimate a home-range size. To use a larger sample of owls, we excluded only owls with fewer than 20 radio locations within a breeding season. Fifteen of 21 owls at S-CON, 7 of 12 at S-OAK, and 9 of 15 at L-CON met this criterion. The mean number of locations among these owls as $37.6 (\pm 10.6)$ and they were tracked over an average period of 116.0 days (± 39.1 , range = 56-184 days).

Home ranges were significantly larger at S-CON than at S-OAK during both seasons (table 6B). A two-way ANOVA for these two sites indicated significant effects of study site ($F = 13.9$, d.f. = 1, 50, $P < 0.001$) and season ($F = 4.2$, d.f. = 1, 50, $P < 0.05$) on AK home-range size, with an interaction effect. The interaction effect was due to larger home ranges in the nonbreeding than in the breeding season at S-CON, but home ranges at S-OAK were larger during the breeding season. The difference in home-range size between seasons at L-CON was not significant ($t = 1.4$, d.f. = 14, $P > 0.15$), but owls at L-CON had home-range sizes about twice those at S-CON in both seasons. Home-range sizes did not differ significantly between sexes at any site during either season.

Owls at S-CON exhibited variable behavior during the winter. Individual birds either migrated, occupied nearly the same home range in winter as in summer, enlarged their home range in winter but still used most or all of the summer home range as well, or shifted their home range for the winter but still overlapped a portion of the summer home range (Chapter 4). Among 21 owls radio-tagged at this site, six were classified as year-round residents, two as enlargers, five as shifters, five as migrants, and three as unknown. Differences in nonbreeding home-range sizes among these categories of birds were significant ($F = 12.4$, d.f. = 3, 17, $P < 0.001$). Shifters had the largest home ranges ($\bar{x} = 13,254 \pm 4,984$ acres), followed by enlargers ($\bar{x} = 5,960 \pm 3,031$), and residents ($\bar{x} = 3,302 \pm 781$). Only one migrant passed the site-fidelity test, and its home range was 9,146 acres.

Annual home ranges were calculated for owls that passed the site-fidelity test both seasons, were tracked over a period of at least 150 days during the nonbreeding season, and had ≥ 20 radio locations during the breeding season (table 6B). Owls at S-CON had significantly larger annual home ranges than those at S-OAK ($t = 2.5$, d.f. = 19, $P < 0.05$). As with breeding and nonbreeding home-range sizes, annual home-range sizes at L-CON were more than twice the size of those at S-CON.

Seasonal home-range sizes of pairs were calculated only when both members of pairs passed the site-fidelity test, were tracked for at least 150 days during the nonbreeding period, and had ≥ 20 radio locations during the breeding period (table 6B). Only one pair at L-CON met these criteria, precluding further analysis of pair home-range data. A two-way ANOVA for S-CON and S-OAK indicated no significant differences between the nonbreeding and breeding periods ($F = 1.1$, d.f. = 1, 12, $P > 0.30$), but pair home ranges were larger at S-CON than at S-OAK ($F = 3.9$, d.f. = 1, 12, $P = 0.07$). The mean proportion of home-range overlap between members of pairs did not differ significantly by study site ($F = 0.3$, d.f. = 1, 12, $P > 0.60$) or by season ($F = 0.2$, d.f. = 1, 12, $P > 0.60$). At both sites in the Sierra NF, pairs had more overlap in their areas of use during the nonbreeding period ($\bar{x} = 51 \pm 18$ percent) than during the breeding period ($\bar{x} = 47 \pm 12$ percent).

Spotted owl home ranges shifted seasonally. Overlap between breeding and nonbreeding periods, using 95-percent AKs of individual home ranges, was 34 ± 18 percent at S-CON, 54 ± 5 percent at S-OAK, and 38 ± 8 percent at L-CON.

Table 6B--Means ($\bar{x}$) and standard deviations (SD) of home-range sizes of California spotted owls studied from 1987-1990 in the northern and central Sierra Nevada. Study sites were in conifer forest on the Lassen NF (L-CON) and in conifer forest (S-CON) and riparian/hardwood forest (S-OAK) on the Sierra NF. Estimates were determined using foraging locations and the 95-percent adaptive kernel method; 100-percent minimum convex polygon estimates of home-range sizes are in parentheses; n = number of individuals or pairs of owls.

Birds	Total home-range size (acres)					
	L-CON		S-CON		S-OAK	
	$\bar{x} \pm \text{SD}$	<i>n</i>	$\bar{x} \pm \text{SD}$	<i>n</i>	$\bar{x} \pm \text{SD}$	<i>n</i>
Individual birds						
Breeding	7,061.2 $\pm$ 5,992.5 (5,422.6 $\pm$ 5,194.4)	9	2,366.8 $\pm$ 740.0 (1,798.7 $\pm$ 787.2)	24	985.0 $\pm$ 745.0 (714.6 $\pm$ 624.4)	7
Nonbreeding	11,601.0 $\pm$ 6,664.1 (14,676.7 $\pm$ 8,251.8)	7	6,834.5 $\pm$ 5,138.3 (5,943.3 $\pm$ 4,529.5)	18	661.0 $\pm$ 510.1 (761.7 $\pm$ 495.7)	5
Annual	12,473.5 $\pm$ 7,305.5 (12,927.2 $\pm$ 10,132.2)	6	5,715.1 $\pm$ 4,289.9 (5,968.8 $\pm$ 4,639.9)	16	874.1 $\pm$ 644.2 (1,042.6 $\pm$ 865.7)	5
Pairs-breeding period						
Total area	3,869.3 (3,014.4)	1	3,420.5 $\pm$ 858.1 (2,514.8 $\pm$ 873.6)	8	720.5 $\pm$ 402.9 (457.4 $\pm$ 274.4)	2
Area shared	1,869.3 (1,164.9)		1,544.5 $\pm$ 364.8 (1,027.5 $\pm$ 317.6)		397.9 $\pm$ 341.6 (278.6 $\pm$ 225.8)	
Pairs-nonbreeding period						
Total area	9,871.8 (17,292.5)	1	9,730.8 $\pm$ 10,168.0 (7,201.0 $\pm$ 6,901.2)	4	573.3 $\pm$ 271.0 (818.8 $\pm$ 251.4)	2
Area shared	1,407.9 (563.2)		4,021.2 $\pm$ 3,929.3 (3,766.0 $\pm$ 4,355.4)		321.3 $\pm$ 160.1 (297.6 $\pm$ 133.9)	
Pairs-annual						
Total area			8,253.0 $\pm$ 7,872.6 (7,709.4 $\pm$ 7,184.0)	4	778.0 $\pm$ 405.8 (875.6 $\pm$ 303.8)	2
Area shared			4,443.0 $\pm$ 4,626.1 (4,492.2 $\pm$ 4,945.2)		447.6 $\pm$ 318.9 (459.9 $\pm$ 201.3)	

Habitat Use

Habitat Composition Within Home Ranges

During the breeding season, 13 and 63 percent of the habitat types available within individual home ranges were medium and large sawtimber (≥ 21 inches in d.b.h.) at S-CON and L-CON, respectively (tables 6C-6E), and 91 percent of the habitat types available within owl home ranges at S-OAK were classified as old-growth. Percentages were similar during the nonbreeding season in all areas. The mean proportions of individual home ranges that were ≥ 40 percent dominant canopy closure varied among sites (table 6F); proportions were similar at L-CON and S-CON, but they were about two times greater at S-OAK. Proportions for ≥ 40 percent total canopy closure were similar among all sites. Mean percentages of home ranges that were "suitable" habitat using R5 definitions were 4 (S-CON), 27 (S-OAK), and 26 (L-CON) at the three sites during the breeding season.

Habitat-Use Patterns Within Home Ranges

Among all of the owls during the breeding season, 10 and 82 percent of the radio locations were in medium and large sawtimber at S-CON and L-CON, respectively, and 92 percent were in old-growth at S-OAK; 21, 70, and 99 percent of the locations were in these size classes at the three sites, respectively, during the nonbreeding season (tables 6C-6F). More use occurred in small than in medium and large sawtimber at S-CON 87 percent and 73 percent of the radio locations during the breeding and nonbreeding seasons, respectively. The proportions of radio locations that were in dominant canopy closure ≥ 40 percent were again similar at L-CON and S-CON, but nearly twice as high at S-OAK. Higher proportions of locations occurred in total canopy closure ≥ 40 percent, and results were similar among the sites. Use of R5 suitable habitat was low--means of radio locations in this habitat class were 4 percent (S-CON), 47 percent (L-CON), and 49 percent (S-OAK) during the breeding season (table 6F). Use was greater than availability for most site-season comparisons and definitions of suitable habitat (fig. 6A). Use of R5 suitable habitat at S-CON was equal

Table 6C. Means ($\bar{x}$) and standard deviations (SD) of areas, proportions of home ranges, and proportions of foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the S-CON study site in the central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for 1987-1989 breeding and nonbreeding seasons.

Habitat type	Breeding period ¹						Nonbreeding period ¹					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Tree size-class d.b.h. in inches)												
No trees	9.1	35.8	0.003	0.01	0	0	736.3	1,828.5	0.058	0.14	0.031	0.08
<5	0	0	0	0	0	0	0	0	0	0	0	0
5 - 10	66.4	82.3	0.029	0.04	0.027	0.05	101.8	109.9	0.020	0.02	0.023	0.04
11 - 20	1,666.0	976.1	0.839	0.17	0.870	0.22	4,028.8	2,826.9	0.671	0.18	0.732	0.19
21 - 35	230.0	319.1	0.095	0.11	0.065	0.16	1,281.7	998.1	0.192	0.10	0.141	0.11
>35	59.0	143.8	0.032	0.08	0.038	0.08	477.5	684.4	0.054	0.07	0.073	0.12
Dominant canopy closure (percent)												
< 10	98.8	254.4	0.027	0.06	0.007	0.02	245.8	492.0	0.022	0.03	0.013	0.03
10 - 19	164.7	154.9	0.076	0.06	0.040	0.04	568.6	509.8	0.080	0.05	0.043	0.03
20-39	1,147.8	776.1	0.537	0.18	0.416	0.24	3,117.6	2,220.8	0.492	0.14	0.442	0.19
40 - 69	605.4	311.0	0.354	0.22	0.537	0.25	1,945.9	977.6	0.342	0.14	0.471	0.19
70 - 100	4.2	16.3	0.002	0.08	0	0	13.1	35.1	0.001	0	0	0
Total canopy closure (percent)												
<10	32.9	70.1	0.010	0.02	0.002	0.01	124.2	215.9	0.012	0.01	0.007	0.01
10 - 19	111.1	230.7	0.038	0.06	0.015	0.03	288.2	367.3	0.035	0.02	0.019	0.02
20 - 39	306.5	293.2	0.137	0.07	0.076	0.08	999.4	1,172.8	0.126	0.07	0.077	0.06
40 - 69	1,318.0	618.5	0.677	0.12	0.685	0.21	3,534.6	1,943.9	0.598	0.14	0.644	0.15
70 - 100	252.9	188.5	0.132	0.09	0.222	0.21	944.3	560.7	0.164	0.06	0.222	0.13

¹ Breeding period-- n = 24 owls with a total of 1,583 locations; nonbreeding period-- n = 18 owls with a total of 1,358 locations. An individual owl may contribute to n more than once if it was radio tracked during multiple breeding or nonbreeding seasons.

to or less than availability, but note the small amounts of this type available at S-CON

Nearly half of the owls at all three sites had significant Chi-square tests of habitat use for tree size-class, and nearly three-fourth of the owls had significant tests for use of canopy-closure classes. Differences in the proportion of owls that demonstrated habitat selection between the breeding and nonbreeding seasons were neither large nor consistent (fig. 6B). Fewer owls selected for tree size-class than for canopy-closure classes, and more selected for dominant canopy closure than for total canopy closure. Fewer owls had significant tests for habitat use when only foraging locations were used than when foraging and roosting locations were pooled. Summed across the three study areas (foraging and roosting locations pooled), 14 of 39 owls had significant tests for use of tree size-class, 26 owls for total canopy closure, and 29 owls for dominant canopy-closure classes during the breeding season. During nonbreeding season, 14 of 29 owls at the three study sites selected significantly for three size-class, 20 owls for total canopy closure, and 20 owls for dominant canopy-closure classes.

We tested whether owls used "suitable" habitat more than expected based on FS, R5, definitions (fig. 6A). Results were similar for L-CON and S-OAK: seven of eight birds at L-CON had significant tests during the breeding season, and four of six birds tested significant during the nonbreeding season. At S-OAK, six of seven birds and four of five birds had significant tests during the breeding and nonbreeding seasons, respectively. On the other hand, at S-CON, only four of 24 owls during the breeding season and six of 18 owls during the nonbreeding season had significant tests for use of suitable habitat.

Patterns of habitat use were weak and inconsistent among the subset of owls that passed the test of habitat selection (figs. 6C-6E). Most owls at all three sites used habitat types in proportion to their availability. Patterns were clearer and stronger for canopy closure than for tree size-class. More than half of the owls used poor cover classes less than expected and many used canopy closure ≥ 40 percent more than expected. Differences between dominant and total cover were minor. Patterns of selection for canopy closure did not appear to be stronger during the breeding than during the nonbreeding season. Use of tree size-class

Table 6D—Means ($\bar{x}$) and standard deviations (SD) of areas, proportions of home ranges, and proportions of foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the S-OAK study site in the central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for the 1989 breeding and nonbreeding seasons.

Habitat type	Breeding period ¹						Nonbreeding period ¹					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Tree size-class (d.b.h. in inches)												
No trees	6.2	10.6	0.005	0.01	0	0	0	0	0	0	0	0
<5	0	0	0	0	0	0	0	0	0	0	0	0
5-10	0	0	0	0	0	0	0	0	0	0	0	0
11 - 20	67.7	138.1	0.083	0.15	0.080	0.18	7.7	11.1	0.014	0.02	0.006	0.01
21 - 35	703.2	577.5	0.912	0.15	0.920	0.18	647.6	556.5	0.986	0.02	0.994	0.01
>35	0	0	0	0	0	0	0	0	0	0	0	0
Dominant canopy closure (percent)												
<10	26.4	55.3	0.021	0.03	0	0	52.6	76.6	0.055	0.04	0.024	0.03
10 - 19	127.9	161.3	0.132	0.14	0.081	0.09	156.6	145.7	0.210	0.16	0.108	0.09
20 - 39	102.0	167.7	0.105	0.11	0.033	0.04	125.0	244.3	0.113	0.14	0.068	0.13
40 - 69	444.8	312.7	0.542	0.23	0.494	0.36	239.6	152.2	0.391	0.10	0.378	0.17
70 - 100	69.4	32.4	0.194	0.24	0.391	0.36	81.8	39.8	0.231	0.23	0.422	0.32
Total canopy closure (percent)												
<10	26.4	55.3	0.021	0.03	0	0	52.6	76.6	0.055	0.04	0.024	0.03
10 - 19	99.0	141.5	0.093	0.09	0.069	0.08	102.8	145.7	0.112	0.08	0.060	0.06
20 - 39	76.6	80.0	0.106	0.10	0.027	0.03	113.9	86.4	0.170	0.07	0.057	0.06
40 - 69	455.0	400.4	0.501	0.27	0.416	0.30	268.5	293.9	0.347	0.11	0.385	0.23
70 - 100	114.1	49.6	0.273	0.26	0.488	0.31	117.6	43.0	0.316	0.25	0.474	0.32

¹ Breeding period-- $n = 7$ owls with a total of 498 locations; nonbreeding period-- $n = 5$ owls with a total of 548 locations.

showed stronger patterns at L-CON than at S-CON and S-OAK. More than half of the birds at L-CON used small sawtimber (<11 inches in d.b.h.) less than expected, and medium and large sawtimber more than expected, during the breeding season. These results were weaker during the nonbreeding season.

Discussion

Home-Range Size

Estimates of home-range size among California spotted owls are extremely variable. All available data indicate that they are smallest in habitats at relatively low elevations that are dominated by hardwoods, intermediate in size in conifer forests in the central Sierra Nevada, and largest in true fir forests in the northern Sierra Nevada.

Home-range sizes of owls in our studies at L-CON, S-CON, and S-OAK varied among areas and between seasons. The mean area used was about twice as large in the northern compared to

the central Sierra Nevada, and was two to 10 times larger in high-elevation conifer forests compared to low-elevation oak woodlands in the central Sierra Nevada. Median home-range estimates for pairs of northern spotted owls were 3,000 to 5,000 acres (Thomas et al. 1990)—less than half the size of pair home ranges of California spotted owls at L-CON (12,500 acres) but about the same as the pair estimates at S-CON. California spotted owls in the foothill riparian/hardwoods and oak woodlands at S-OAK used less than 900 acres, or approximately 20-30 percent of the area used by northern spotted owls.

Two pairs of owls radio tracked in the San Bernardino Mountains used home ranges averaging more than 5,300 acres (100-percent MCP-LaHaye pers. comm.) (table 6G). Home-range sizes of pairs during the breeding period averaged 4,569 acres on the Tahoe NF (100-percent MCP, $n = 2$; Call 1990, p. 21) and 4,759 acres on the Eldorado NF [100-percent MCP, $n = 4$ (excludes two pairs with relatively few radio locations); Laymon 1988, p. 187]. These estimates, with those of 3,869 acres for the Lassen NF ($n = 1$, table 6B) and 3,421 acres for the Sierra NF ($n = 8$, table 6B), give an overall estimate of about 4,200 acres (grand mean, unweighted for sample size) for home-range sizes of owl pairs during the breeding period in Sierran conifer forests.

Table 6E—Means ($\bar{x}$) and standard deviations (SD) of areas, proportions of home ranges, and proportions of foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the L-CON study site in the northern Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for breeding (1990) and nonbreeding (1989-1990) seasons.

Habitat type	Breeding period ¹						Nonbreeding period ¹					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Tree size-class (d.b.h.in inches)												
No trees	515.0	913.2	0.049	0.04	0	0	1,368.4	1,241.2	0.112	0.09	0.007	0.01
<5	9.9	17.5	0.001	0	0	0	39.3	38.8	0.003	0	0.002	0.01
5 - 10	207.7	332.5	0.023	0.01	0.011	0.02	608.9	383.8	0.046	0.02	0.029	0.04
11 - 20	2,659.2	3,724.8	0.300	0.15	0.172	0.11	3,502.0	2,340.1	0.247	0.12	0.261	0.12
21 - 35	1,394.8	962.3	0.251	0.10	0.298	0.15	2,755.5	1,490.4	0.224	0.10	0.220	0.05
> 35	2,371.9	2,287.2	0.377	0.12	0.519	0.17	4,644.8	2,164.0	0.368	0.09	0.480	0.10
Dominant canopy closure (percent)												
<10	1,296.3	1,797.4	0.160	0.04	0.072	0.08	2,198.5	1,469.6	0.165	0.06	0.064	0.04
10 - 19	1,598.6	2,003.9	0.204	0.04	0.142	0.07	2,859.0	1,329.1	0.223	0.05	0.131	0.13
20 - 39	2,043.2	2,230.9	0.303	0.10	0.329	0.21	3,266.3	1,415.1	0.255	0.03	0.318	0.14
40-69	1,607.0	1,461.7	0.251	0.11	0.350	0.17	2,436.2	1,439.3	0.187	0.06	0.318	0.12
70 - 100	532.8	614.3	0.076	0.03	0.108	0.08	1,294.3	840.3	0.094	0.03	0.165	0.11
Total canopy closure (percent)												
<10	679.5	1,191.5	0.067	0.05	0.033	0.06	1,088.0	985.8	0.079	0.06	0.006	0.01
10 - 19	300.8	403.4	0.041	0.02	0.012	0.02	666.9	618.7	0.048	0.04	0.013	0.01
20 - 39	1,595.1	1,983.9	0.211	0.06	0.105	0.06	1,983.2	1,359.0	0.145	0.05	0.117	0.04
40 - 69	2,038.2	2,369.7	0.263	0.09	0.204	0.16	3,268.1	1,630.2	0.257	0.08	0.185	0.11
70 - 100	2,464.3	2,063.7	0.411	0.09	0.647	0.15	5,048.4	2,205.2	0.396	0.05	0.675	0.11

¹ Breeding period-- $n = 8$ owls with a total of 479 locations; nonbreeding period-- $n = 6$ owls with a total of 402 locations.

The smallest estimated use areas of California spotted owls (means for pairs ranging from 98 to 243 acres) were based on known sizes of small stringers of dense riparian/hardwoods in the Cleveland, Angeles, and Los Padres NFs (table 6G). Owls in these stringers were not radio-tagged. Perhaps some of them used more than one canyon bottom, but the Forest Biologists who made these estimates reported that, in some cases, other individuals or pairs of owls occupied the riparian stringers in adjacent canyons. Most canyon sides above the riparian zones were covered by dense chaparral. We believe it is most unlikely that the owls can use the chaparral, as it is too dense for safe or effective flight.

We strongly suspect that the large differences in home-range sizes reported here are related, at least in part, to differences in the primary prey of the owls in different localities. Consistently, California spotted owls with the smallest observed home ranges prey primarily on woodrats, but those with the largest home ranges specialize on flying squirrels. Woodrat densities generally tend to be much greater than flying squirrel densities, and woodrats weigh nearly twice as much as flying squirrels (Chapter 4). Similar relations are suggested in recent studies of northern spotted owls by Carey et al. (1992).

Habitat Selection

Here we evaluate habitat quality based on use versus availability of types (Thomas et al. 1990, appendix F). We regard as suitable those habitats selected in excess of availability by most owls. Marginal habitats are seldom or never used in excess of availability, used in proportion to availability by many owls, and used less than expected by many other owls. Habitat types used less than expected by most owls are considered to be poor in quality and are classed as unsuitable habitat.

Spotted owls in this study more consistently selected for high canopy closure than for large tree size-class. Chi-square values were consistently higher for canopy closure, and more owls had significant tests for selection of high canopy closure than for tree-size class in 18 site-season comparisons. Differences between total and dominant canopy closure were minor, but because more owls exhibited significant selection for high dominant cover than for high total cover, dominant cover may be a better measure of suitable habitat for California spotted owls.

The amount of medium and large sawtimber in individual home ranges did not appear to be a good indicator of the amount of that habitat needed to sustain California spotted owls, unlike the case for northern spotted owls (see Thomas et al. 1990). Nearly half of the California spotted owls had significant tests of

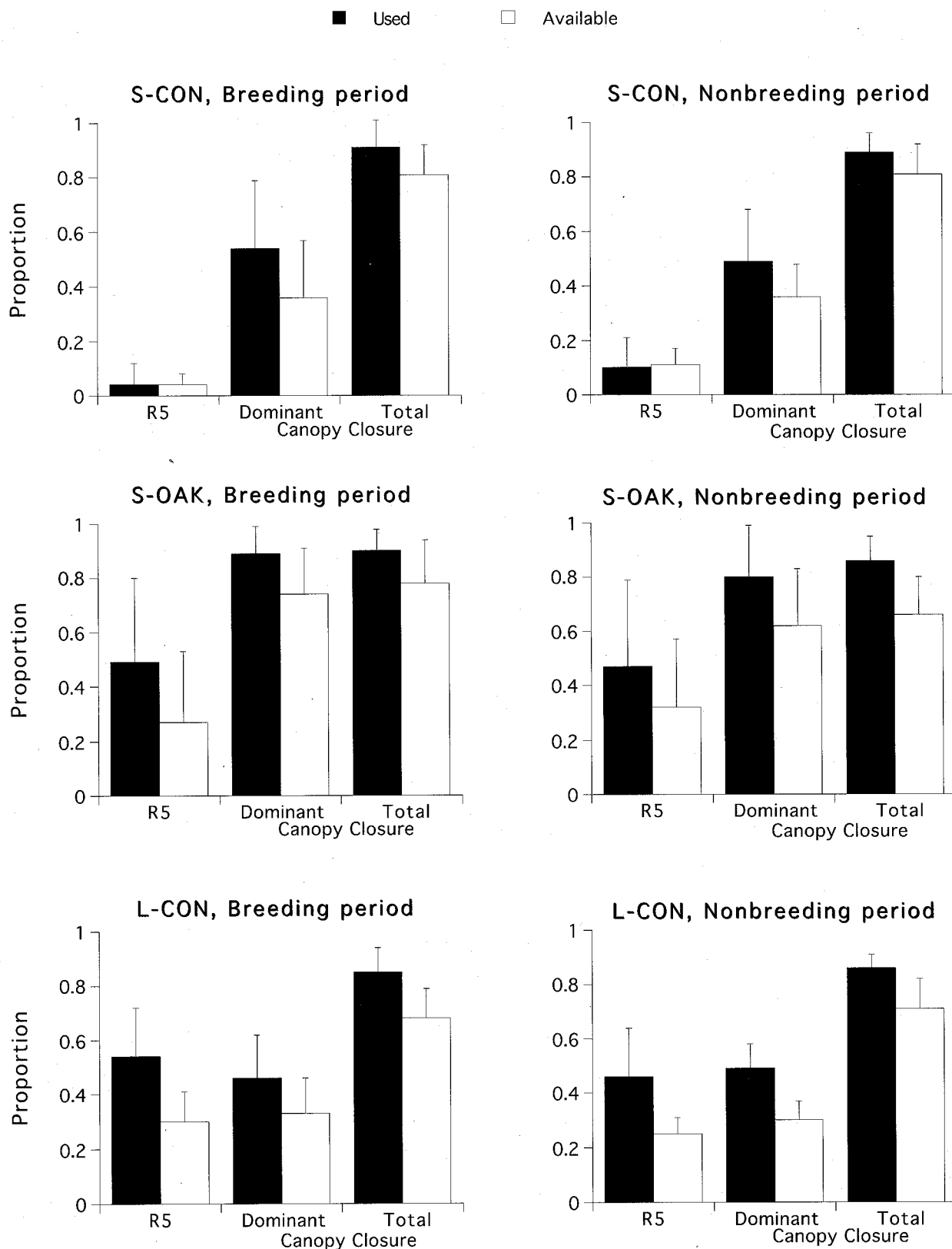


Figure 6A—Mean proportions of suitable habitat available in home ranges of California spotted owls in relation to proportions used by radio-tagged birds in different seasons and study sites. Study areas were in conifer forests of the Sierra (S-CON) and Lassen (L-CON) National Forests, and in hardwood/riparian forests of the Sierra (S-OAK) National Forest. Three categories of suitable habitat were tested: (1) R5 = Forest Service (Region 5) definition—medium or large sawtimber, dominant canopy closure poor or higher, and total closure >69 percent; (2) canopy closure of dominant trees ≥ 40 percent; and (3) total canopy closure ≥ 40 percent. Error bars are standard deviations (SD). The 95-percent adaptive kernel was used to delineate home ranges.

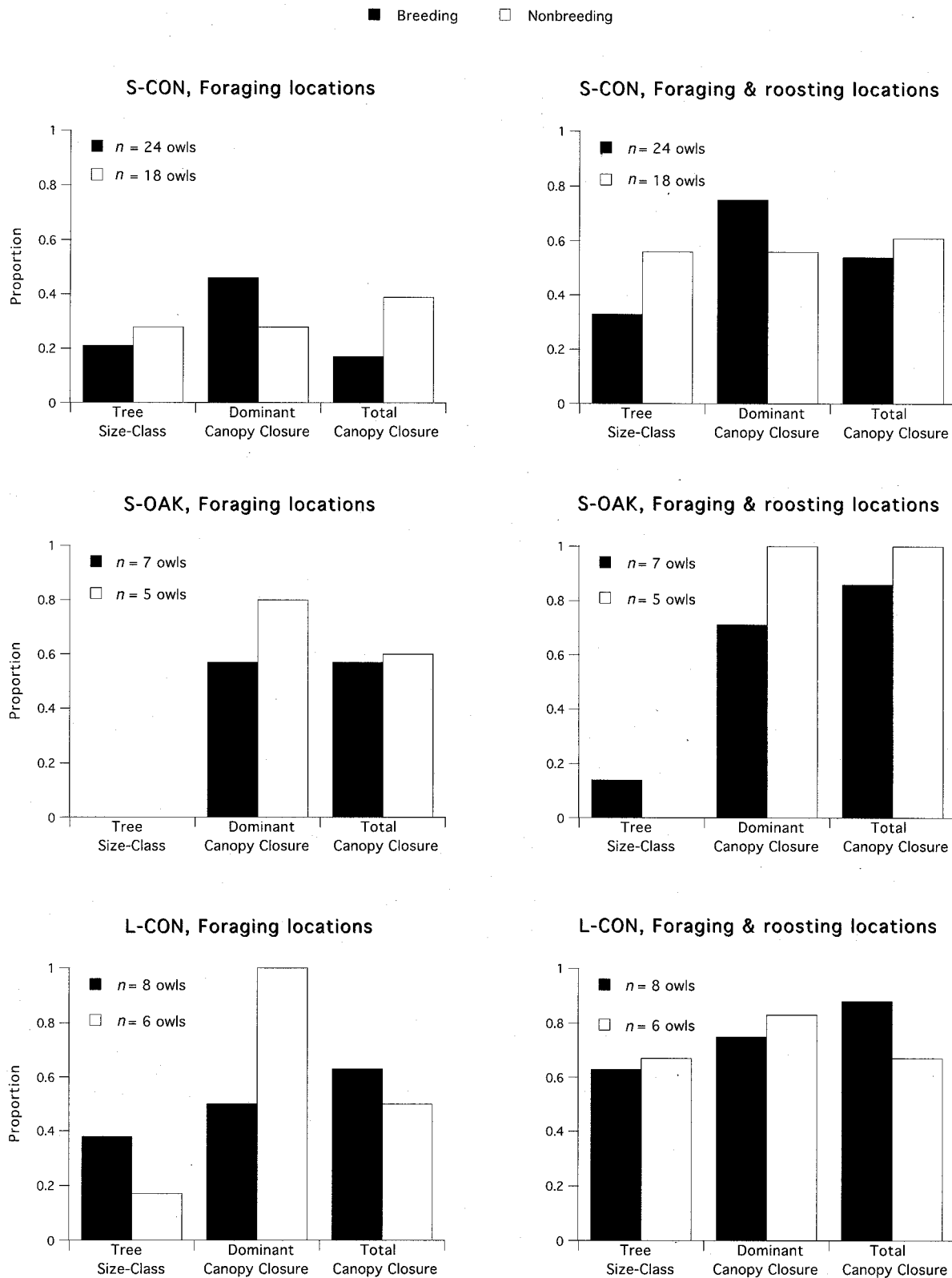


Figure 6B—The proportion of California spotted owls with significant ($P \leq 0.05$) Chi-square tests for selection of habitats based on tree size-classes, dominant canopy closure, and total canopy closure. Study areas were in conifer forests of the Sierra (S-CON) and Lassen (L-CON) National Forests, and in hardwood/riparian forests of the Sierra (S-OAK) National Forest. Tests were done separately for breeding and nonbreeding periods using foraging locations alone, and using foraging and roosting locations pooled.

selection for tree size-class, but most of them used all size classes in proportion to availability in the central Sierra Nevada. Patterns were stronger at L-CON during the breeding season, when about half of the birds used medium and large sawtimber more than expected. By contrast, old-growth was used in greater proportion than its availability, for nesting, roosting, and foraging, by most northern spotted owls in Oregon and Washington, and it was never used less than expected. Throughout their range and across all seasons, northern spotted owls consistently showed foraging and roosting patterns significantly associated with old-growth stands or mixed stands of mature and old-growth trees. Among California spotted owls, however, patterns of habitat use for tree size-class were weaker, and they were not consistent among study areas.

Canopy closure ≥ 40 percent was used by many California spotted owls greater than expected, by a few less than expected, and by many equal to its availability. Canopy closure ≤ 39 percent was used by most owls less than expected and in proportion to availability by many others. Based on these results, then, suitable habitat for California spotted owls appears to include canopy closure ≥ 40 percent, and habitat with ≤ 39 percent canopy closure is marginal to unsuitable.

The R5 definition of suitable habitat does not appear to be appropriate across the range of the California spotted owl. Most owls at L-CON (79 percent) and S-OAK (83 percent) used R5-defined suitable habitat in excess of availability. But results were quite different for owls in the conifer forest at S-CON, where this habitat type was generally not available within home ranges. At S-CON, most birds used R5-defined suitable habitat in proportion to availability, a few used it more than expected, and a few less than expected.

Habitat Selection and Population Stability

Habitat selection by owls at S-CON was generally less evident than at L-CON, even though both sites were in Sierran conifer forests. We also determined that only 13 percent of the forest in the study area at S-CON was in medium and large sawtimber, whereas the L-CON site had 63 percent of its forest in those timber size classes and several of the owls there exhibited significant selection for those timber stands. During the breeding periods of 1987, 1988, and 1989, owl crews on the Lassen and Sierra NFs monitored the occupancy status and breeding activity of owl pairs in Spotted Owl Habitat Areas (SOHAs) managed for the owls. Over that period on the Lassen NF, an absence of pairs was confirmed in 8 of 27 cases (30 percent) and breeding was confirmed in 8 of 27 cases (30 percent). During the same period on the Sierra NF, an absence of pairs in SOHAs was confirmed in 8 of 11 cases (73 percent) and breeding was confirmed in only 1 of 11 cases (9 percent). Because we lack sufficient information to determine whether California spotted owls in any part of the Sierra Nevada are reproducing at a rate that can maintain the population (Chapter 8), we cannot be certain that habitats used by owls either at L-CON or S-CON were adequate to provide for a balance between births and deaths. The data suggest, however, that the habitat available to spotted owls on the Sierra NF may be less adequate than that on the Lassen NF. Indeed, it may be that

spotted owls on the Sierra NF cannot maintain their numbers, and that perhaps they are maintained in part by immigration from populations in the neighboring NPs. Note that the Sierra NF shares its northern border with Yosemite NP and its southern border with Sequoia/Kings Canyon NPs (fig. 4B).

Power of Chi-square Tests

The power of Chi-square tests of habitat selection is influenced by classification error (telemetry and/or mapping), the resolution of habitat classification, and by the number of locations available to estimate use. These factors may reduce the likelihood of detecting habitat selection when, in fact, it is occurring (type-II error-see White and Garrott 1986). In addition, the power of a test depends on the "effect size" (Cohen 1988) or, in the case of habitat selection, the degree to which differences exist between proportions of available and used habitat types. The smaller the effect size, other things being equal (significance level, desired power), the larger the sample size needed to detect selection. The small number of locations in our data could have reduced the likelihood of detecting habitat selection when it occurred. Owls with significant Chi-square tests for selection of canopy-closure classes had a mean of 72 (± 23) radio locations, but owls with insignificant tests had a mean of only 57 (± 19) locations. The difference between these, sample sizes was significant (t test = 2.8, d.f. = 78, $P < 0.01$), indicating that small sample sizes may have been associated with our failure to detect habitat selection by radio-tagged owls. On the other hand, the difference between the number of locations between owls that passed ($\bar{x} = 69 \pm 24$) and failed ($\bar{x} = 62 \pm 21$) tests of selection for tree size-class was not significant ($t = 1.3$, d.f. = 68, $P > 0.20$).

The number of radio locations approximately doubled when we pooled foraging and roosting locations. More owls had significant Chi-square tests of habitat use for the pooled data set than was the case for the foraging locations alone. The difference in Chi-square results between these two groups was apparently due primarily to differences in habitat use by foraging and roosting owls, and less so to the increase in sample size. Roost sites were more distinct from available sites than was the case for foraging sites. For example, 18 of 18 owls at S-CON used sites that had ≥ 40 percent canopy closure more than expected for roosting during the breeding period, and 83 percent had significant tests of habitat selection. Use of sites that had ≥ 70 percent canopy closure for roosting was similar: 16 of 18 owls had significant tests of habitat selection, and 11 of 18 owls used, these stands more than expected (G. N. Steger pers. observ.). By contrast, only 7 of 24 owls at S-CON had significant tests for use of foraging sites with dense canopy during the breeding period, and only seven owls foraged more than expected in sites with ≥ 40 percent canopy closure.

Effect size increases with the size of the difference between proportions of available and used habitat types, providing a useful index to identify where habitat selection is greatest. We found higher effect sizes for canopy closure than for tree size-class, and for foraging and roosting locations combined than for foraging locations alone. These results support the conclusion that the owls had differential use patterns between daytime roosting

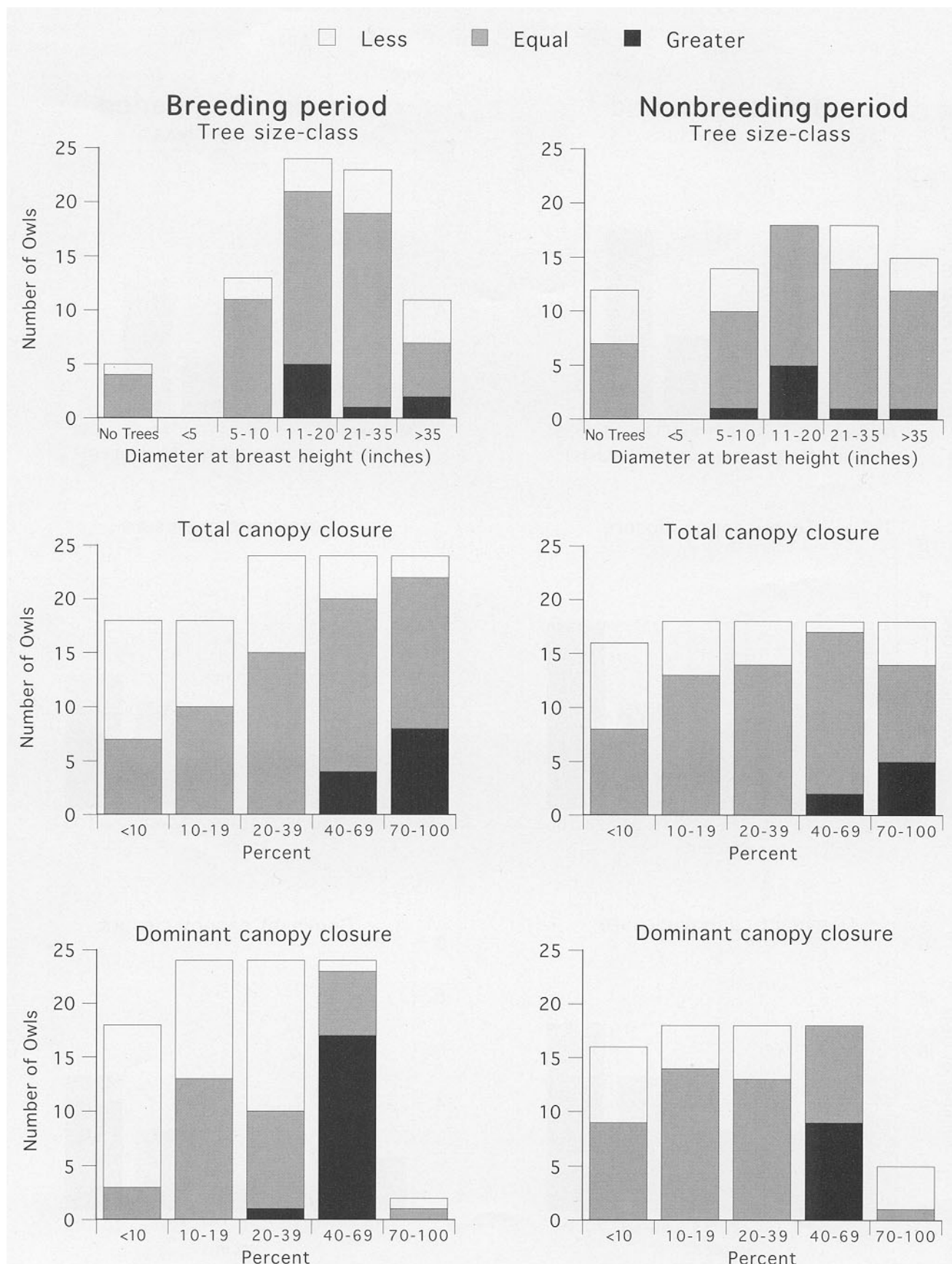


Figure 6C—The number of California spotted owls at S-CON (conifer forest study area in the Sierra National Forest) that used tree size-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

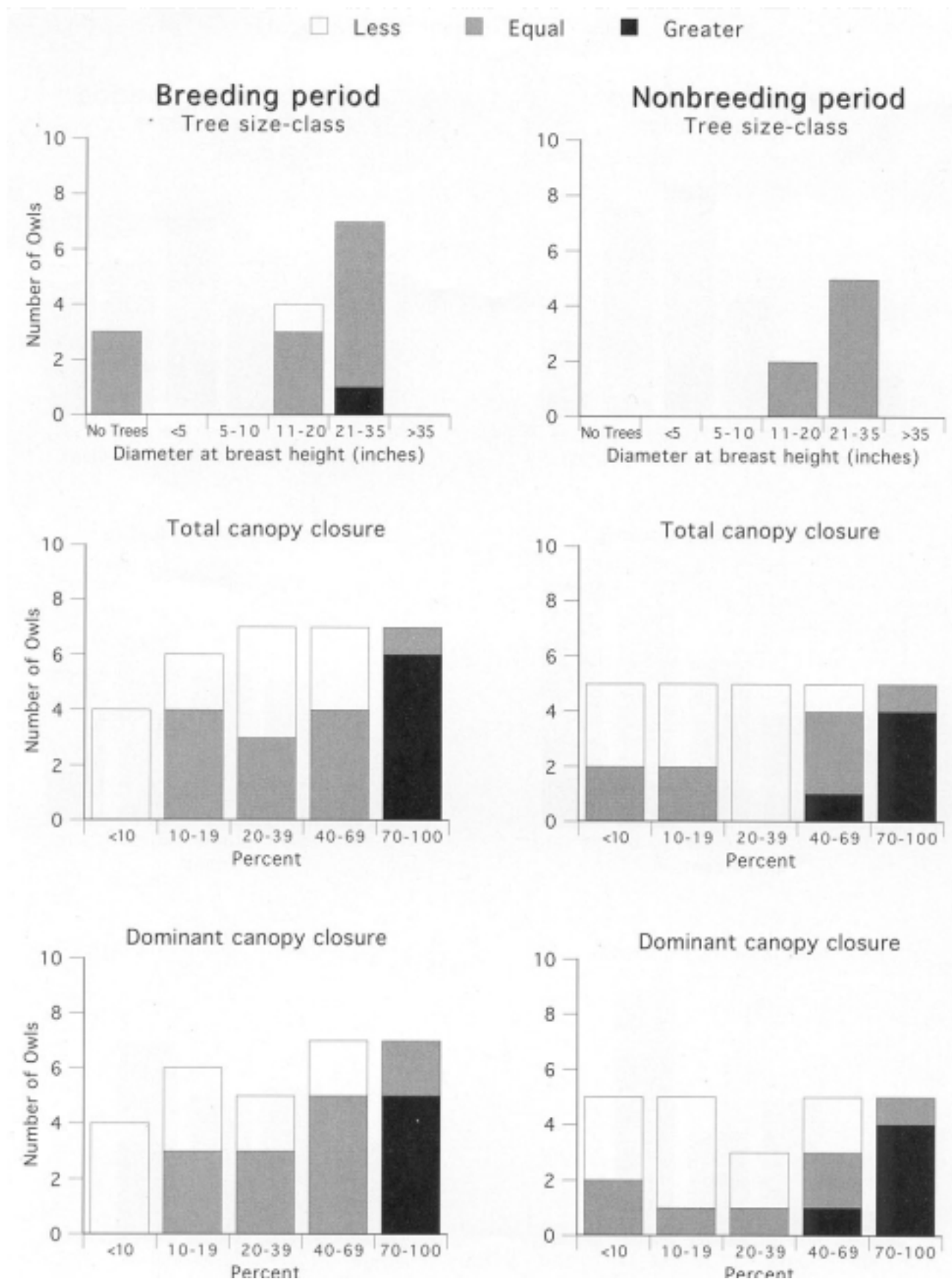


Figure 6D—The number of California spotted owls at S-OAK (riparian/hardwood forest study area in the Sierra National Forest) that used tree size-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

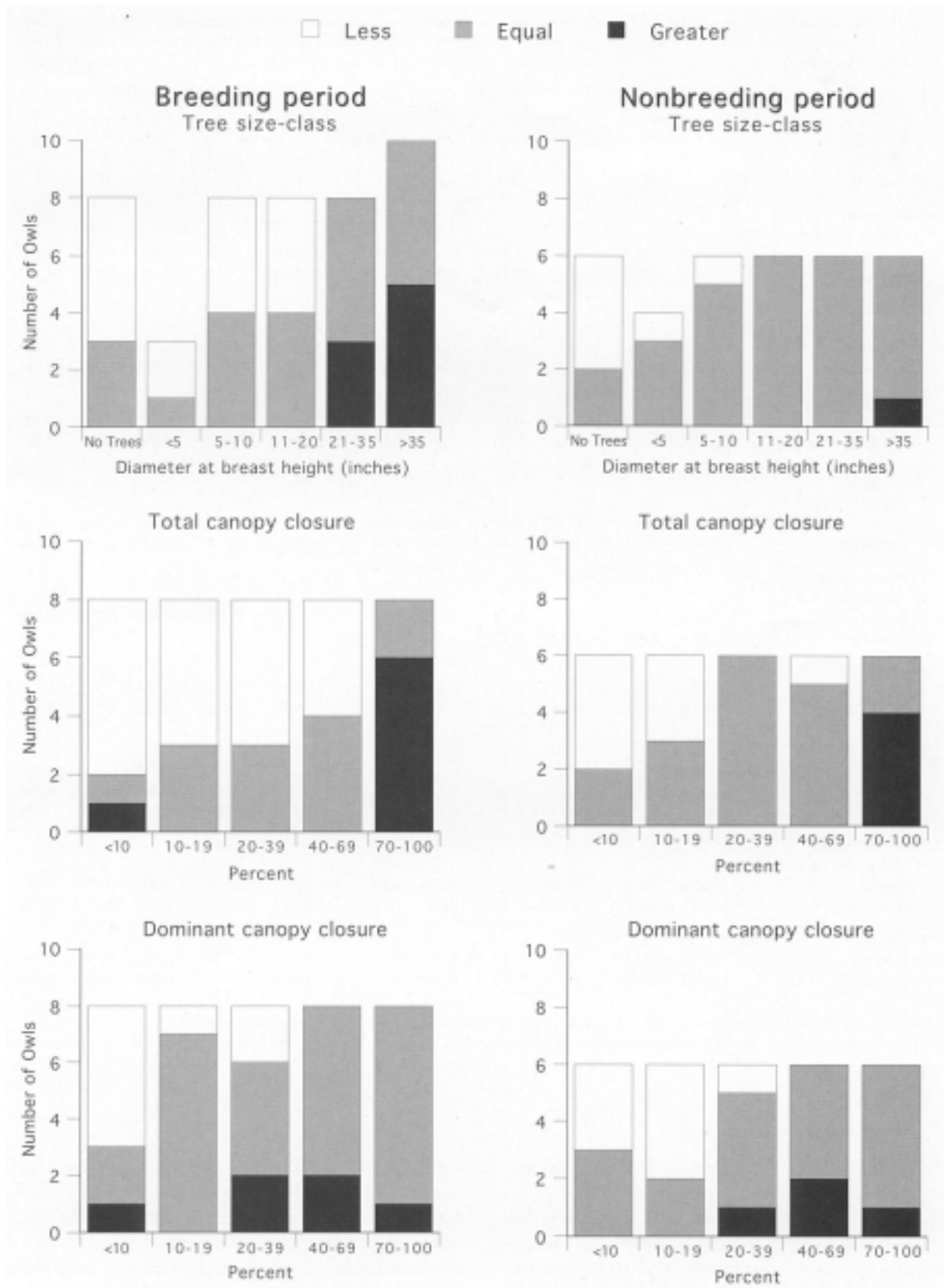


Figure 6E—The number of California spotted owls at L-CON (conifer forest study area in the Lassen National Forest) that used tree diameter-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

Table 6F--Means ($\bar{x}$) and standard deviations (SD) of total area, proportions of home ranges, and proportions of foraging and roosting radio locations in suitable and unsuitable habitat for California spotted owls that passed the site fidelity test for the 1987-1990 breeding and nonbreeding period at L-CON, S-CON, and S-OAK study sites in the northern and central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges (n = number of individual owls).

Study site Habitat type		Breeding period ¹								Nonbreeding period ¹					
		<i>n</i>	Area (acres)		Proportion of home range		Proportion of locations		<i>n</i>	Area (acres)		Proportion of home range		Proportion of locations	
			$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD		$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
S-CON	Total canopy closure ≥40 pct	24							18						
	Suitable		1,570.7	734.1	0.813	0.11	0.907	0.10		4,478.9	2,378.6	0.806	0.11	0.893	0.07
	Unsuitable		450.5	540.9	0.187	0.11	0.093	0.10		1,412.1	1,734.4	0.194	0.11	0.107	0.07
	Dominant canopy closure ≥40pct	24							18						
	Suitable		609.6	308.0	0.357	0.22	0.537	0.25		1,959.0	991.5	0.361	0.12	0.487	0.19
	Unsuitable		1,411.6	1,095.7	0.643	0.22	0.463	0.25		3,932.0	3,053.7	0.639	0.12	0.513	0.19
	Region 5 ²	24							18						
	Suitable		93.6	126.5	0.039	0.05	0.037	0.08		655.8	499.9	0.105	0.06	0.105	0.11
	Unsuitable		1,927.6	1,117.4	0.961	0.05	0.963	0.08		5,256.2	3,560.3	0.895	0.06	0.895	0.11
S-OAK	Total canopy closure ≥40 pct	7							5						
	Suitable		569.1	365.8	0.779	0.16	0.904	0.08		386.1	256.4	0.663	0.14	0.859	0.09
	Unsuitable		202.0	261.1	0.221	0.16	0.096	0.08		269.2	299.4	0.337	0.14	0.141	0.09
	Dominant canopy closure ≥40 pct	7							5						
	Suitable		514.5	284.5	0.740	0.17	0.886	0.10		321.3	122.0	0.623	0.21	0.799	0.19
	Unsuitable		256.6	349.8	0.260	0.17	0.114	0.10		334.2	439.9	0.377	0.21	0.201	0.19
	Region 5 ²	7							5						
	Suitable		113.6	49.6	0.273	0.26	0.488	0.31		117.6	43.0	0.316	0.25	0.474	0.32
	Unsuitable		657.5	599.5	0.727	0.26	0.512	0.31		538.0	592.8	0.684	0.25	0.526	0.32
L-CON	Total canopy closure ≥40 pct	8							6						
	Suitable		4,502.6	4,425.3	0.679	0.11	0.851	0.09		8,316.5	3,739.6	0.709	0.12	0.864	0.05
	Unsuitable		2,575.2	3,557.8	0.321	0.11	0.149	0.09		3,737.9	2,750.8	0.291	0.12	0.136	0.05
	Dominant canopy closure ≥40 pct	8							6						
	Suitable		2,140.0	2,059.0	0.328	0.13	0.458	0.16		3,730.4	2,114.3	0.304	0.07	0.487	0.09
	Unsuitable		4,938.0	6,005.8	0.672	0.13	0.542	0.16		8,323.7	3,986.6	0.696	0.07	0.513	0.09
	Region 5 ²	8							6						
	Suitable		1,465.5	883.5	0.262	0.10	0.468	0.13		2,238.8	971.0	0.252	0.09	0.415	0.17
	Unsuitable		5,167.5	5,269.0	0.738	0.10	0.532	0.13		7,898.8	4,339.5	0.749	0.09	0.585	0.17

¹ An individual owl may contribute to n more than once if it was radio tracked during multiple breeding or nonbreeding periods.

² Region 5 definition--suitable habitat = medium or large sawtimber, dominant canopy closure poor or higher, and total closure > 69 percent; unsuitable habitat=all other types.

locations and nighttime foraging locations-they were less selective among habitats when foraging than when roosting.

The small number of radio locations among our owls did not result in low power to reject the null hypothesis for canopy closure. Estimates of power ranged from 70 to 90 percent for canopy closure. We had high likelihood of detecting habitat selection for canopy closure when it occurred. Our power to detect selection for tree size-class was lower-70 percent at L-CON, 59 percent at S-CON, and 29 percent at S-OAK. Thus, even if selection for tree size-class occurred, we had low power to detect it, especially in the oak woodlands at S-OAK. The number of radio locations for canopy closure and tree size-class

was the same; the differences in power were due to differences in effect size. To achieve 80 percent power at an 0.05 level of significance, with 4 degrees of freedom, given the effect size we observed for tree size-class (0.20 at S-OAK), 298 radio locations would be needed; if the effect size were 0.30, only 133 locations would be needed (see Cohen 1988, p. 258).

Effect size can also be strongly influenced by the definition of the available sampling frame. In general, the more widely defined the available frame, the greater the likelihood of demonstrating selection. By using the AK method to define the available sampling frame for each home range, we decreased the likelihood of demonstrating selection relative to a less restrictive

Table 6G Estimated areas of use by California spotted owls that were not radio tracked. Data are tabulated by National Forest (NF), and some Ranger Districts, as minimum breeding-season estimates. Estimated areas of use were based on the sizes of drainages occupied by owls during summer surveys.

Areas of use	Total area used (acres)		
	$\bar{x} \pm SD$	Range	<i>n</i>
Cleveland NF			
All sites	133.4 ± 70.0	38.0 - 294.0	15
Chaparral sites	159.5 ± 85.9	38.0 - 294.0	8
Oak/Pines sites	103.6 ± 29.4	70.0 - 155.0	7
Angeles NF			
All sites	225.8 ± 148.1	37.0 - 689.0	71
Saugus Ranger District	172.6 ± 156.7	48.0 - 530.0	14
Tujunga Ranger District	235.4 ± 123.3	119.0 - 405.0	8
Arroyo Seco Ranger District	304.6 ± 144.1	37.0 - 689.0	21
Mount Baldy Ranger District	185.6 ± 134.3	46.0 - 496.0	14
Valyermo Ranger District	195.3 ± 139.7	65.0 - 600.0	14
All pairs	242.5 ± 147.4	54.0 - 600.0	38
Singles	206.5 ± 148.7	65.0 - 600.0	33
Los Padres NF			
All sites	89.3 ± 52.2	25.0 - 200.0	21
All pairs	98.4 ± 50.4	25.0 - 200.0	16
Singles	60.0 ± 51.9	25.0 - 150.0	5
San Bernardino NF¹			
All pairs	5,329.0 ± 4,941.0	1,835.0 - 8,823.0	2
All individuals	3,450.1 ± 2,504.6	674.0 - 6,294.0	4

¹ Owls on the San Bernardino NF were radio tracked. Home-range estimates were determined using the 100-percent minimum convex polygon.

definition of availability based on, for example, the 100-percent MCP. This occurred because the AK algorithm tightly fits the actual distribution of points with an irregular polygon. In the limiting case with many data points, the AK could fit just the used distribution of points and exclude other habitats that truly may have been available.

Thus, failure to reject the null hypothesis (that habitat use = habitat available) in some of our tests of selection may have resulted from the effects of small samples and the use of the AK algorithm, rather than demonstrating a lack of selection. The extent to which this occurred is unknown. It is clear, however, that failure to detect habitat selection should be interpreted, for those tests with low power, in terms of a high likelihood of type-II errors. Given these limitations, it may be that confirmed selection for particular attributes (for example, canopy closure or tree size) by even a few owls should be considered strong evidence for selection in our studies. An incorrect inference would be to conclude that failure to detect significant habitat selection proves a lack of selection. For these reasons, we believe the most significant insights to spotted owl biology are provided by the habitat-use results, rather than results of tests for selection.

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Chapter 7

Patterns of Habitat Use By California Spotted Owls in Logged Forests of the Northern Sierra Nevada

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The radio-tracking study area on the Lassen National Forest (NF) reported in Chapter 6 was coincidentally an area for which we were able to locate nearly complete records of logging. It was also an area for which we had much information about the vegetation. Based on these records, we have visually examined patterns of habitat use by radio-tagged spotted owls in relation to stand histories near the geographic center of our telemetry study area. We have assumed that a low density of owl locations in an area indicated an aversion by the owls to the habitat there. Conversely, a high density of locations was interpreted to indicate selection for a particular area.

We have not attempted any statistical analyses of use vs. availability for these data, as done in Chapter 6. Logging practices were unique enough on the various study sites that we could not stratify them into meaningful categories for rigorous use-versus-availability tests. Instead, we based our evaluations of spotted owl use patterns on visual inspections of owl locations in relation to known histories of logging in stands. Such case studies may serve to enlarge our general understanding of how the owls are affected by different stand treatments.

Study Area

The Lassen NF study area was located in the northern Sierra Nevada, east of Lassen National Park. It was dominated by red and white fir at high elevations (approximately 5,800-6,900 feet) and pine (Jeffrey, ponderosa, sugar, and lodgepole) at lower elevations (approximately 5,000-5,800 feet). The predominant silvicultural method there has been selective logging. For this chapter, we focus on the high-elevation, true fir zone. The condition of this forest in the early part of the 20th century was markedly different before logging began in the 1930s. Sierran mixed-conifer forest covered the mid-mountain slopes and red fir dominated higher elevations, except for shrub fields on the south side of Swain Mountain. The forest was dominated by large trees—average diameter at breast height (d.b.h.) of the various species was 25-34 inches for white fir, 32-35 inches for Jeffrey pine, and 28-32 inches for red fir (Boerker 1912, Evans 1919).

Methods

The cutting history within the study area was determined using records and timber sale maps from the U.S. Department of Agriculture, Forest Service (FS) and private timber companies. This information was then transferred to U.S. Geologic Survey topographic maps. Cut-unit polygons were subsequently digitized and stored in a Geographic Information System (GIS). Each cut-unit polygon contained historical information, including year of cut, type of harvest (overstory removal, group selection, thinning, sanitation, salvage, partial cut), and species removed. Radio-telemetry points from daytime roosting and nighttime foraging locations of spotted owls (Chapter 6) were overlaid onto the cut-history maps using GIS. Vegetation types (table 6A), determined from large-scale color aerial photographs and 1:24,000 black-and-white orthophotoquads, were then overlaid onto the owl telemetry points and the cut-unit maps. Vegetation polygons were classified by diameter size-class of the dominant trees (structural size class) and canopy closure class of dominant trees. For this chapter, we classified structural size class into two categories: <21 inches in d.b.h. (size classes 0-3) and ≥21 inches d.b.h. (size classes 4 and 5). Similarly, canopy closure was categorized as <40 percent cover (open, sparse, or poor) or ≥40 percent cover (normal or good). Polygons were reclassified as suitable or unsuitable spotted owl habitat based on current FS definitions. Suitable stands were those in which the diameter size-class of dominant trees was ≥21 inches, canopy closure of dominant trees was ≥20 percent, and total canopy closure was ≥70 percent.

We present three figures for each area of interest with owl radio locations overlaid on each of three vegetation types—suitable spotted owl habitat according to the FS; structural size class ≥21 inches in d.b.h.; and canopy closure ≥40 percent. Cut units and areas of owl use have been numbered in the sequence in which they are discussed in the results. For one area, we also present a 1980 orthophotograph for a visual inspection of the landscape. Timber-sale boundaries delineated on the figure do not always align with boundaries on the orthophoto. The figure represents sale maps or planned cuts, but the orthophoto depicts actual cut boundaries after logging was done. Cut units delineated on the figures are minimum representations of actual areas that were logged. Many areas were entered with light removal outside of the units we mapped, but the FS generally did not keep detailed records of such light cuts.

Results

We examined four areas located near the center of our owl home-range and habitat-use study and where much logging had occurred (fig. 7A). These areas are designated here as Griffith Hill (fig. 7B), Swain Mountain (fig. 7C), Silver Lake (fig. 7D), and Star Butte (fig. 7E). Most logged areas on Swain Mountain were little used by owls, and some heavily logged areas at Griffith Hill, Silver Lake, and Star Butte were avoided by the owls, but other logged areas were used extensively.

Griffith Hill

The Griffith Hill area was dominated by a strip of FS land approximately 3/4 of a mile wide and 2 miles long, lying between two areas of private land (figs. 7B and 7F). Canopy cover on FS land was mostly ≥ 40 percent. The FS land was characterized by selectively logged true fir and mixed-conifer forests. Several sites (numbers 1, 2, 3, and 4) were selectively logged in the mid-1960s by overstory removal and group selection. Private land south of this section (site 5), on the other hand, has been logged much more heavily, and canopy cover there was < 40 percent. Site 5 was rarely used by the owls. Pine and fir were harvested there in 1960; in 1973 trees > 24 inches were removed and the site was salvage-logged for merchantable timber; and trees of all species < 20 inches in d.b.h. were thinned in the 1970s-1980s (McCrory pers. comm.). Site 5 currently has sparsely scattered trees ≥ 21 inches in d.b.h. in the eastern section. The adjacent private land (site 6) is owned by the same company but, according to their records, it has not been entered. The Susan River drainage, which runs through this area to the south of Lake Road (site 7), was logged by overstory removal and group selection in 1966 and 1968. It now has canopy cover ≥ 40 percent, but trees there are small and the site is classified as unsuitable owl habitat.

In general, spotted owl use at Griffith Hill occurred mostly on FS land. The more open private land to the north and south were used relatively little. Several owl telemetry fixes were in site 6, characterized by trees ≥ 21 inches in d.b.h. and a canopy closure ≥ 40 percent. An owl pair nested in the fir stand covering the eastern half of site 1. The owls apparently did not use the western half of site 1, which had been heavily logged and was very open. The eastern half of site 1 was "group cut" (in small areas < 1 acre), and the western half was cut using overstory removal (J. D. Johnston pers. observ.).

Swain Mountain

This area covers Swain Mountain Experimental Forest (SMEF) and adjacent forests (fig. 7C). Most of SMEF lies above 5,800 feet in elevation and is dominated by forests of red and white fir. Numerous small patch cuts were made across SMEF in 1958 and from 1970 to 1972. Several stands were also selectively logged during the early 1970s. The large south-facing

slope of Swain Mountain burned frequently in the past and was planted with Jeffrey pine in 1978. Today the area is dominated by a thick cover of ceanothus, chinquapin, manzanita, and small Jeffrey pines. Much of SMEF was shelterwood-logged from 1982 to 1985. Those cuts underwent intensive site preparation following logging-units were either broadcast burned or tractor-piled and burned. Most of the residual trees there today are large, old-growth firs, with densities ranging from 5 to 15 trees per acre. Several intact stands of old-growth still remain on SMEF.

Spotted owls did not use the large areas of shelterwood cuts (site 8) or the large pine plantation on the south side of Swain (site 9). Figure 7C shows that most owl locations were in habitat classified as suitable (sites 10, 11, 12, and 13), and many were in the intact old-growth stands. Most owl locations on SMEF occurred during the nonbreeding period. One owl pair had a linear home range along a road just southwest of the pine plantation (site 14). The forest along this road, and to the west of it, has been selectively logged but is still dominated by trees ≥ 21 inches in d.b.h. and canopy cover ≥ 40 percent.

Silver Lake

The Silver Lake area (fig. 7D) lies just west of the Griffith Hill area and northwest of SMEF. Its eastern part includes private land that was heavily logged in the past (fig. 7B, site 5). The area currently has a very open canopy and few stands with large trees remain. Relatively few owl locations occurred there. To the northwest and southwest were FS lands that had been selectively logged to varying degrees. Owls used this heterogeneous landscape extensively, avoiding the most open areas--sites 15, 16, and 17. Those sites formed a continuous, broad strip of land that has been logged heavily. Stands between the private land (site 5) and logged sites 15 and 17 contained suitable habitat with large trees. Cutting occurred there in small blocks, but the owls regularly used the area. Several owl locations were in high-elevation ($> 6,400$ feet) stands that were relatively open but dominated by large-diameter firs (site 18).

Star Butte

The Star Butte area (fig. 7E) has also been selectively logged to varying degrees using overstory removal and group-selection methods. Most of this area was extensively used by spotted owls, even though much of it was not classified as suitable spotted owl habitat. The only relatively undisturbed stand of old-growth fir in the Star Butte area was used for nesting by a pair of owls in 1990 (site 19). The more heavily logged areas (site 21) and the area around Star Butte (site 22) were both used infrequently by the owls. Site 21, on private land, was logged repeatedly in the 1930s, 1940s, 1950s, and 1970s. It was logged for culls in 1980, and it has been thinned in the past 3 years (Briggs pers. comm.). Star Butte (site 22) had small pockets of large trees but was unsuitable owl habitat. It contains a 6,700-foot peak with shrubfields along its upper slopes and small firs on its lower slopes. The area southeast of Star Butte had been heavily logged and appeared to be avoided by owls.

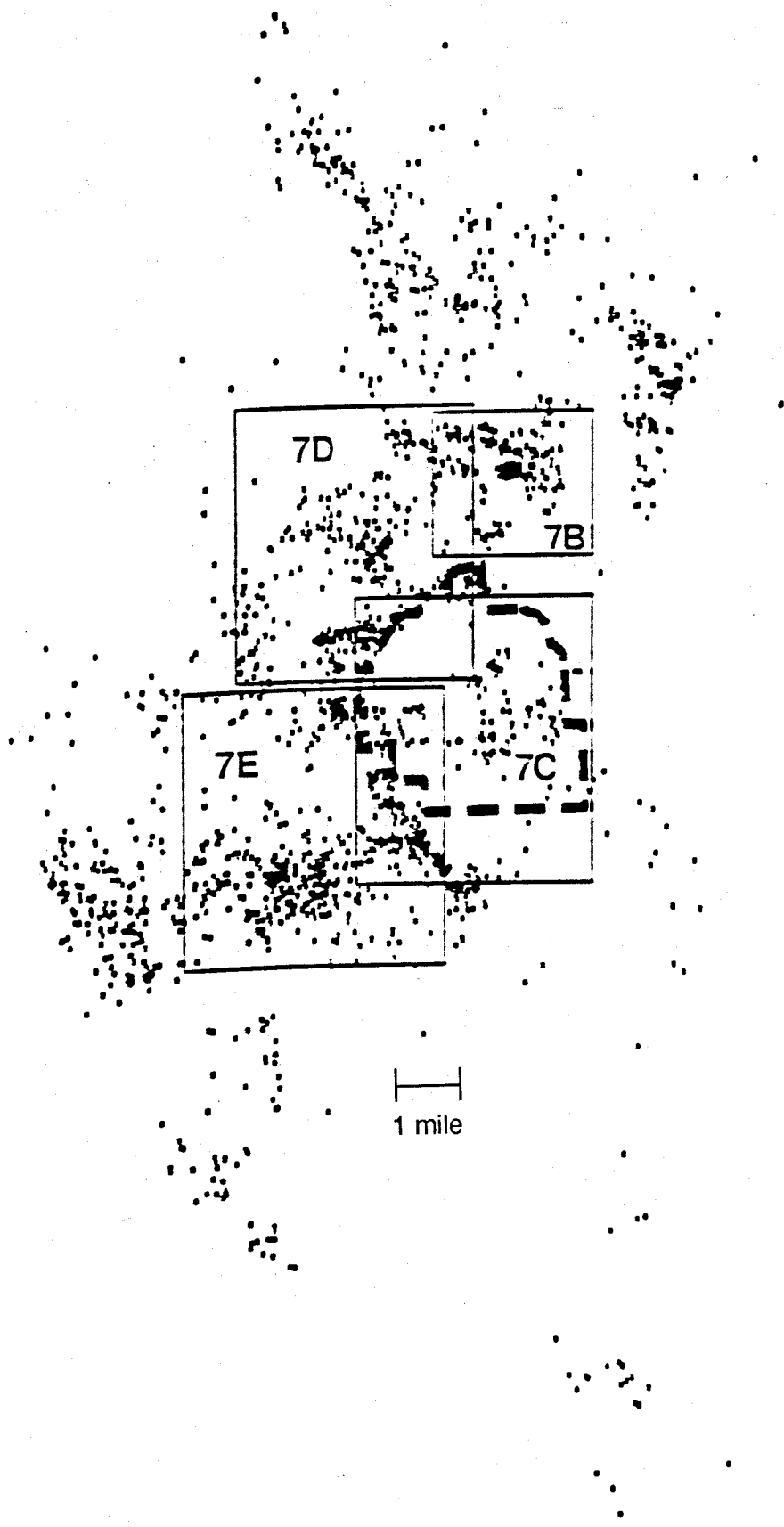


Figure 7A—Locations of study areas (7B, 7C, 7D, and 7E) on the Lassen National Forest. Radio-telemetry points from daytime roosting and nighttime foraging locations of California spotted owls are indicated. The boundary of Swain Mountain Experimental Forest is delineated as a dashed line. Study area numbers correspond to descriptive figures 7B-7E, similarly numbered.

1,000 feet



Suitable habitat

Size-class ≥ 21 inches in d.b.h.

Canopy closure ≥ 40 percent

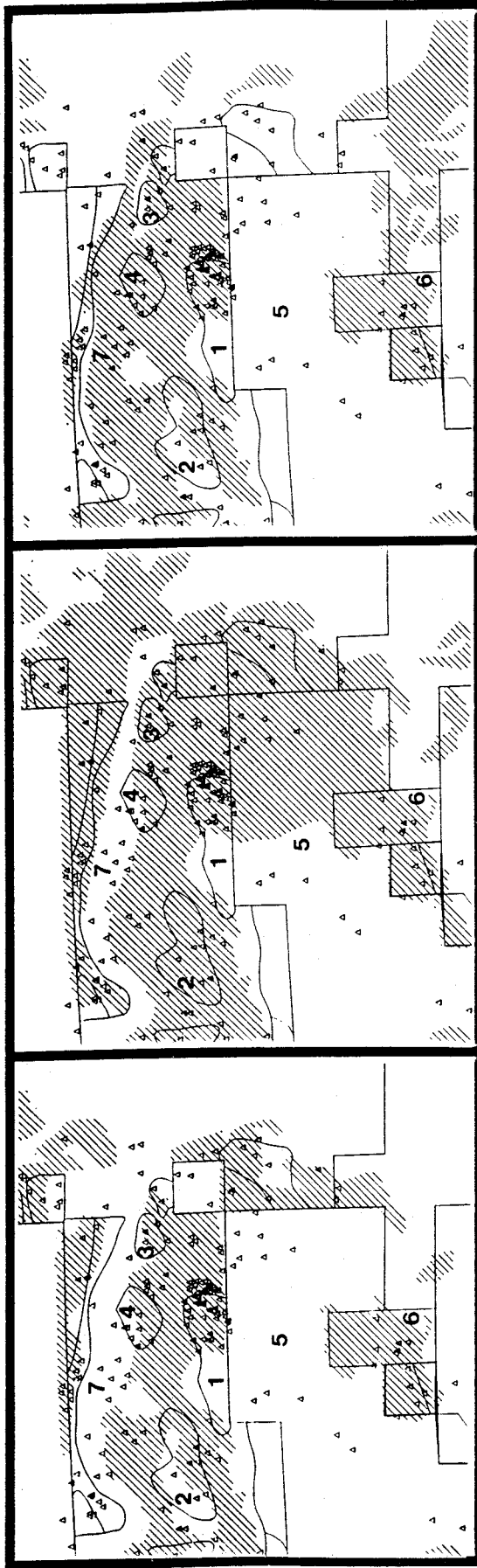


Figure 7B—Griffith Hill study area. Timber sale boundaries and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations (open triangles) are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥ 21 inches; and (3) stands in which canopy cover of dominant trees was ≥ 40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

1,000 feet



Canopy closure ≥ 40 percent

Size-class ≥ 21 inches in d.b.h.

Suitable habitat

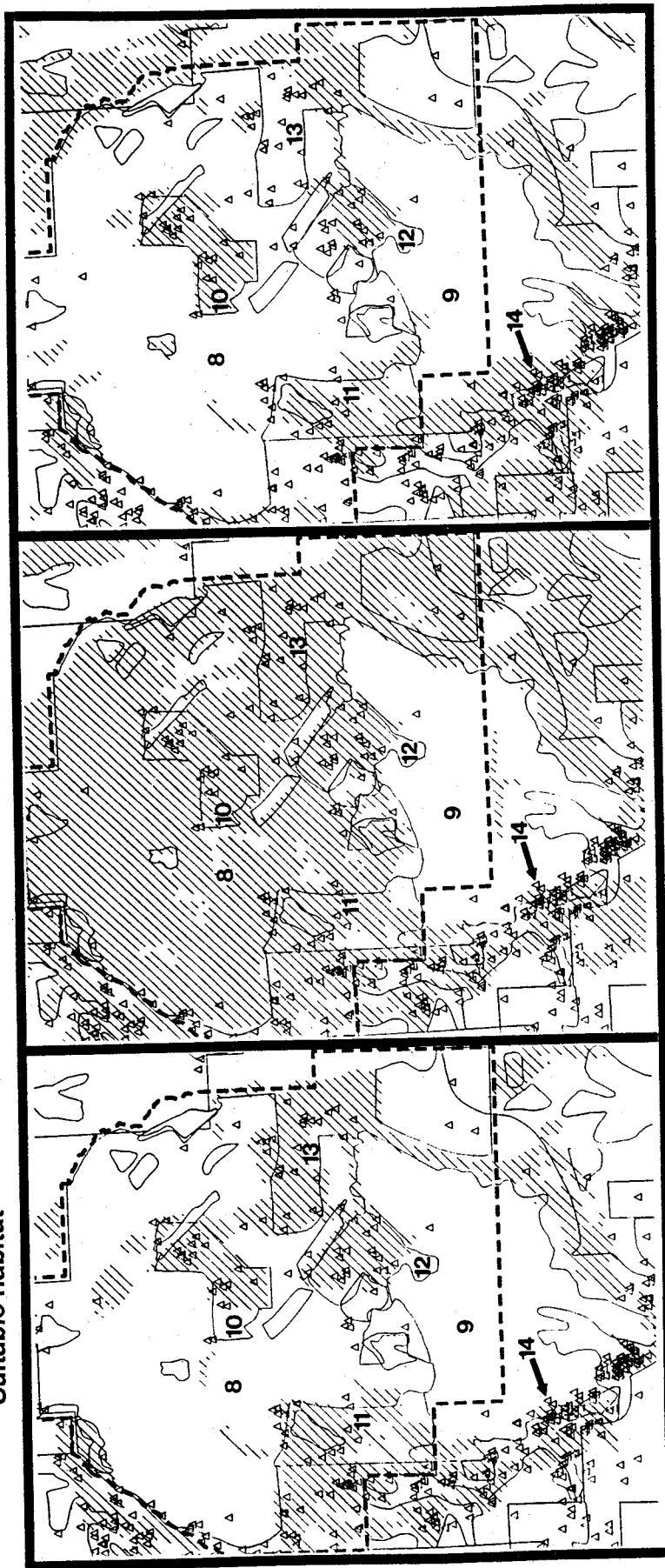


Figure 7C—Swain Mountain study area. The boundary of Swain Mountain Experimental Forest is indicated as a dashed line. Timber sale boundaries and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥ 21 inches; and (3) stands in which canopy cover of dominant trees was ≥ 40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

1,000 feet


Suitable habitat

Size-class ≥ 21 inches in d.b.h.

Canopy closure ≥ 40 percent

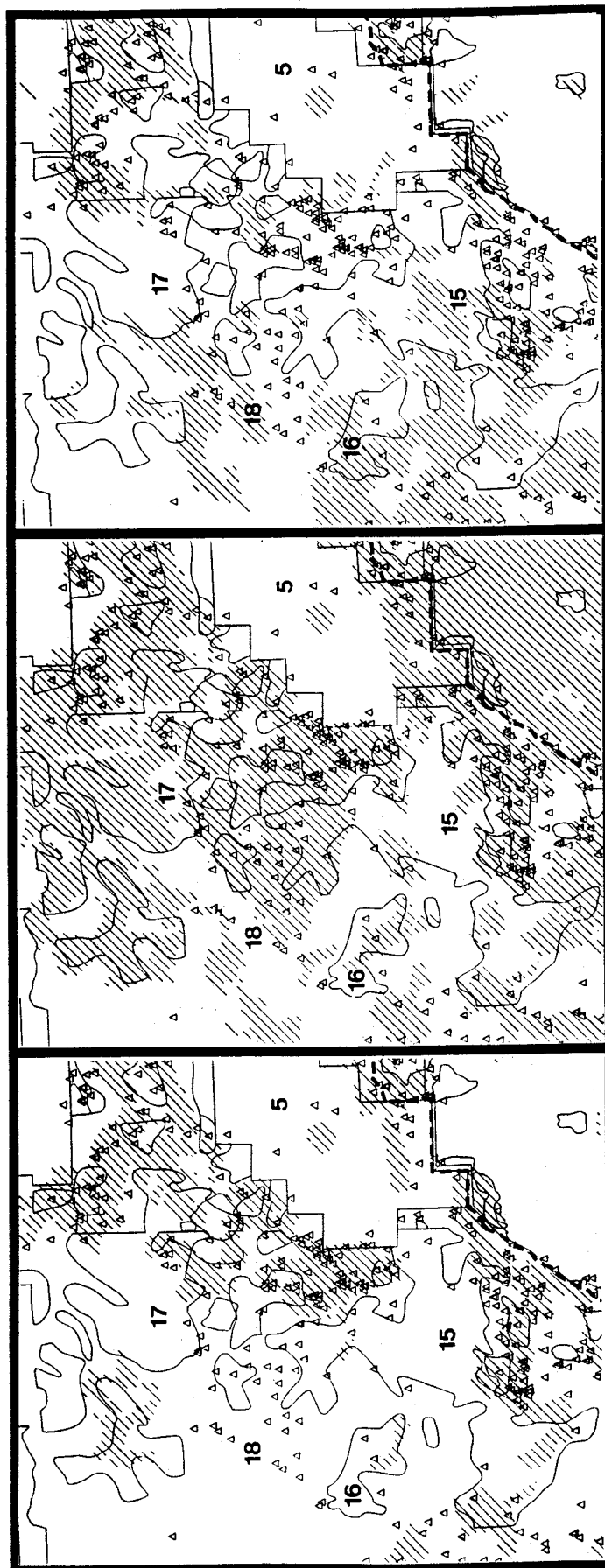


Figure 7D—Silver Lake study area. Timber sale boundaries and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥ 21 inches; and (3) stands in which canopy cover of dominant trees was ≥ 40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

1,000 feet



Canopy closure ≥ 40 percent

Size-class ≥ 21 inches in d.b.h.

Suitable habitat

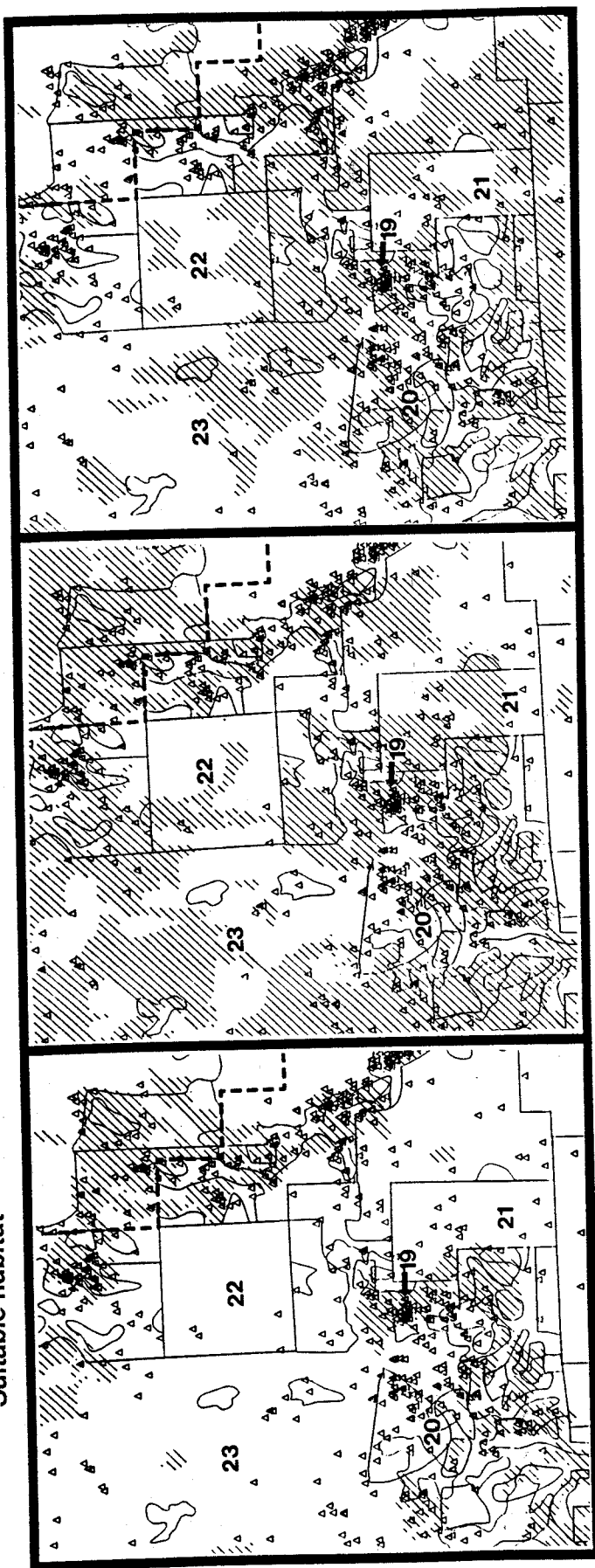


Figure 7E—Star Butte study area. Timber sale boundaries, and section boundaries between private and National Forest lands are delineated. California spotted owl radio-telemetry locations are overlaid onto three vegetation types indicated by diagonal lines: (1) suitable spotted owl habitat, based on current Forest Service (Region 5) definitions; (2) stands in which diameter size-class of dominant trees was ≥ 21 inches; and (3) stands in which canopy cover of dominant trees was ≥ 40 percent. Numbers on each study area map refer to specific logging sites and areas of owl use.

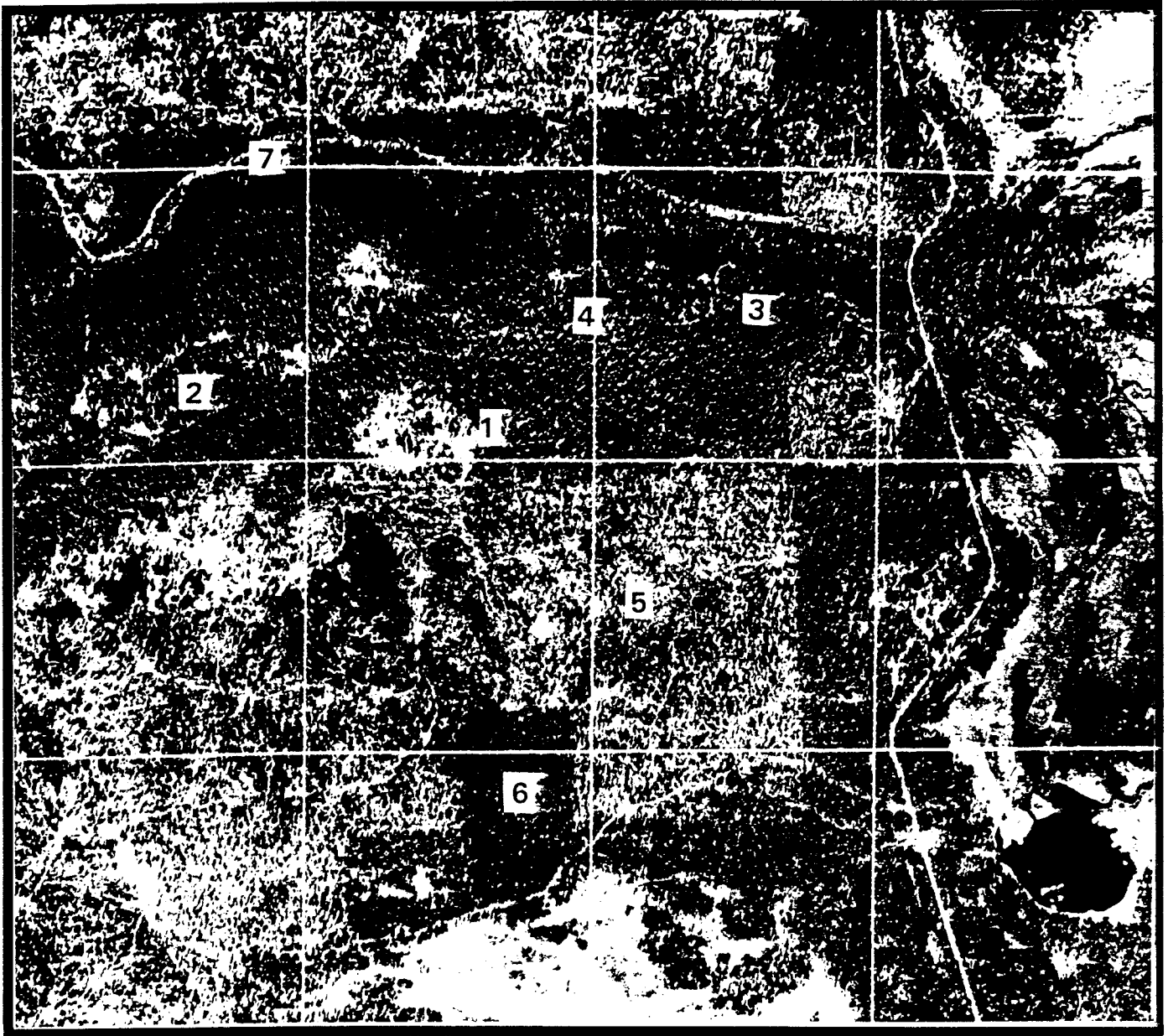


Figure 7F—Orthophotograph of Griffith Hill study area (fig. 7B). Cut units and areas used by California spotted owls are numbered in the sequence in which they are discussed in the results section of this chapter.

Site 14, near the southwest corner of SMEF, is an extension of an owl pair's linear home range referred to in the discussion of Swain Mountain. It has been selectively logged, but it was still suitable habitat and was heavily used by a pair of owls. Site 23, like site 18 (fig. 7D), is an uncut, high-elevation site that was used by owls even though it was unsuitable habitat. It also had areas of sparse, large trees where owl locations tended to occur, and pockets of high canopy cover were present.

Discussion

Decades of selective logging and wildfire on the Lassen NF have resulted in a complex and heterogeneous landscape. Unlike landscapes in the Pacific Northwest, where even-aged management has produced stands that differ primarily in stand age and size, uneven-aged management on the Lassen NF and throughout most of the Sierra Nevada has produced landscapes in which stands vary according to several factors. They vary in the number of times they have been entered for logging, the species of

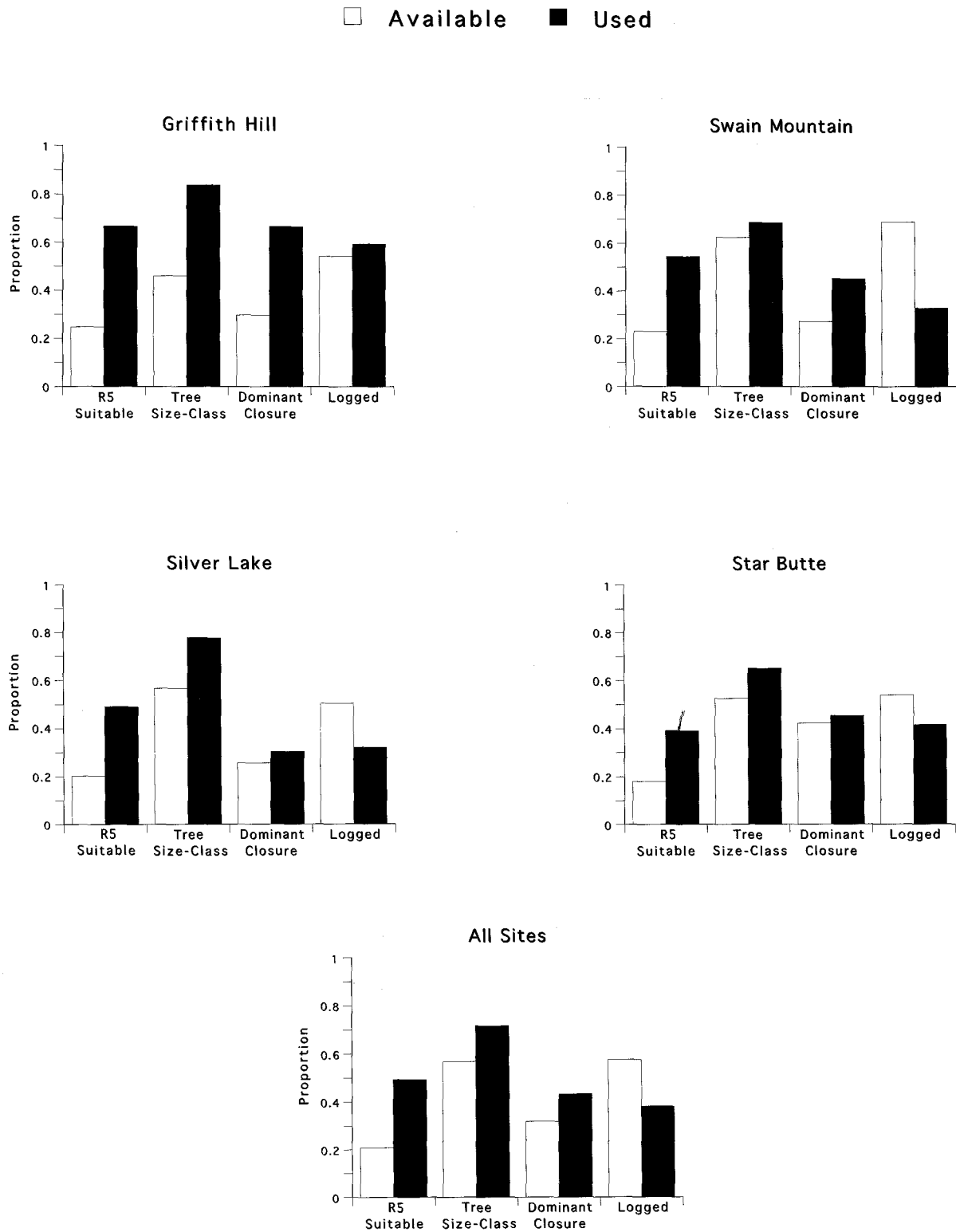


Figure 7G—Proportions of habitat types available in relation to the proportions used by radio-tagged California spotted owls at four study areas in the Lassen National Forest. Four categories of habitat were tested: (1) R5 suitable = Forest Service (Region 5) definition—medium or large sawtimber (≥ 21 inches in diameter at breast height), dominant canopy closure poor or higher, and total closure >69 percent; (2) structural size-class ≥ 21 inches in diameter at breast height; (3) dominant canopy closure ≥ 40 percent; and (4) logged stands.

trees taken, the diameter distribution of trees removed, and in the total volume logged. As a result, it is more difficult to compare stand structure and composition in landscapes dominated by uneven-aged management than is the case where even-aged management has occurred.

The areas we examined were predominantly logged by overstory removal and group-selection techniques in the late 1960s. It is apparent from these results that spotted owls tend to avoid altogether some forest conditions resulting from logging, but that they will use other types for foraging. Logged areas used by owls contained predominantly large trees (≥ 21 inches), and most of them had retained enough structure and canopy closure to be classified as suitable owl habitat (for example, site 14). Owl use of sites with large trees, dense canopy cover, and with suitable habitat (R5 definition), was greater than expected from the availability of such sites at all four study areas (fig. 7G). Some areas of low canopy cover were used where large trees were present and stands of high and low cover were interspersed (sites 2, 3, and 13). Pockets of large trees were also used when they were in areas of high canopy cover (sites 4, 20, and 21). It appears as if spotted owls will use logged sites if pockets of suitable habitat are interspersed among stands with low canopy or small trees. We cannot, however, quantify the total acreage or proportion of a site that must be in such stands before owls will use the site. These results indicate that logging by overstory removal and group selection can be compatible with spotted owl management in the red fir zone, if logged areas are small and interspersed with varying size classes and levels of canopy closure.

Use of logged sites was less than expected from the availability of such sites at three of four study areas (fig. 7G). Logged sites that were avoided by owls included large areas of sparsely distributed, big trees with low canopy cover (sites 5, 8, and 17), and large areas with dense canopy cover but small trees (sites 15 and 16). Most of the logged areas that were not used by owls had not returned to suitable owl habitat.

Spotted owls in the true fir zone used some naturally occurring sites classified as unsuitable owl habitat (see Chapter 6). These included areas at high elevations with large trees that were sparsely distributed (for example, Silver Lake site 18 and Star Butte site 23). In contrast, areas that were unsuitable habitat as a consequence of logging were often not used by owls. Examples include shelterwood-logged stands at SMEF (site 8) and private land that was heavily thinned north of Swain Mountain (site 5). Areas near site 18 and site 23 were used by owls even though they were far from the center of any concentration of owl locations. Yet, heavily logged areas (sites 5 and 8) were not used, even though they were adjacent to sites with concentrations of owl locations.

Unsuitable habitat in the Silver Lake area (site 18) was used by five individual owls during the nonbreeding period. These owls moved upslope into the higher elevations during the fall and remained there throughout the winter. Similarly, four owls

used the high-elevation, uncut stands in SMEF (sites 10, 11, 12, and 13) during the fall and winter. These owls did not fly across the shelterwood-logged stands during the summer, but they did so during the winter to access uncut, old-growth stands (sites 10, 11, and 12).

This is a first attempt to determine cut patterns that spotted owls will use. Strong patterns of aversion were apparent in the data, but preference patterns were not so clear. The silvicultural prescriptions described here did not adequately convey what was removed from cut units. All the units we examined had overstory removal and group selection, yet aerial photographs indicated that different volumes of timber were removed. Some units now have dense stands of large trees, while others have sparsely distributed, large trees. A micro-scale approach, with precise measurements of stand characteristics, may be needed to better understand what logging prescriptions are compatible with spotted owls. Attributes that may have been impacted by site preparation but were not considered in the analyses presented here, such as amounts of coarse woody debris, may also be important. Such attributes may influence prey abundance and distribution, and indirectly influence use of harvested areas by spotted owls (Chapter 4).

These results indicate that cutting patterns other than clearcuts, such as heavy overstory removal, can make sites unsuitable for spotted owl foraging in the red fir zone. We do not know how these patterns may extend into Sierran mixed-conifer forests. Home-range sizes of California spotted owls were larger in the high-elevation, red fir zone (Chapter 6), which was underused for nesting (Chapter 5) compared to mixed-conifer forests. High-elevation red fir may be marginal for California spotted owls, and owls living there may be more sensitive to logging than owls in mixed-conifer forests. These results may not be applicable to other forests types. A similar study with good quantitative information on what was logged, and how, needs to be done in mixed-conifer forests.

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Chapter 8

Estimates of Demographic Parameters and Rates of Population Change

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Detailed analyses of a species' life-history structure are essential to understand its population dynamics, provide insights to effective management, and also suggest directions for future research. In this chapter, we present analyses of available demographic data on the California spotted owl, using life-history and demographic information in an approach similar to that of Mertz (1971), Nichols et al. (1980), Noon and Biles (1990), and Thomas et al. (1990, appendix L). Our objectives were (1) to characterize the life-history structure of the California spotted owl, (2) to estimate values of the demographic parameters needed to compute rates of population change, (3) to test the sensitivity of the rate of population change to each of the demographic parameters, (4) to infer which parameters may be most influenced by management decisions, and (5) to suggest future research priorities, as indicated by the demographic analyses.

Methods

Demographic studies of spotted owls were conducted at five locations for periods ranging from 2 to 6 years—Lassen National Forest (NF), Eldorado NF, Sierra NF, Sequoia/Kings Canyon National Parks (NPs), and San Bernardino NF (table 8A). Density studies were conducted at four of those sites and at three additional sites (table 8B). The territorial behavior of spotted owls allows researchers to survey their populations by listening for and eliciting vocalizations. The usual procedure is to locate owls at night, then to follow up the next day with visual confirmation and, for demographic studies, to capture and uniquely

Table 8A—Summary information on the five demographic study areas.

Location	Approximate size (square miles)	Years of marking	Total individuals marked
Lassen National Forest	500	1990-91	130
Eldorado National Forest	136	1986-91	72
Sierra National Forest	160	1990-91	82
Sequoia/Kings Canyon National Parks	130	1988-91	62
San Bernardino National Forest	730	1987-91	367

Table 8B—Density estimates (owls per square mile) of spotted owls in California.

Study area	Size in square miles	Crude density ¹	Reference
Northern spotted owl			
Six Rivers National Forest	113	0.609	Franklin et al. 1990a
Simpson Timber Company	94	0.990	Diller 1989
California spotted owl			
Eldorado National Forest	137	0.259	Lutz 1992
Yosemite National Park	156	0.518	Roberts et al. 1988
Sierra National Forest	160	0.526	Verner et al. 1991
Sequoia/Kings Canyon National Parks	132	0.440	Roberts 1989; Verner et al. 1991
San Bernardino National Forest	207	0.347	LaHaye et al. in press
Mount San Jacinto	67	0.466	Gutiérrez and Pritchard 1990
Palomar Mountain	13	1.657	Gutiérrez and Pritchard 1990

¹Estimated number of owls/total study area. Much of the area included was not suitable habitat, and the proportion of unsuitable may have varied markedly from one study area to another.

color band each bird to allow individual identification in the field without recapture. The sex of adults was determined from their vocalizations, and reproductive status was determined by a protocol in which live mice were fed to the owls and they were then observed to determine whether they eventually carried a mouse to a nest site (Forsman 1983). Captured spotted owls can be placed into one of four age-classes: juvenile ($x < 1$), first-year subadults ($1 \leq x < 2$), second-year subadults ($2 \leq x < 3$), and adults ($x \geq 3$) based on plumage characteristics (Moen et al. 1991). Model structure, however, seldom has been based on all four age-classes because parameter estimates do not differ among classes, or because of insufficient data. Second-year subadults and adults are often collapsed into a single age-class (see below).

Parameter Estimation

Estimates of density (owls per square mile) assumed complete enumeration of all owls within a defined area. Usually when owls were counted, they were also color-banded to minimize the likelihood of double counting. Because territorial owls tended to vocalize regularly and to be spatially restricted within their home ranges, they were more likely to be detected than

nonterritorial owls (floaters). To the extent that many floaters occurred in an area, true density may have been underestimated.

Ideally, we would use precise and accurate estimates of three classes of parameters (s_x , b_x , and a) to compute the finite population growth rate, or λ :

1. s_x = probability of survival from age x to $x + 1$.

Previous demographic analyses of spotted owls generally assumed that s differed for at least three age-classes—juveniles (s_0), first-year subadults (s_1), and adults (s). The adult class, defined on the basis of age at first reproduction ($a = 2$ years), thus included second year subadults. The juvenile stage ends at the age of 1 year for spotted owls. In our analyses we did not partition juvenile survival rate into preand postdispersal probabilities, as done by Lande (1988). The subadult stage for the northern spotted owl covers the second year of life (age 1 to age 2) and is assumed to be an age interval in which the birds typically do not breed. The adult stage was thus anything older than 2 years (Noon and Biles 1990). Ideally, survival rates of these stages can be computed directly for each population modeled, using data from that population. Using program JOLLY (Pollock et al. 1990), we could estimate juvenile survival rate (s_0) only for the San Bernardino study area, because data were insufficient for the Eldorado and Sequoia study areas. Consequently, the San Bernardino value for s_0 was used as an approximation for the other two locations. It is similar to estimates of s_0 from several studies of northern spotted owls (Franklin 1992; USDI, FWS 1992), and λ is not especially sensitive to variations in s_0 . The true value of s_0 for these sites, however, is unknown.

Data were also insufficient to compute separate estimates of s_1 and s for the Eldorado and Sequoia/Kings Canyon study areas, and these two values were statistically indistinguishable for the San Bernardino study area. Therefore, in demographic analyses reported here, we used survival estimates for only two age-classes— s_0 (juvenile) and s ("nonjuvenile," combining subadult and adult age-classes). The probability of survival to age x was thus computed as $l_x = s_0 s^{x-1}$ (by definition $l_0 = 1.0$) (table 8C).

Table 8C—Spotted owl life history (age at first reproduction is 2 years).

x^1	l_x^2	b_x^3	$l_x b_x^4$
0	1.0	0	0
1	s_0	0	0
2	$s_0 s_1$	b	$s_0 s_1 b$
3	$s_0 s_1 s$	b	$s_0 s_1 s b$
4	$s_0 s_1 s^2$	b	$s_0 s_1 s^2 b$
.	.	.	.
.	.	.	.
.	.	.	.
x	$s_0 s_1 s^{x-2}$	b	$s_0 s_1 s^{x-2} b$

¹ x denotes age in years.

² l_x denotes the probability that an individual aged 0 (a newly hatched bird) will survive to enter age class x .

³ b_x denotes the expected number of female fledglings produced by a surviving female aged x .

⁴ $l_x b_x$ denotes the net maternity function. At this time for the California spotted owl, $s_1 = s$.

2. b = fecundity, the expected number of female fledglings produced per female per year; b_x is the fecundity of a female of age x .

Fecundity values were calculated by halving the number of young fledged per territorial female, assuming an even sex ratio among fledglings. Because ages of females breeding, or attempting to breed, were seldom known, we assumed a constant reproductive rate for females of all ages: $b_x = b$ ($x \geq 2$ years).

3. a = age at first reproduction.

Apparently female spotted owls rarely breed when only 1 year old; most do not begin until at least 2 years old (Franklin 1992). Therefore, we used $a = 2$ years in demographic analyses reported here.

Estimates of age-specific survival rates from study areas with ≥ 4 years of data came from capture histories of marked birds using Program JOLLY (Pollock et al. 1990). Because some studies suggest that reproduction by spotted owls may be affected by radio transmitters attached with back-pack harnesses (Paton et al. 1991, Foster et al. 1992), estimates of survival and reproductive rates used in this demographic analysis were based solely on banded birds. To increase the precision of the estimates, we estimated the minimum number of parameters that adequately fit the data. When sufficient data were available, we tested for differences between adjacent age-classes to justify pooling of capture histories. In most cases, however, data were insufficient, so we pooled values for all individuals at least 1 year old to compute a survival rate for adults. Because the Lassen and Sierra studies have been underway for only 2 years, their data were insufficient for statistically reliable estimates of survival rates. For these sites, we simply estimated survival rates empirically, pooling data from all males and females at least 1 year old.

Analysis

Standard Lotka-Leslie methods (Leslie 1945, 1948; Lotka 1956) were applied to the estimates of vital rates (age-specific birth and death rates) to make inferences about rates of population change. In addition to assumptions identified above, we assumed (1) that reproduction was characteristic of a "birth-pulse" population—one with a single, well-defined, annual breeding period (Caughley 1977, p. 6), (2) a stable age (stage) distribution, and (3) no density dependence—a change in population density did not affect the values of the vital rates. This assumption was probably valid within the limits of the population densities modeled here. Preadult survival rate (l_2) was the probability of survival from fledging (age when leaving the nest) to age 2 and was given by the product of s_0 and s .

Estimates of all parameters needed for a completely age-specific Leslie matrix (Leslie 1945, 1948) were not available for any of the populations modeled. Often such data are limited for long-lived species, and estimates of all the age-specific parameters are impossible to attain or have large sampling variances because of small sample sizes. Repeated multiplication of imprecise estimates in fully age-specific models is likely to lead to uncontrolled error propagation (Dobson and Lyles 1989). The

Lefkovich stage-projection matrix model (Lefkovich 1965) is a useful approximation to an age-structured model. The dynamics of the two models are usually similar, but the Lefkovich model is more tractable (Boyce 1987). A stage is simply a category (age-class) within which birth and death rates are assumed to be constant. Consequently, estimating the population dynamics of spotted owls with a stage matrix would yield misleading conclusions only if the birds manifest an age-related decline in reproductive rate (senescence) before about 15 years old (Noon and Biles 1990). Given the current high estimates of s , early senescence seemed unlikely.

Our application here of the Lefkovich model uses only two stages juveniles (J) and nonjuveniles (NJ), as defined above. Time was expressed as an interbreeding interval of 1 year, and age at first reproduction was set at 2 years. Given that populations were based on census estimates corresponding to a period shortly after the breeding period, the Lefkovich matrix had the following structure (details in Noon and Sauer 1992):

$$\begin{pmatrix} J_{t+1} \\ NJ_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & sb \\ s_0 & s \end{pmatrix} \begin{pmatrix} J_t \\ NJ_t \end{pmatrix}$$

The location of s along the diagonal of the matrix reflects our assumption of constant adult survival and no senescence. The possibility of very old owls in the population had little effect on our estimate of λ assuming that adult survival was estimated, irrespective of adult age, from an unbiased sample of all adults in the population (Boyce 1987). We believe this assumption was valid for all populations modeled here.

The basic characteristic equation of the matrix is given by

$$\lambda^2 - s\lambda - s_0sb = 0. \quad (1)$$

The dominant, real-valued solution (λ_1) is an estimate of the annual, finite rate of change of the population. Vital rates suggest an increasing population if $\lambda > 1.0$, a stable population if $\lambda = 1.0$, and a declining population if $\lambda < 1.0$. We urge caution in using the computed estimates of λ to forecast future population sizes or to infer sizes of historical populations. Lambda estimated how the population was changing only during the period of study. Using the estimate of λ to project future population size would assume, unrealistically, that current estimates of vital rates are constant over time.

Hypothesis Tests of Lambda

We had estimates of fecundity and adult survival from three study areas and, in addition, an estimate of juvenile survival from one study. Based on these parameter estimates, and assuming s_0 to be equal at all locations, we computed λ from the Eldorado NF and Sequoia/Kings Canyon NPs in the Sierra Nevada Province, and from the San Bernardino NF in the Southern California Province. The sensitivities (partial derivatives) of λ with respect to individual life-history characteristics indicate which parameters most affect variation in population growth rate (Lande 1988, Noon and Biles 1990). In addition, sensitivi-

ties are needed to estimate the standard error of λ and to perform hypothesis tests. Sensitivities were computed by implicit differentiation of the characteristic equation (Goodman 1971, Lande 1988). Sensitivities for the two-stage Lefkovich model are:

$$\begin{aligned} s_0: \partial\lambda/\partial s_0 &= sb/(2\lambda - s); \\ s: \partial\lambda/\partial s &= (\lambda + s_0b)/(2\lambda - s); \text{ and} \\ b: \partial\lambda/\partial b &= s_0s/(2\lambda - s). \end{aligned}$$

For all areas, change in population growth rate was most sensitive to variation in adult survival rate. It was much less sensitive to variation in first-year survival rate and fecundity; sensitivity to these two parameters was about equal.

Sensitivities of λ appear in the formula that approximates the sampling variance of the estimate of λ (Lande 1988, p. 602):

$$\sigma^2_{\lambda} = \sum (\partial\lambda/\partial p)^2 \sigma^2_p \quad (2)$$

where p represents each of the parameters and σ^2_p their sampling variance. The variances of juvenile and nonjuvenile rates were estimated according to the methods of Jolly (1965) and Seber (1965). Variance of annual fecundity was based on variance among females across the years of study, divided by the appropriate sample size. For the power analyses (see below), we assumed the survival probability to have a binomial sampling distribution.

Equation (2) is based only on sampling variance, but the data include both sampling and temporal variance. Also, equation (2) neglects possible covariances among the demographic parameters and fails to account for between-year changes in vital rates. Year-to-year changes, estimated by factoring out the temporal component of variation from the total variance estimates of the vital rates and λ cannot yet be estimated for the California data.

Components of the sampling variance of λ were computed by using equation (2), based on the sensitivities and estimates of the vital rates. The standard error of λ , computed as the square root of the variance, was used to construct a confidence interval around λ . For example, the 95 percent confidence interval on λ was computed as: $\lambda \pm 1.96 \sigma_{\lambda}$. An estimate of λ and its standard error also allowed tests of hypotheses. Of most interest, relative to concern for the species' persistence, was whether λ was significantly < 1.0 . We tested the null hypothesis: $H_0: \lambda \geq 1$, versus the alternative hypothesis: $H_A: \lambda < 1$. The appropriate test statistics followed a Z-distribution, given by: $Z = |(\lambda - 1)/\sigma_{\lambda}|$. Tests were one-tailed with a specified probability of a type-I error = 0.05 (only a 5 percent chance of concluding a decline when none actually occurred).

Power of the Tests on Lambda

When a test fails to reject the null hypothesis (H_0), it is important to estimate the power of the test, which is the probability that H_0 will be rejected when a particular alternative hypothesis (H_A) is true. Failure to reject a false H_0 (that is, the popula-

tion is in decline) is known to statisticians as a type-II error. To estimate the power of the test when H_0 was not rejected, we used a method outlined by Taylor and Gerrodette (in press). The method involves estimating two sampling distributions, one based on a specified value of λ for H_A , the other on the value of λ for H_0 ($\lambda = 1.0$). Under H_A we specified a $\lambda = 0.95$, that is, a 5 percent annual rate of population decline. This rate of decline would result in a loss of >40 percent of the population over a decade. If the two distributions are completely disjoint, the power of the test is 1.0. If the two distributions are coincident, the power is 0. Power increases as the difference between the specified value of λ and the hypothesized λ value (for example, $\lambda = 1.0$) increases, or as the variance of the distributions decreases. The probability of a type-II error (β) is estimated as a function of the overlap between these two distributions. The power of the test is then $1 - \beta$. To estimate power, we generated simulated distributions of λ under each hypothesis (H_A and H_0) based on 16,000 randomizations.

Results

Density Estimates

Estimates of crude density (number of owls/total acreage of study area) were available from seven areas within the range of the California spotted owl, four in the Sierra Nevada Province

and three in the Southern California Province (table 8B). Densities varied from a high of 1.657 owls per square mile on Palomar Mountain to a low of 0.259 owls per square mile on the Eldorado NF. Overall, estimates of crude density for the California spotted owl tended to be slightly lower than those for the northern spotted owl (table 8B; see also Bart and Forsman in press).

Comparison of Demographic Study Areas

Demographic studies were done at five locations widely spaced over the range of the California spotted owl. Two studies have collected data for only 2 years, and the longest study has been in place for only 6 years (table 8D). All studies, however, are planned to continue for 3-5 more years. Some significant highlights from a comparison of the demographic attributes in the five areas (table 8D) include extensive among- and within-site variation in the proportion of nesting pairs and mean fecundity, and pronounced among-site variation in pair turnover rates (proportion of banded adults and subadults that are replaced on their territory by another bird) and nonjuvenile survival rates. Components that contributed to the observed variance in annual fecundity at a given site arose from variation in both the proportion of females nesting and in their productivity. Among-site variation in survival rates of nonjuvenile owls was particularly relevant, as even small changes in survivorship of adult females greatly affect rates of population change (Noon and Biles 1990).

Table 8D—Summary of demographic attributes of California spotted owls.

Attributes	Lassen National Forest	Eldorado National Forest	Sierra National Forest	San Bernardino National Forest	Sequoia/Kings Canyon National Parks
Years of banding	2	6	2	5	4
Mean proportion of pairs nesting ¹	0.52	0.31	0.65	0.59	0.51
Range of proportion of pairs nesting	0.38-0.70	0.0-1.0	0.63-0.67	0.50-0.76	0.18-0.80
Mean total fecundity ^{1,2}	0.48	0.94	1.02	0.59	0.53
Range of total fecundity ^{1,2}	0.36-0.64	0.37-1.50	0.75-1.22	0.35-0.80	0.08-1.50
Mean subadult turnover rate	0.57	0.14 ³	0.75	0.28 ³	--
Mean adult turnover rate	0.21	0.14 ³	0.19	0.28 ³	0.24
Mean empirical survival rate of subadult females	0.33	0.73	0.50	0.72 ^{2,3}	0.80 ^{2,3}
Mean empirical survival rate of adult females	0.84	0.73	0.74	0.72 ^{2,3}	0.80 ^{2,3}
Mean nonjuvenile survival	*	0.83 ^{2,3}	*	0.75 ^{2,3}	0.89 ^{2,3}

¹ Weighted by yearly sample size.

² Males and females combined.

³ Subadult and adult age-classes combined.

* Inadequate sample.

Hypothesis Tests on Lambda (λ)

Eldorado National Forest

This study has been underway for 6 years, with estimates of nonjuvenile survival rates based on capture histories of 72 birds >1 year old, and fecundity estimates based on reproductive performances of 66 territorial females (table 8E). The estimate of λ (equation 1) was 0.947, suggesting about a 5 percent annual rate of population decline during the period of study (1986-91). This value was not significantly <1.0 ($\alpha = 0.05$, $P = 0.1271$), so the statistical test did not reject the null hypothesis that the population is not declining ($H_0: \lambda \geq 1.0$). The test, however, had a power of only 0.30, setting the probability of a type-II error at about 0.70. The low power of the test was a result of a relatively small number of marked birds, and the large standard errors of parameter estimates (table 8E).

Sequoia/Kings Canyon National Parks

This study has been underway for 4 years, with estimates of nonjuvenile survival rates based on capture histories of 45 birds >1 year old, and fecundity estimates from the reproductive performances of 45 territorial females (table 8F). The estimate of λ was 0.969, suggesting about a 3 percent annual rate of population decline during the period of study (1988-91). As in the Eldorado study, the statistical test ($\alpha = 0.05$, $P = 0.2709$) failed to reject the null hypothesis ($H_0: \lambda \geq 1.0$). In this case, the test had a power of only 0.30, with an 70 percent probability of failing to detect a real decline of this magnitude. The very low power of the test was a consequence of the small number of marked birds and, to a lesser extent, the standard errors of parameter estimates (table 8F).

San Bernardino National Forest

This study, underway for 5 years, was unique among demographic studies of spotted owls in sampling, almost in its entirety, an insular population (LaHaye et al. 1992). It provides an estimate of juvenile survival rate of 0.296, based on capture histories of 130 owls banded shortly after fledging (table 8G). The estimate of nonjuvenile survival rate is based on capture histories of 184 birds > 1 year old, and the fecundity estimate comes from reproductive histories of 328 territorial females. Lambda was estimated at 0.827, suggesting about a 17 percent annual rate of population decline during the period of study (1987-91). The statistical test ($\alpha = 0.05$, $P \leq 0.0001$) strongly rejected the null hypothesis ($H_0: \lambda \geq 1.0$) of a nondeclining population.

Table 8E--Estimates of the annual finite rate of population change (λ) for the California spotted owl in the Eldorado National Forest, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimate	Sample size	Standard error	P
Juvenile survival (s_0) ¹	0.296	130	0.055	--
Nonjuvenile survival (s) ²	0.826	72	0.039	--
Fecundity (b) ³	0.470	66	0.054	--
Population change (λ)	0.947	--	0.046	0.1271

¹ LaHaye (pers. comm.).

² Combined estimate for males and females, adults and subadults.

³ Number of female young per territorial female.

Table 8F--Estimates of the annual finite rate of population change (λ) for the California spotted owl in Sequoia/Kings Canyon National Parks, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimate	Sample size	Standard error	P
Juvenile survival (s_0) ¹	0.296	130	0.055	--
Nonjuvenile survival (s) ²	0.895	45	0.047	--
Fecundity (b) ³	0.267	45	0.059	--
Population change (λ)	0.969	--	0.051	0.2709

¹ LaHaye (pers. comm.).

² Combined estimate for males and females, adults and subadults.

³ Number of female young per territorial female.

Table 8G--Estimates of the annual finite rate of population change (λ) for the California spotted owl in the San Bernardino National Forest, with test statistics and P value for the test of the null hypothesis that $\lambda \geq 1.0$ vs. $\lambda < 1.0$.

Parameter	Estimate	Sample size	Standard error	P
Juvenile survival (s_0)	0.296	130	0.055	--
Nonjuvenile survival (s) ¹	0.747	184	0.024	--
Fecundity (b) ²	0.297	328	0.087	--
Population change (λ)	0.827	--	0.035	0.0000

¹ Combined estimate for males and females, adults and subadults.

² Number of female young per territorial female.

Discussion

Owl Densities

Because we were able to estimate only crude density for most study areas at this time, interpretations of results are tentative. This is true because crude density does not adjust for the amount of unsuitable habitat in a study area. If one area has a higher proportion of unsuitable habitat than another, but the amounts are unknown, estimates of crude density for the two areas are not comparable. With this caution in mind, density estimates at least suggest some questions that need to be resolved.

The Eldorado study area is mostly forested. The apparent low density of spotted owls there may result from the fact that much of the area is in classic, alternate-section, checkerboard ownership between NF and private timberlands that have been intensively managed for timber production. For example, Bias and Gutiérrez (1992) reported that most roost sites and all nest sites in the Eldorado study area were on public lands. The private lands have not been generally clearcut, however, so owls probably forage in much of the private ownership.

Various hypotheses can be advanced to account for the apparent high density of owls on Palomar Mountain: (1) Crude density may have been overestimated. We know from other studies, for example, that density estimates of spotted owls are affected by the size of the study area, with positively biased estimates in study areas <40 square miles (Franklin et al. 1990b). Based on a regression equation and a proportional adjustment from the asymptotic density in Franklin et al. (1990b, fig. 4), the density estimate for Palomar Mountain should be adjusted downward to about 1.1 owls per square mile. But this is still higher than estimates for all other areas. (2) An extensive fire destroyed much owl habitat on Palomar Mountain in 1987, 1 year before the density survey (Gutiérrez and Pritchard 1990). Several previously occupied owl sites were lost in the fire and an unknown number of additional birds may have been displaced. As a result, densities may have increased temporarily from packing by displaced birds into remaining habitat. (3) Home-range sizes of spotted owls in much of southern California are considerably smaller than they are in conifer forests of the Sierra Nevada or in the San Bernardino Mountains (Chapter 6). Over much of the owls' distribution in southern California, however, suitable habitat tends to be concentrated in small, relatively isolated ravines and canyons; most of the intervening habitat is unsuitable. The crude density of owls there could be similar to that where home ranges are larger but where suitable habitat is more continuous. This is the case, for example, between the foothill woodland and conifer forest segments of the Sierra NF study area (Verner et al. 1991). If suitable habitat is more continuously distributed on Palomar Mountain, but owl home ranges there are relatively small (for example, because the owls specialize on woodrats as a prey source), the observed high

density at Palomar could be a real difference from all other density studies of the California spotted owl.

Sources of Bias in Estimates of Lambda

Juvenile Survival

"Estimates of juvenile survival rate can be biased low if some juveniles leave the study area, survive a full year, and never return. To the extent that these three events occur, juvenile survival rate is underestimated and the estimates of λ are too low" (USDI, FWS 1992, appendix C). If emigrating juveniles do not survive their first year, or if they survive but are subsequently detected, then no bias occurs. To provide a statistically reliable estimate, we estimated s_0 using the maximum-likelihood procedure from Program JOLLY (Pollock et al. 1990) for the San Bernardino study (LaHaye pers. comm.). We believe the estimate from that study is reliable. First, it was based on a sample of 130 owls banded as fledglings. Second, the study area covers almost the entire San Bernardino Mountain Range, and the population was largely isolated from other owl populations (LaHaye et al., 1992). Consequently, the area covered by dispersing juveniles was more restricted and the entire area was surveyed each year. These factors greatly increased the likelihood of reobserving banded juveniles. Finally, the estimate of s_0 (0.296) is nearly the same as that for the five northern spotted owl study areas ($s_0 = 0.311$) (USDI, FWS 1992) based on longer-term studies.

Nonjuvenile Survival

As for estimates of juvenile survival, nonjuvenile survival rate would be underestimated if many banded birds permanently left a study area and survived at least 1 year. Thomas et al. (1990, appendix L) investigated this potential bias by computing the number of emigrations per bird-year in studies of radio-tagged, adult spotted owls. A bird-year was defined as one adult bird tracked for one calendar year. From radio-tracking studies near Roseburg, Oregon, only one permanent emigration occurred in >100 bird-years. Similarly, in northwestern California, one permanent emigration occurred in 60 bird-years. These findings suggest that estimates of adult survival rate for the northern spotted owl were essentially unaffected by permanent emigration from study areas. Although we lack comparable data from the California spotted owl, we have no reason to believe that permanent emigration by adults would be more common for that subspecies.

Senescence

The effects of age-related decline in reproductive potential of spotted owls have been explored by Noon and Biles (1990). Failure to account for senescent declines could result in a significant overestimate of λ . Conversely, incorporating senescence when it does not occur can result in significant underestimates of λ . We do not know the life span of spotted owls or whether fecundity remains constant through life. The high, observed

estimates of s would not likely arise, however, if spotted owls lived <15 years. If reproductive senescence occurs at earlier ages, the decline in λ would be increasingly pronounced.

Researchers often assume that birds do not experience senescent declines in fecundity and survival rates (Deevey 1947). An estimate of mean generation length (Caughley 1977, p. 124) without reproductive senescence and assuming $s = 0.92$, however, suggests the unlikely average age of mothers at the birth-pulse = 53 years. Given the magnitude of this estimate, we believe that senescent declines must occur in reproduction and/or adult survival rate. Invoking reproductive senescence at ages of 16 or 26 years yields more reasonable estimates of generation length ($\cong 8$ and $\cong 12$ years, respectively), but it lowers the estimates of λ . Reproductive senescence is not likely to occur much before 16 years; rather, we would expect strong natural selection against the evolution of early senescence in a species with life-history characteristics like the spotted owl's.

Stable Stage Distribution

Calculation of λ from equation (1) assumes a stable stage distribution. If the vital rates are constant, the convergence to a stable distribution is asymptotically exponential (Caswell 1989, p. 70). If the vital rates vary stochastically, or are time-dependent, then the assumption of a stable stage distribution is invalid. At this time we have insufficient data to estimate the degree of stochasticity in the vital rates for the spotted owl, or to determine if the year-to-year differences among projection matrices represent time-dependency or simply sampling variation. In the absence of this information, we assumed mean values for the vital rates. We can, however, examine the likelihood of introducing a bias into the estimate of λ by assuming constant vital rates, and thus a stable stage distribution.

If the growth of a given population is time-dependent, then the growth of that population is described by the product of a sequence of projection matrices. In the special case of independent matrices (that is, independent environments), population growth rate is equivalent to the dominant eigenvalue (λ) of the projection matrix based on the mean values of the vital rates (Tuljapurkar 1982). Unfortunately, under stochastic conditions, the growth rate of the average population may be a misleading indicator of population stability. This occurs because the distribution of population sizes from stochastic projection matrices is approximately lognormal (Tuljapurkar and Orzack 1980). A property of lognormal distributions is that the modal or most likely population size will always be smaller than that based on mean values of the vital rates (Gerrodette et al. 1985). Under conditions of stochasticity, the realized trajectory of any single population is simply one of an infinite number of possible outcomes. Thus, the actual growth rate of any single population with stochastic vital rates is always less than or equal to the growth rate estimated from mean values of the projection matrix (Cohen et al. 1983).

The likely consequence of our assumption of a time-invariant, mean projection matrix, therefore, was to overestimate the growth rate (λ) experienced by any given population, unless the environmental variability was negligible. In general, as the environmental variability becomes small, the average growth rate of

a stochastic population approaches (from below) that described by the dominant eigenvalue of the mean projection matrix (Caswell 1989, p. 222). There are some exceptions to this general rule. For example, in nonstochastic, periodic environments, Tuljapurkar (1989) found that variation can increase population growth rate if the period of the environmental oscillation is roughly equivalent to the generation length of the organism being modeled. We emphasize that this is an unlikely outcome for any climatically induced variation in the vital rates of a given species (see, for example, figs. 8A and 8B). The general observation that, in stochastic environments, a probability of extinction exists even when the mean growth rate, λ , is >1.0 (Lande and Orzack 1988) should temper any overly optimistic interpretation of λ values.

Tests on Lambda

Although the null hypothesis of a stable population was not rejected for either the Eldorado or the Sequoia/Kings Canyon study area, we could not correctly conclude that these populations were stable during the periods of study. The power of our statistical tests was disturbingly low for both areas, and there was a high likelihood of failing to detect real annual declines of 5 percent or less. The greater uncertainty that accompanied a smaller sample of banded birds and a shorter time series of capture histories is clearly illustrated by comparison with the northern spotted owl. The estimate of λ for the northern spotted owl on lands managed by the Bureau of Land Management near Roseburg, Oregon, was nearly identical to that for the Eldorado study area ($\lambda = 0.941$ vs 0.947 , respectively). In the Roseburg study, however, the null hypothesis of a stable population was strongly rejected (probability of a type-I error <0.0005 -USDI, FWS 1992, appendix C). In contrast to the Eldorado study, the Roseburg study was based on a larger sample of birds (589 vs 72) and a longer time series (7 years vs 6 years).

Given the high likelihood of accepting false null hypotheses of stable populations in the Sierra Nevada studies, the correct inference to draw from the statistical tests is that, at this time, we are uncertain about true trends of the Eldorado and Sequoia/Kings Canyon populations during the periods of study.

If the California spotted owl has experienced gradual declines in habitat quality in the Sierra Nevada, these effects may be subtle and, therefore, more difficult to detect than those experienced by the northern spotted owl. With the exception of the mid-1980s, very little clearcut logging was practiced in the Sierra Nevada. Even the heavy cutting that occurred on private timberlands near mills and railroad lines usually left some large trees standing that could eventually serve as nest sites in regenerating stands. In contrast, within the range of the northern spotted owl, most logging has been by clearcutting, and most of the decline in suitable owl habitat has been compressed into the interval since about 1950 (Murphy and Noon 1992). As a result, the landscape pattern for northern spotted owls is coarse-grained, with clear distinctions between suitable and unsuitable habitat. Selective logging of the largest trees from the most productive sites in the Sierra Nevada has resulted in significant changes in diameter distributions and produced a more fine-grained landscape pattern for the California spotted owl (Chapter 11).

The effects of changes in forest structure and landscape pattern on owl demographics are unknown. If changes in habitat quality accompany selective logging methods, however, it seems obvious that they would produce less pronounced declines in the vital rates than clearcut logging. As a result, only very long-term studies involving a large number of banded birds would be able to detect such effects.

We do not know the reason(s) for the significant decline of about 17 percent in numbers of territorial owls in the San Bernardino study area from 1987 to 1991. Much logging occurred there in the 1960s, but we doubt whether that disturbance can explain the current decline. A more plausible hypothesis involves either direct or indirect effects of the drought in southern California. For example, precipitation from 1987 through 1990 averaged about 60 percent below normal at a weather station at the western end of Big Bear Lake, in the San Bernardino Mountains (fig. 8A) and 67 percent of normal at the east end (fig. 8B). Rainfall in 1991 was above normal at both of these sites, but almost all of it occurred in March, after the owls would have initiated breeding. One working hypothesis is that dusky-footed woodrats, the primary prey of the owls in the San Bernardino Mountains (Chapter 4; LaHaye pers. comm.), have experienced marked population declines as a result of the drought. For example, Linsdale and Tevis (1956) and Spevak (1983) reported depressed woodrat populations in California during droughts, although Kelly (1989) failed to find a decline in woodrats during a drought at Hastings Natural History Reservation in Monterey County in the late 1980s.

If the recent drought has contributed in some way to the decline of the owl population in the San Bernardino Mountains, it suggests that the population is subject to high levels of environmentally induced variation in its demographic parameters. As the population declines, individuals may be lost from marginal habitats, where survival and reproduction are possible only

during "good" times (for example, see O'Connor 1986). Individuals that survive, and even reproduce, during the decline may be those that occupy better, more stable habitats, as where more mesic conditions prevail (for example, riparian areas). Such refuges would be particularly important to the species' long-term persistence, and any destabilization of them-by logging, water diversion, depression in ground water levels, or excessive development of recreational activities-could pose a significant threat to the species' survival.

Future Research Needs

Based on a three-stage model, estimates of parameter sensitivities from all three study areas suggest that λ values were most sensitive to estimates of adult survival rate (s), distantly followed by first- and second-year survival rates (s_0 , s_1) and fecundity (b) (fig. 8C). The sensitivity coefficient associated with age at first reproduction was small (Noon and Biles 1990). The much steeper slope for adult (≥ 2 years) survival rate demonstrates the importance of precise estimates of adult survival to produce precise estimates of λ . Introducing senescence at age 16 increases the slopes for fecundity and prereproductive survival rates, but s is still most important (fig. 8D). For a fixed recapture probability, more precise estimates of s can be attained only by having a larger sample of banded birds.

A comparison of figures 8C and 8D indicates that it may be important to know whether spotted owls exhibit senescent decline in fecundity or survival. Noon and Biles (1990) showed that estimates of population growth rate (λ) were strongly influenced by the age at which reproductive senescence was assumed. Without detailed information on reproductive histories of marked individuals, insights into senescent declines in the owl's vital rates cannot be detected.

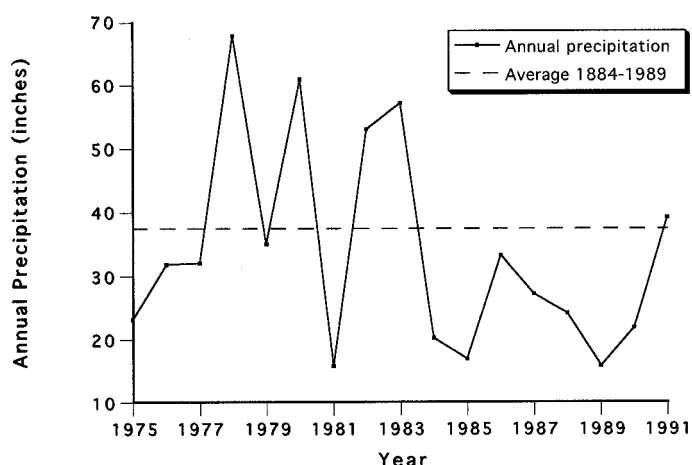


Figure 8A-Annual precipitation (inches) from 1975-91 as measured at the western end of Big Bear Valley, in the San Bernardino Mountains (Lundy pers. comm.).

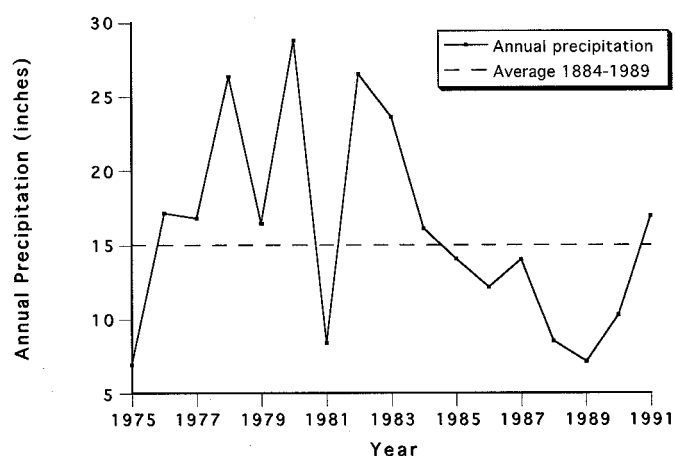


Figure 8B-Annual precipitation (inches) from 1975-91 as measured at Big Bear City, in the San Bernardino Mountains, 7 miles east of the weather station for results reported in figure 8A (Lundy pers. comm.).

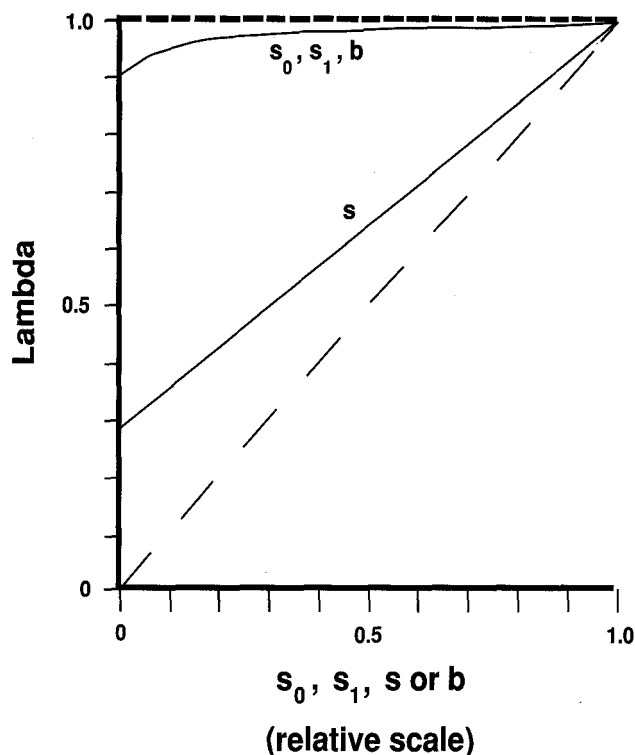


Figure 8C-Population growth rate (lambda) for a stage-structured model of the California spotted owl. The figure shows the effects on lambda (λ) of a proportional decline in a specific demographic rate, with all others held constant. Empirical estimates of mean survival rate have been scaled by $1/\lambda$ to yield an initial starting point of $\lambda = 1.0$ on the abscissa.

Two sources of information are relevant to a species' rate of population change (λ). One is the sensitivity of λ to variation in the vital rates as reflected in coefficients of parameter sensitivity. The other concerns those life-history attributes that show the most natural variation. Variation in population growth rate (λ) may be more closely associated with attributes that are naturally more variable than with attributes that are less variable but to which growth rate is mathematically more sensitive. We cannot yet estimate the magnitude of natural variation in demographic parameters of California spotted owls. Estimates that confound sampling error and true annual variation from the five demographic study areas (table 8D), however, indicate that fecundity exhibits the greatest annual variation. Fecundity combines two important components: productivity per breeding female and the proportion of females ≥ 2 years of age that breed. The latter is particularly variable (table 8D).

Factors contributing to the low and variable reproductive rates of spotted owls also need investigation. We do not know whether the extensive annual variation in reproductive success is due to variable resource levels (prey base), variable climatic conditions, or some combination. Nor do we know whether reproductive rates or adult survival rates can be increased by direct management for prey populations; this is also an important research question.

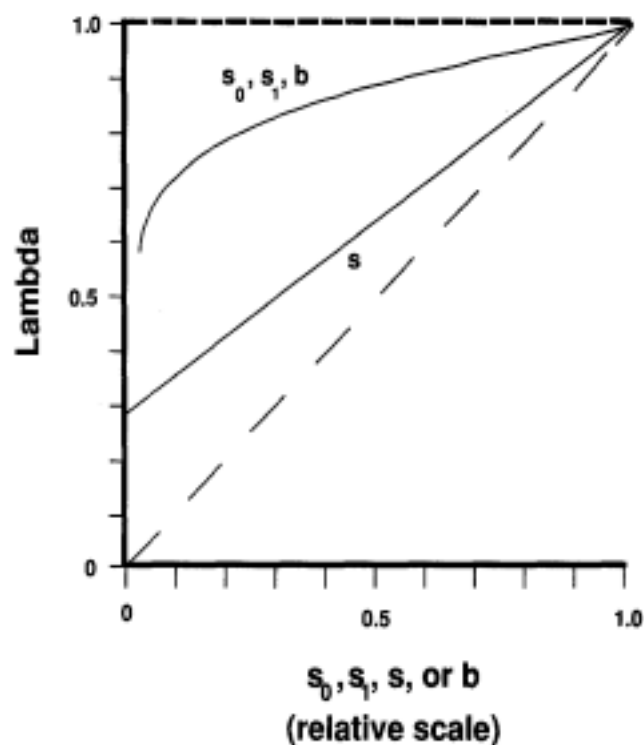


Figure 8D-Population growth rate (lambda) for an age-structured model of the California spotted owl. The figure shows the effects on lambda (λ) of a proportional decline in a specific demographic rate, with all others held constant. Empirical estimates of mean survival rate have been scaled by $1/\lambda$ to yield an initial starting point of $\lambda = 1.0$ on the abscissa.

Finally, as suitable spotted owl habitat becomes more fragmented, it will become increasingly important to estimate dispersal capabilities of California spotted owls (Chapter 4) and to identify factors that affect survival during dispersal. This includes influences on the survival of juvenile birds dispersing from their natal territories, as well as adult birds displaced by habitat loss.

Management Implications

Implications of the demographic results for management involve decisions that may differentially affect adult and pre-adult birds. The life-history pattern of the spotted owl suggests that it must have evolved in an environment stable with respect to adult survivorship. The much greater sensitivity of λ to variation in adult than preadult survival rates indicates strong natural selection to maintain low adult mortality rates. Further, the low fecundity rate suggests that recruitment may always have been variable. In spite of this, high adult survivorship has allowed the

spotted owl to persist through long periods of low reproductive output. A consequence of this trade-off is of great concern when considering management for spotted owls. Namely, low fecundity precludes rapid recovery from a population decline. Any management action that lowers adult survival rate, particularly when coupled with a reduction in population size, markedly increases the likelihood of local extinction.

Although λ is relatively insensitive to changes in s_0 and b (figs. 8C and 8D), we cannot infer that these attributes are unimportant when developing management plans. Adult survival rate is relatively high and may not be amenable to further increases. Assuming no reduction in adult survival rate, increasing first year survival or fecundity by direct management activity may be the most feasible way to increase the growth rate of spotted owl populations. For example, certain silvicultural prescriptions may increase the availability of the owl's preferred prey and somewhat ameliorate the otherwise negative effects of logging. But these prescriptions are still unknown and untested.

Given the spotted owl's life history structure, an evaluation of management decisions in terms of persistence likelihoods are possible only when viewed over the long-term (50-100 years). With a high adult survival rate and an apparently long life span, the Spotted Owl may be able to persist over the short-term even in the face of extensive reduction in the amount of its suitable habitat. Thus, significant time lags may occur in responses of spotted owl populations to declining environmental carrying capacity. By themselves, therefore, short-term survey results, even those including observations of breeding owls, are insufficient to allow inferences about population viability.

Rapid rates of population decline in either deterministic or stochastic analyses are not surprising when the finite rate of increase (λ) is <1.0 . Leslie-Lefkovich projection matrices and life table models yield simple exponential models of population growth or decline (see discussion in Noon and Sauer, 1992). For this reason, it is inappropriate to use estimates of λ to project future population size without strict qualifications. Most natural populations presumably demonstrate density-dependence in one or more life history parameters. Many examples exist of bird species shown to exhibit density-dependent effects on vital rates. These include the gray partridge (Blank et al. 1967), the mallard (Hill 1984), the tawny owl (Southern 1970), and the European sparrowhawk (Newton 1988). No empirical data for spotted owls presently indicate a relation between population density and values of vital rates. Nevertheless, on the basis of a simple nonspatial model, Boyce (1987) argued that spotted owl populations at low densities should exhibit density-dependent increases in survival and reproduction that could stabilize the populations. Very different inferences are drawn, however, from models that include the additional reality of spatial structure, such as the

uncertainties of successful dispersal and mate finding in spatially structured populations. Lande (1987) and Lamberson et al. (in press) found that owls at low population densities may experience negative effects of low densities that further depress survival and fecundity. In fact, their models indicate that if population densities are very low, or the amount of suitable habitat is greatly reduced, a threshold point exists beyond which the owl populations collapse to extinction.

We believe there are implications for the management of California spotted owls. Future management activities, for example, must not increase the mean nearest-neighbor distances among suitable pair sites. Subtle factors that uniformly decrease habitat quality, or increase fragmentation, will act to reduce population density and incrementally increase the uncertainties associated with successful dispersal and mate-finding. Habitat-induced changes in vital rates, such as declines in first-year survival and in the proportion of breeding females, will lead to declines in population growth rate. If suitable habitat is allowed to decline and become fragmented, as for the northern spotted owl, the uncertainty of successful dispersal will become progressively more relevant to the subspecies' long-term population dynamics and likelihood of persistence. Should this pattern ensue for the California spotted owl, then the most effective way to assure its long-term persistence may be to create a connected network of habitat conservation areas (HCAs) as was proposed for the northern subspecies (Thomas et al. 1990). Large HCAs provide stable areas of high population density that promote a balance between pair turnover and colonization of pair sites, either through internal recruitment of dispersing juveniles or the emigration of owls from neighboring HCAs. Implementing such a strategy, however, would risk an increasing threat of stand-destroying fires in areas maintained primarily for the owls.

Finally, it is important to recognize that rates of population change (λ) and the values of the owl's vital rates are ultimately determined by habitat quality at both local and landscape scales. For example, habitat quality at the scale of the home range may determine the survival and birth rates for an individual pair of owls. At a larger scale, the number of suitable pair sites and their spatial arrangement may determine the persistence of local populations. And, at a regional scale, providing habitat for a large number of local populations distributed widely across the landscape will increase overall persistence of the subspecies by decreasing the likelihood of populations simultaneously experiencing negative environmental effects. Thus, to ensure stable owl populations in the Sierra Nevada and Southern California Provinces will require specific management prescriptions, implemented at local to regional scales, to retain the amount and spatial pattern of habitat that will provide for a long-term balance between birth and death rates.

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Chapter 9

Stability Properties of the Spotted Owl Metapopulation in Southern California

Barry R. Noon and Kevin S. McKelvey

Spotted owls in the Southern California Province have an insular population structure characterized by large (about 200 pair sites) to small (about 2-4 pair sites) local populations distributed among discrete mountain ranges (fig. 9A, table 9A). The distribution of habitat "islands" is discontinuous across the landscape, reflecting natural discontinuities in vegetation structure and composition, in topographic conditions, and in the effects of extensive human-induced habitat disturbance and fragmentation. Lowland areas surrounding these mountain ranges are primarily desert scrub and chaparral habitats that are unsuitable for spotted owls. Relatively narrow gaps between populations, like the 6-mile separation at Cajon Pass, between the San Gabriel and San Bernardino populations (fig. 9A), are probably not complete barriers to dispersing owls. Longer separations, however, such as that of about 30 miles through the Los Angeles

Basin, between populations in the San Bernardino and Santa Ana Mountains (fig. 9A), may present significant survival risks to dispersing owls such that successful colonization is very unlikely. The degree to which these gaps act to severely reduce or eliminate demographic rescue between populations is unknown. To date, however, no banded spotted owl has been located within any population outside that of its origin (LaHaye pers. comm.). The most significant gaps between owl populations are discussed in table 3K and shown on a distribution map in that chapter (fig. 3A).

Even within many of the mountain ranges, the distributions of habitat and owl sites are discontinuous. For example, in the Cleveland and Los Padres National Forests (NFs), most suitable spotted owl habitat is patchily distributed because it is restricted to deeply dissected canyons dominated by oaks and surrounded

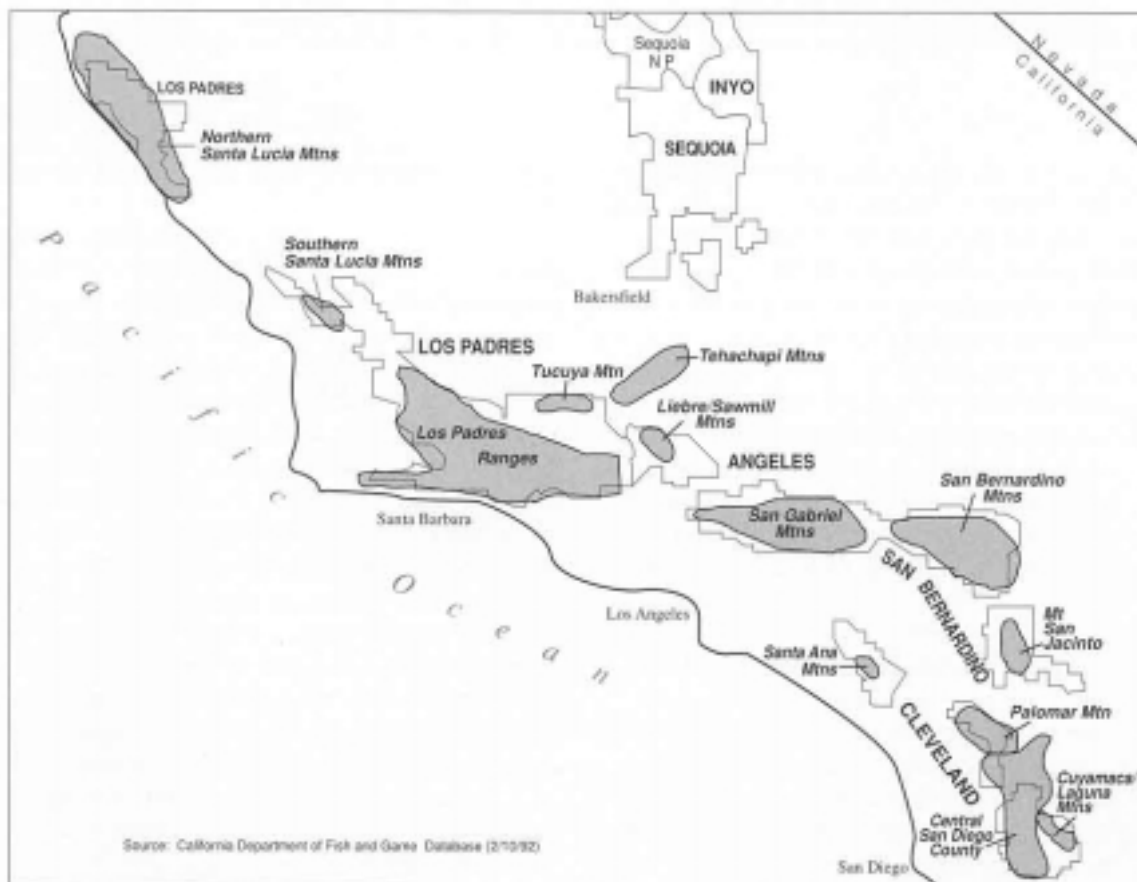


Figure 9A-"Island" populations that comprise the southern California metapopulation of spotted owls. Estimated numbers of owl sites for each "island" are given in table 9A.

Table 9A-Owl sites,¹ pairs and status of pairs on these sites, and nearest neighbor distances of California spotted owl populations in southern California (from Stephenson 1991 and Chapter 3). Compare values tabled here with the locations of these areas, shown in figure 9A.

Area	Owl sites (all years)	Pairs since 1987	Breeding since 1987	Potential population ² (no. sites)	Nearest neighbor distances ³
San Diego Ranges	37	18	6	76	18 - 33 miles
Palomar Mountain	(18)				
Central San Diego County	(9)				
Cuyamaca/Laguna Mountains	(10)				
Santa Ana Mountains	2	1	-	12	30 - 40 miles
San Jacinto Ranges	20	16	9	29	11 - 18 miles
San Bernardino Mountains	124	114	66	125	6 - 11 miles
San Gabriel Mountains	54	22	5	95	6 - 20 miles
Liebre/Sawmill Mountains	14	10	2	20	12 - 20 miles
Tehachapi Mountains	4	0	-	12	unknown
Tecuya Mountain area	5	3	-	10	9 - 12 miles
Los Padres Ranges	65	32	17	100	8 - 12 miles
So. Santa Lucia Mountains	12	6	2	19	32 - 45 miles
No. Santa Lucia Mountains	39	22	1	80	45 miles
Southern Monterey	(14)				
Northern Monterey	(25)				
Total	376	244	108	578	

¹ See glossary in Appendix B for a definition of "owl site."

² If each site were assumed capable of supporting a pair, the total population would be the number of sites times 2.

³ Where two distance values are shown (that is, 12-20 miles), they represent the distances to the two closest neighboring populations.

by unsuitable chaparral habitat. Thus, many of these populations have an insular structure at both landscape and local scales. The present modeling study was prompted by the need for a better understanding of the potential effects on population persistence of isolation between subpopulations, and changes in habitat continuity within otherwise continuous habitat islands.

Although spotted owl records in southern California exist from the early part of this century (Stephens 1902, Clay 1911), careful population studies are recent. LaHaye et al. (1992) have studied the demography of the owl population in the San Bernardino Mountains, and Gutiérrez and Pritchard (1990) reported on surveys done on Mt. San Jacinto and Palomar Mountain. In addition, infrequent surveys in NF lands provide a cumulative record of spotted owl locations outside of these study areas (Gould et al. 1987, Stephenson 1991).

The largest population occupies the San Bernardino Mountains (about 124 owl sites), with considerably smaller populations in the other ranges (table 3H). The cumulative total number of known owl sites within the southern California "archipelago" is estimated at 376 (table 9A), with an approximate population of 300-350 pairs at any point in time. The population trend is known for only one location. During the interval 1987-91, the resident, territorial population in the San Bernardino Mountain study area declined by about 17 percent per year (LaHaye et al. 1992; Chapter 8). If this rate of decline were to continue, the

territorial population would decline by 50 percent in about 4 years.

Based on theory and limited empirical data (reviewed in Gilpin and Hanski 1991), we believe the ultimate stability of this metapopulation will depend upon several factors. These include the persistence of one or more populations large enough to escape the negative effects of demographic and environmental stochasticity, and with demographic characteristics resulting in a production of excess individuals to serve as potential colonists for other local populations. Many of the small, isolated populations that occur in southern California are probably maintained by occasional immigration from these more productive source areas (see Pulliam 1988 and Howe et al. 1991 for a discussion of source-sink dynamics). In addition, given a high likelihood of significant environmental variation (for example, wildfires, prolonged periods of drought, or rapid urbanization) at least two source populations will be needed, and they should be sufficiently separated to minimize the likelihood of their simultaneously experiencing negative perturbations.

The human population in southern California continues to expand into the forested mountain habitats of the spotted owl. In the San Bernardino Mountains, for example, the human population has grown from about 19,000 in 1970 to over 40,000 in 1992, with 5 million annual visitors (Dib and Griffone 1991). Accompanying this growth is a reduction in the quality and

amount of forested habitat for spotted owls—a consequence of urbanization, highways and smaller roads, and recreational developments. Although we lack earlier estimates of spotted owl population sizes or densities, we nonetheless consider it likely that spotted owls have declined in both number and distribution from historic levels.

Given the metapopulation structure of the southern California spotted owl population, recent declines within the largest and most contiguous population in the region, and significant threats to loss of suitable habitat due to rapid human population growth, we believe that a specific conservation strategy is warranted for the subspecies in this part of its range.

This chapter has two main purposes: to explore, in a general sense, the stability properties of the southern California metapopulation structure, and to make specific recommendations for conservation of the subspecies in this part of its range. Toward this end, we make frequent reference to pertinent population theory and use results of simulation models to explore conservation alternatives. Our goal was not to estimate extinction likelihoods—we believe it is premature to conduct such analyses at this time. Currently, the only estimate of population change from this region suggests a rapid decline in the territorial population (Chapter 8). Under a strict assumption of constancy in the vital rates, projecting forward at this rate shows a rapid decline to extinction. Until more is known about natural fluctuations in vital rates of populations, however, such projections are unwarranted.

Rather, our goal was to explore the geometry of the metapopulation, including both habitat and owls, to gain insights into what spatial arrangement of habitat would minimize future extinction risks. In this chapter we present the results of our efforts to integrate, in the form of computer simulation models, the species demography with variations in the amount, distribution, and quality of owl habitat. The computer simulation models were developed specifically to aid the development of a conservation plan for spotted owls (Thomas et al. 1990, appendix M; Lamberson et al. in press; McKelvey et al. in press). We used the results of computer simulations to test basic principles of reserve design (Murphy and Noon 1992) and to provide guidance about the necessary spatial design of a reserve system implemented on real landscapes.

Methods

Parameter estimates and model structure were based on information from the study of marked populations (LaHaye et al. 1992; Chapter 8). Owls were captured during the breeding season, aged, sexed, and individually marked. Reproductive status was determined for all individuals using methods outlined by Forsman (1983). Young were counted after fledging had occurred (that is, after they left the nest). Individuals were initially

placed into four age classes (juvenile, first-year subadult, second-year subadult, adult) according to criteria developed by Moen et al. (1991). Because of similarity in survival rates, first- and second-year subadults were pooled with adults and collapsed into a single stage. Annual survival rates for banded juveniles, subadults, and adults were calculated using Jolly-Seber capture-recapture models for open populations (Jolly 1965, Seber 1965) using program JOLLY (Pollock et al. 1990).

The estimate of fecundity combines two important components—the number of females fledged per nest and the proportion of females ≥ 2 years of age that breed. Thus, "adult" refers to ages subsequent to the second year of life. Fecundity was estimated each year as the mean number of young fledged per pair, assuming a 1:1 sex ratio at birth. Within the adult age class, survival rate was assumed to be constant, and we assumed no reproductive senescence. For our simulation models, we divided the population into three stages: juveniles, subadults, and adults. Time was expressed on an interbirth interval of 1 year, and we assumed an age at first reproduction of 2 years (that is, birds just beginning their third year of life).

Lambda (λ), the estimated annual, finite rate of population change from the San Bernardino study was 0.827 (table 8G), indicating that the territorial population there was in precipitous decline. Because λ represents a simple exponential rate of change, using the vital rates estimated from this study to project future populations would be a trivial exercise. All populations would decline exponentially regardless of the amount and distribution of suitable habitat. To evaluate possible effects of variation in landscape geometry, we initially adjusted the survival rates by multiplying them by $1/\lambda$ to yield a $\lambda=1.0$ in suitable habitat. All demographic rates were again slightly increased to allow for the possibility of a 2 percent annual rate of population growth ($\lambda = 1.02$). This scaling of the survival rates allowed for a growing (source) population in suitable habitat. Differences in model results based on the landscape model (see below) would, therefore, reflect the effect of differences in distribution and amount of suitable habitat, and not an assumption of depressed demographic rates. Based on current field studies (Chapter 8), however, the adjustments we made to the demographic rates for suitable habitat were optimistic.

Dynamic Projection Models

No natural population is exposed to purely deterministic forces. Thus, population dynamics of the spotted owl should be examined relative to both demographic and environmental stochasticity. Further, simple deterministic analyses are also limited in that they provide no insight into the dynamics of mobile populations in real landscapes. That is, they incorporate no information on the movement behavior of animals in heterogeneous environments and the uncertainties of finding suitable habitat and mates. Failure to account for the spatial component

of both animal locations and their habitat distributions ignores the covariance between demographic rates and habitat variation.

A conservation strategy for any species is ultimately described by a map that integrates information on the species' distribution; the distribution of current and potentially suitable habitat; and economic, political, and legal constraints (Thomas et al. 1990; Murphy and Noon 1992). To develop a general set of conservation recommendations for the southern populations of the California spotted owl, we needed insights into how the landscape-scale arrangement of owls and their habitat affected their population dynamics. The data available to us lacked detail and were imprecise (see Chapter 3). As a result, we could explore the effects of landscape geometry and variation in the distribution of habitat types only in a nonspecific way, and make general recommendations about the significance of different components of the landscape.

To provide a framework to guide the conservation evaluation of the California spotted owl, we drew general inferences from several simulation models incorporating various degrees of spatial information. Our approach, which investigated the effects of variable dispersal efficiencies on the population dynamics of territorial animals occupying heterogeneous landscapes, had its foundation in previous work by Lande (1987, 1988). Lande's model was based on a hypothetical species with a monogamous, territorial breeding system and with obligate juvenile dispersal from the natal area. This model was directly applicable to the life history structure of the spotted owl.

Nonexplicit Spatial Models

In the following, we briefly review the structure and assumptions of two models used to assist in the design of a reserve strategy for the northern spotted owl (see Thomas et al. 1990, appendix M). We do not discuss these models exhaustively but simply make reference to results from those models that are most applicable to the conservation of spotted owls in southern California. Additional details can be found in Thomas et al. (1990, appendix M), Lamberson et al. (in press) and McKelvey et al. (in press).

The Individual-Territory Model

Model Description

This model (Lamberson et al. in press) extended that of Lande (1987) by relaxing the assumption of demographic equilibrium and allowing the simulated landscape to be dynamic. Life history was expressed as a three-stage, two-sex projection model. The model assumes that all newly fledged juveniles disperse, and that adult birds who experience loss of their territory (for example, due to logging) also disperse. Lande's model allowed some likelihood of a juvenile's inheriting its natal terri-

tory. Based on the settling patterns of owls first banded as juveniles, however, inheritance of the natal site is a very rare event. Our model focuses on a landscape with a fixed spatial extent and with a fixed number of potential territories (or "sites"). Sites were either suitable for survival, mate attraction, and reproduction, or they were unsuitable. Only the suitable sites were capable of being occupied. The key response variable in our model is the occupancy rate of sites by pairs. As in Lande's model, this model lacks realism because of the global nature of juvenile and adult search—all cells had an equal likelihood of being sampled.

The search process was simulated as sampling with replacement. The key equation describing search success in our model (see Lande 1987) was

$$\text{Pr}(\text{success}) = 1 - (1 - \text{unoccupied suitable sites}/\text{total sites})^m, (1)$$

where m is the number of sites that can be searched prior to mortality (additional equations describing the model dynamics are given in Lamberson et al. [in press]).

A nesting pair will annually produce young (according to a deterministic or stochastic likelihood), and these will disperse at the end of the season, the males seeking an unoccupied site and the females seeking a site occupied by a solitary male. Dispersal success is density-dependent, calculated by assuming random search of accessible sites. Search capabilities, together with the occupancy ratio of searched sites, determines the bird's potential for successful dispersal (consistent with Lande 1987).

Relevant Model Results

The most significant conclusions from Lande (1987) and Lamberson et al. (in press) are (1) that the occupancy of suitable habitat declines with a declining proportion of the landscape that is suitable habitat (fig. 9B), and (2) that if the amount of suitable habitat declines below some threshold value, the population will become extinct (fig. 9C, curve A). That is, because of uncertain-

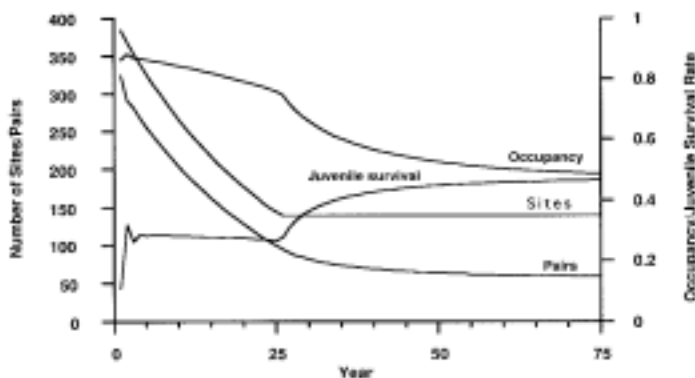


Figure 9B—Trend in the number of pairs of spotted owls, number of sites, site occupancy by pairs, and juvenile survival rate based on a 75-year simulation. The simulation assumed that 4 percent of the suitable owl habitat was lost per year until 14 percent remained, and that juvenile owls could search 20 sites.

ties associated with search and mate finding, a species can be critically habitat-limited even in the presence of suitable but unoccupied habitat.

New findings, beyond those reported by Lande (1987), resulted from the model of Lamberson et al. (in press), because of its dynamic and nonequilibrium nature. First, survival probability, as a function of the percent of suitable habitat, is affected by environmental variation. Once again the deterministic case shows a staircase function, with the jump from 0 to 1 occurring at the threshold point (fig. 9C, curve A). Adding environmental variance makes the extinction threshold less abrupt (fig. 9C, curves B and C). Second, in a scenario involving incremental loss of suitable habitat (for example, by logging), the crowding of older owls into remaining suitable habitat is likely to produce temporarily high occupancy rates-much higher than expected under long-term stable conditions (fig. 9B). Thus, predicting long-term population status from short-term occupancy data can be very misleading.

The Territory-Cluster Model

The primary limitation of the individual-territory model was the global nature of search. In reality, organisms search locally and are primarily influenced by the local nature of the landscape rather than its global condition. The basis of the territory-cluster model (Thomas et al. 1990, appendix M; Lamberson and Noon 1992) is a fixed, rectangular array of circular clusters containing a variable number of owl sites (territories). Every site within a cluster, assumed to be of identical size, was either suitable or unsuitable (defined as in the individual-territory model). Clusters could be either totally or partially suitable-the carrying capacity of a cluster equalled the number of suitable sites. For a given simulation, all clusters were the same size (that is, they contained the same number of sites). As in the individual-territory model and Lande (1987), the response variable was the proportion of suitable sites occupied at any point in time.

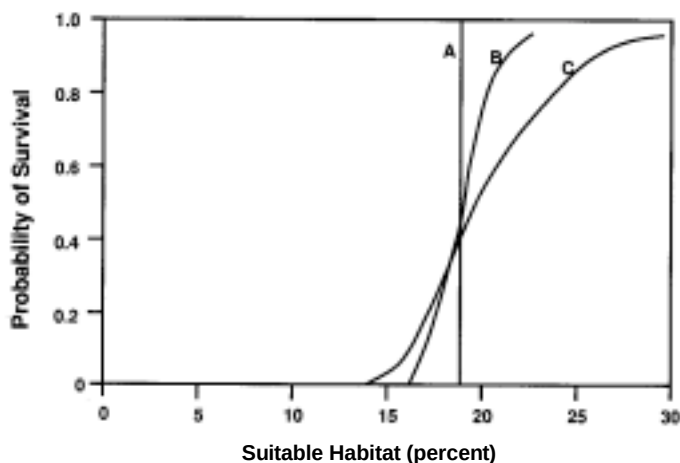


Figure 9C-The 250-year survival probability in relation to the percentage of suitable sites in the landscape. Curves A, B, and C represent the conditions of no, low, and high environmental variability, respectively.

The matrix between clusters was assumed to be entirely unsuitable for owl sites. Assuming a constant percentage of the habitat as potentially suitable Habitat and restricting the habitat to clusters had two important consequences: (1) as cluster size increased, the distance between adjacent clusters increased predictably (fig. 9D); and (2) the dispersal angle between adjacent clusters (see fig. 9E), and the probability of selecting this angle, were independent of cluster size.

The landscape simulated by the model had a "wrap-around" structure to exclude possible anomalous results that might arise from edge effects. The clusters on the right side of the grid were treated within the model just as though they were immediately to the left of those on the left side of the grid. The top and bottom rows of clusters were treated in a similar manner.

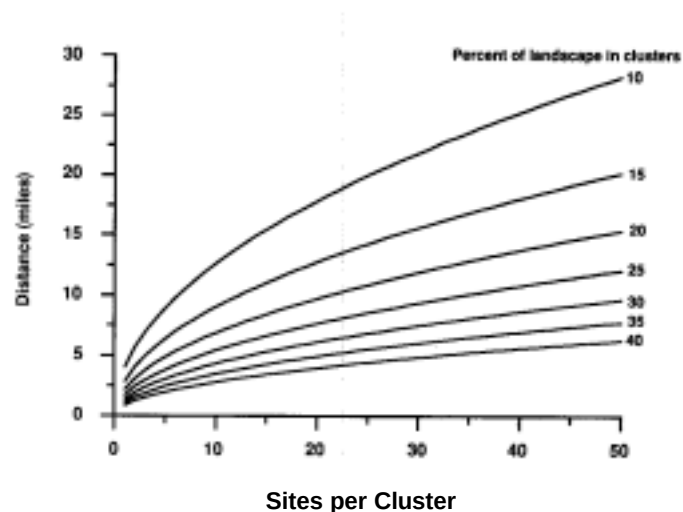


Figure 9D-Nearest-neighbor distance between clusters in relation to cluster size. Each curve represents a different percentage of the landscape assumed to be suitable habitat and located in the clusters.

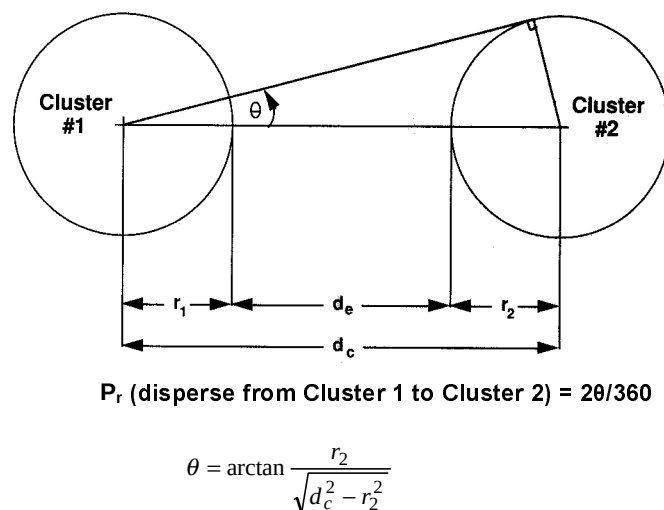


Figure 9E-Method of estimating the angle of intersection between two adjacent clusters in the cluster model. The probability of dispersing in the correct direction is a function of the combined angles of intersection of the six neighboring clusters.

The life history was expressed as a three-stage, female-only projection model. Initial values of the vital rates were based on table 8G, and survival rates were scaled by multiplying by 1/0.827 to provide for a stable local population in suitable habitat. Based on observations of recently fledged young near the nest site (Marcot and Holthausen 1987), a predispersal survival component of 0.6 was assumed for the juvenile survival rate. The dispersal component of first year survival arose from properties of search efficiency and landscape pattern, thus allowing the possibility of a growing population. Fecundity was treated stochastically, based on good years and bad years for reproduction, with expected values equal to field data (table 8G). We assumed complete spatial autocorrelation for the reproductive pulses.

Dispersal Dynamics

As in Doak's (1989) model, our model distinguished between dispersal within and among clusters. All clusters were equally accessible in Doak's model, but we introduced the additional reality that search was spatially constrained and was, therefore, affected by the status of neighboring clusters. Within-cluster dispersal in our model was identical to the individual-territory model, with each dispersing owl allowed to sample with replacement a given number, m , of sites within the cluster (equation 1). To determine the allocation of search effort within a cluster, we assumed a random walk from a random starting point. By simulation, we estimated the expected number of steps taken by a dispersing bird before it crossed the boundary of a circular cluster. The assumption was that an owl could traverse one site in a single time step. Based on 10,000 simulations of circular clusters of various sizes, and regressing the number of steps taken before crossing the circle, we estimated the following relationship:

$$\text{Expected}(m) = 0.41 * \text{number of sites in the cluster.} \quad (2)$$

For clusters with 20 sites, for example, an average of eight sites were searched within clusters before crossing the boundary into the matrix between clusters. The total number of searches across all clusters ($m = 22$) was based on the upper bound of the 90th percentile of the maximum dispersal distance of 56 radio-tagged juvenile spotted owls (Thomas et al. 1990, p. 305) and the assumption that each site had a diameter of about 2 miles.

If a dispersing juvenile did not find a suitable site within its natal cluster (based on a fixed number of searches), it was forced to disperse between clusters. Between-cluster dispersal was modeled as a straight-line path moving away from the natal cluster at a random azimuth. Two sources of mortality were encountered. First, the bird must move in a direction that would intersect a neighboring cluster. The probability of intersection for each adjacent cluster was governed by the following equation (see fig. 9E):

$$\text{Probability}(\text{disperse from cluster 1 to cluster 2}) = 2\theta/360 \quad (3)$$

$$\text{where } \theta = \arctangent \left(r_2 / \sqrt{d_c^2 - r_2^2} \right)$$

Second, if a correct direction was chosen, the likelihood of

successful travel to the neighboring cluster lying a distance d miles away (measured edge-to-edge) was modeled by a declining exponential,

$$\text{Pr}(\text{survive to } d) = \exp(-kd) \quad (4)$$

The value of k was estimated by arranging the maximum straight-line distances attained by the 56 radio-tagged juvenile owls in rank order, then regressing the natural log of the cumulative proportion represented by that distance (dependent variable) on the associated distance and forcing the regression through 0 ($r^2 = 0.97$) (see fig. 4F). Because search begins in the natal cluster and moves through adjacent clusters, the search success in this model, as in nature, is a function of the condition of the landscape near to the bird's natal site.

Model Parallels to the Southern California Metapopulation

The structure of the cluster model crudely approximates aspects of the southern California spotted owl habitat distribution (fig. 9A). Clusters can be considered analagous to local habitat islands, and gaps between local populations are analagous to the matrix-areas that allow dispersal (with inevitable survival risks) but no reproduction. Model results allowed us to make general inferences to (1) the relation between cluster size and local population stability, (2) the effects of variable spacing among clusters on mean pair occupancy, and (3) the most efficient ways to allocate lands to a reserve design.

Relevant Model Results

Because the number of combinations of model parameters is immense, many sensitivity analyses were done (table 9B). The most significant result, however, was based on the relation between mean pair occupancy and cluster size. For a simulation with 60 percent of the sites suitable within a cluster, occupancy did not stabilize until clusters held at least 15 sites (fig. 9F).

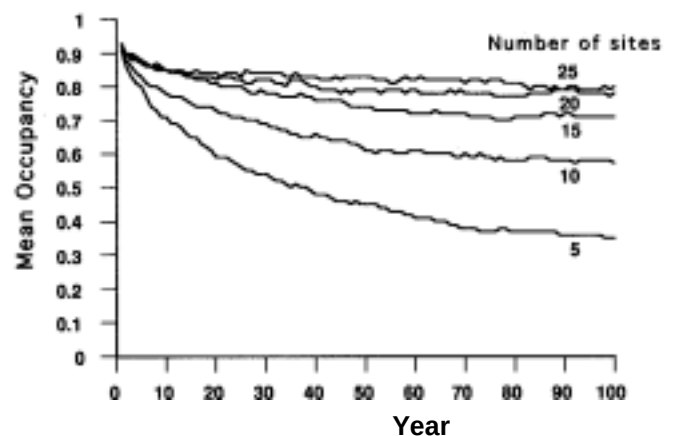


Figure 9F—Mean proportion of cluster occupied in relation to time, based on a 100-year simulation. The number of sites per cluster varied from 5 to 25, and 60 percent were assumed suitable; 35 percent of the landscape was in clusters.

Clusters of 15 sites stabilized at about 70 percent occupancy, while clusters of >20 sites stabilized at about 80 percent, a figure representing nearly full occupancy given adult survival rates. Further increases in cluster size had little effect on occupancy. As the number of suitable sites within a cluster increased, the marginal difference in occupancy among clusters of different sizes became less pronounced.

Based on the relation between the landscape fraction within clusters (habitat islands) and cluster spacing (fig. 9D), different levels of allocation to a reserve system can be viewed in terms of the distance between clusters. We found mean occupancy rate to be strongly affected by increased spacing between clusters for cluster sizes <20 sites (fig. 9G). In contrast, clusters with >25 sites showed minimal distance effects beyond separations of about 20 miles (fig. 9G). Adding low levels of environmental variation in survival rates lowered occupancy rates about 7 percent and suggested slightly larger cluster sizes for the same level of occupancy (fig. 9H).

An alternative approach to choosing an optimal cluster size is to estimate the expected number of owls occupying a fixed amount of suitable habitat. Based on mean occupancies at 100 years from fig. 9F, the efficiency of land use is clearly higher for larger clusters (fig. 9I).

Inferences to Reserve Design from the Nonexplicit Spatial Models

Results from these models suggest that providing for clusters of territories should increase the persistence likelihood of spotted owls, primarily by facilitating juvenile dispersal (compare Doak 1989). If habitat becomes too diffuse at a local scale, populations there will experience extinction events and require recruitment from larger source areas for recolonization (the

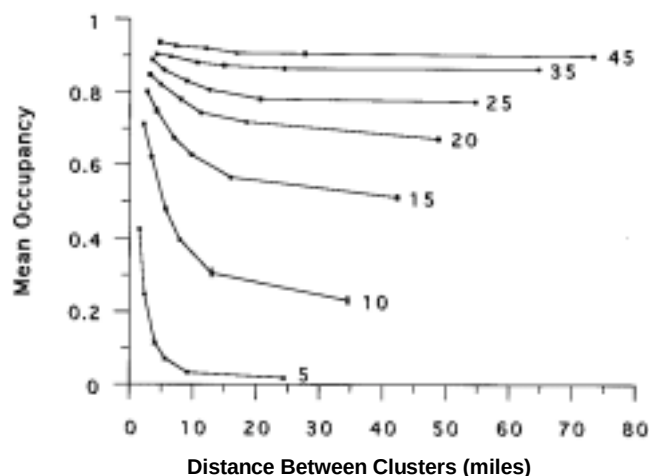


Figure 9G—Mean proportion of clusters occupied as a function of the distance between clusters. The number of sites per cluster varied from 5 to 45, and 60 percent were assumed to be suitable.

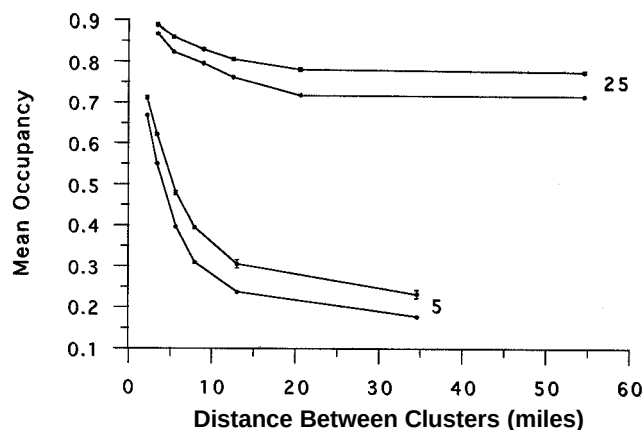


Figure 9H—Mean proportion of clusters occupied as a function of distance between clusters. The number of sites per cluster was either 5 or 25, and 60 percent were assumed to be suitable. The lower curve of each pair represents simulations including environmental variation in survival rates.

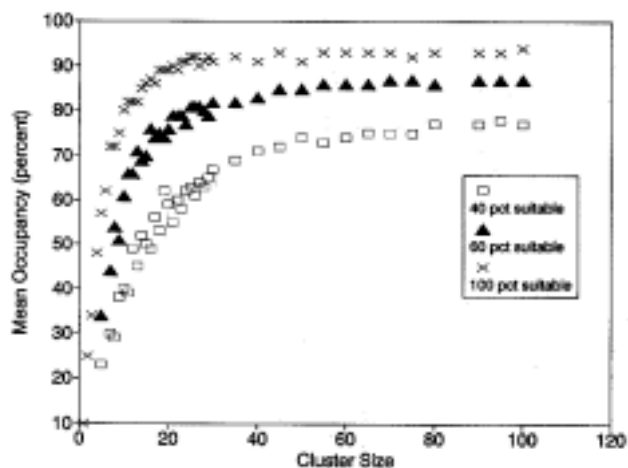


Figure 9I—Steady-state mean occupancy rate in relation to cluster size. The curves represent 40, 60, and 100 percent of the sites within each cluster as suitable habitat.

"rescue effect"). Given assumptions of the cluster model (≥ 60 percent of sites suitable, moderate connectivity among adjacent clusters), clusters with >20 sites should provide for locally stable populations in the absence of catastrophic disturbance. Adding moderate levels of environmental variation in the survival rates, however, raises the desired minimum cluster size to about 25 sites.

Once clusters reach about 35–45 sites, they attain high levels of local stability and become relatively independent of the distance to their nearest neighbor. Within the structure of our model, this occurred because almost all dispersing juveniles found suitable sites within their natal cluster. Given a fixed number of total searches ($m = 22$), and the allocation of within cluster search following equation 2, all search is expended within

Table 9B--Qualitative results of sensitivity analyses for the territory cluster model.

Factor varied	Sensitivity ¹
Within-cluster search efficiency	Low for large clusters; high for small clusters
Resistance to between-cluster dispersal	Low for large clusters; high for small clusters
Search time outside of natal cluster	Low to moderate for large clusters; high for small clusters
Initial population size	Low if population was in large clusters; high if population was in small clusters

¹ Measured in terms of reduction in mean pair occupancy.

the natal cluster when cluster size equals 54 sites. At this point in our model, all clusters are acting as independent subpopulations.

Comparing these general model inferences to estimates of the number of sites in various habitat islands in the Southern California Province (table 9A) provides some significant insights. Based on current estimates of owl sites, many of these habitat islands have <25 sites, are isolated by >10 miles, and are therefore expected to be very unstable. That is, they will be subject to extinction events because of both demographic and environmental variation, or act as sink areas (Pulliam 1988). As such, their occupancy status will depend largely upon immigration from neighboring habitat islands. The possible dependence of these populations on immigration from larger source populations parallels results for insular populations of acorn woodpeckers in the southwestern United States (Stacey and Taper 1992), and red-cockaded woodpeckers in the southern Appalachian mountains (Conner pers. comm.).

The cluster model had several optimistic assumptions. Most important were that (1) no uncertainty was associated with mate finding, (2) only low levels of environmental variation in vital rates were simulated, and (3) clusters were assumed to be circular, thus minimizing the perimeter:area ratio. A circular shape (1) maximizes the density of suitable habitat and, given our within-cluster search algorithm, suggests very high search efficiencies; and (2) it affects the estimate of the probability of leaving the natal cluster in an appropriate direction. For both stability of mean occupancy and to achieve a specified occupancy rate, relaxing these assumptions would generally require larger cluster sizes.

A Spatially Explicit Landscape Model

The landscape model links an organism's survival and reproduction explicitly to its current habitat location. In reality, habitats range in quality from those that support demographic rates resulting in a net gain of births over deaths (source areas) to those that yield a net loss (sink areas). The latter habitats would be unoccupied in the absence of immigration from source areas. As Pulliam (1988) has argued, it may be that habitat-specific demographic rates are more important than age-specific rates to a species' long-term population dynamics. In this model, a population's rates of survival and fecundity will vary based on landscape configuration and the distribution of habitat types. The model, a two-sex, single-organism simulator, assumes that each organism must search the landscape to find new territories and mates. Each organism is born, moves, attempts to find a mate and breed, and dies. This format allows the behavior of each individual to be simulated by following a series of probabilistic rules.

Male and female behavior in this model is similar to that in the territory-cluster model. Males search for territories to occupy. If they find a suitable nest site, they stop moving and become territorial. The likelihood of settling in a given site is a function of the habitat quality of that site. Males remain on their selected site until they die or the site becomes unsuitable for nesting. If the site becomes unsuitable, the males become nonterritorial and reinitiate search. Females are born and disperse from the natal site to seek unpaired, territorial males. When they find a territorial male, they obligately pair. Once paired, females remain on site until they die or the site becomes unsuitable for nesting.

Paired individuals split up when one member of the pair dies, or the site becomes unsuitable for nesting. If the female dies, the male remains territorial and stays on site. If the male dies, the female has no site fidelity and will initiate search for a new mate. If the site becomes unsuitable for nesting, both members search independently for a new site. The movement of females after loss of their mate is supported by field data. In general, females move more often than males, occasionally leaving sites to search for new mates even when their previous mates are still alive.

In the landscape model, by contrast with the previous two models, if a juvenile fails to locate an unoccupied, suitable site it does not die--rather, it becomes a floater. As a consequence, search efficiency has less of a direct effect on juvenile survival rate, but a strong effect on the dynamic movement between the reproductive and nonreproductive stages. To the extent that search inefficiency prevents pair formation, fecundity declines and λ decreases accordingly.

Demographics

All demographic parameters are linked to site quality. Individual mortality and fecundity are determined by the quality of the site occupied at the beginning of each time-step. In keeping with the stage-structured approach, risks are assumed to be constant within a stage over the course of a year. The year is divided into i time-steps, and the risk per step for an owl in stage-class j occupying habitat type k is defined as the i th root of the yearly risk for class j and habitat type k .

In the model analyses described below, we allow a maximum of three habitat types: (1) suitable habitat with associated vital rates from table 8G, initially scaled by $1/\lambda$ to provide for a stable or growing population; (2) sink habitat with reproduction and survival below that needed for a stable population; and (3) unsuitable habitat that allows survival at reduced rates, but no reproduction. The model structure will support additional categories of habitat quality, but available data do not support this degree of resolution.

Movement

The map is divided into a fixed array of grid cells, each representing one territory-sized unit. The grid is hexagonal to allow more realistic movement. The rate of movement depends on the size of the grid cell and the number of time-steps per year. Individual moves are restricted to adjacent cells. The mobile classes of the owl (nonterritorial males and females) have an opportunity to move at each time-step. To ensure that certain birds or areas of the map are not given preferential access to open territories or mates, the order of movement is fully randomized at each time-step.

In its simplest implementation, movement is a random walk. The model, however, allows owls to search with "intelligence"; that is, they may favor movement through good habitat and avoid poor habitat. Similarly, females may move obligately to known territorial males, and nonterritorial males may be averse

to crossing into defended territories. This intelligent behavior is modeled by giving the owls absolute knowledge of the quality of the cell they occupy and partial knowledge of adjacent cells. They have no knowledge of more distant parts of the landscape. This knowledge takes the form of a series of switches and weighting factors that condition the probability of movement (table 9C).

Three boundary conditions can be specified at the map edges: absorbing, reflecting, and wrap-around. In addition, internal reflecting zones can be created by specifying a land type for which the owls show complete aversion.

Fledglings

Fledglings are defined for model purposes as young that survive to disperse. We assume both good and bad years for fledging and complete correlation in reproductive pulses among populations. If it is a good year, then the pair produces fledglings according to a beta random variable ranging from zero to the maximum clutch size. Two levels occur at which variability can affect the number of fledglings. If the area under the beta distribution is concentrated around the mean clutch size, the population will pulse based on the frequency of good years. When a good year occurs, all pairs at all sites will produce at about the mean number of fledglings. If the probability of a good year is 1.0, variability in the number of fledglings will occur on an individual-territory basis and will depend on the parameters of the beta distribution. Both parameters are linked explicitly to habitat quality and the stage-class of the pair. Because this is a two-sex model, the sex ratio of fledglings is also adjustable.

Relevant Inferences to the Southern California Metapopulation

Effects of Cluster Shape

The cluster model assumed circular clusters, but the landscape models allowed us to closely specify the shapes of clusters

Table 9C -A summary of factors that can affect an individual's movement in the landscape model.

Factor	Based on	Sex	Form
Becomes territorial	Habitat quality/occupancy	M	Probabilistic switch
Aversion	Habitat quality	M/F	Weighted probability
Site fidelity	Habitat quality	M/F	Weighted probability
Linear propensity	Behavior	M/F	Weighted probability
Territorial aversion	Occupancy	M	Weighted probability
Female finds male (current cell)	Occupancy	F	Absolute switch
Female finds male (adjacent cell)	Occupancy	F	Probabilistic switch
Global boundary	-	M/F	

(habitat islands). To compare general model results between the two models, the landscape model was used to project population trends from a number of hypothetical landscapes with an identical number of suitable sites (McKelvey et al. in press). Other than suitable habitat configuration, there were no differences in the initial values of any model parameters. The map boundaries were wrap-around so that the exact location of the habitat within the map frame was unimportant. In these simulations, only two habitat qualities were simulated: habitat suitable ($\lambda = 1.0$) and unsuitable for nesting. The movement parameters deviated only slightly from a random walk—birds were twice as likely to choose suitable habitat, males treated occupied habitats identical to unsuitable habitat, and birds were twice as likely to move in the same direction as to choose a different direction.

Model results parallel the territory-cluster model, showing that a clustering of suitable habitat is both more efficient in terms of mean population level and more stable in terms of lowered extinction probabilities than is a random structure. We found, however, that the shape of the cluster had an important effect on its stability properties and mean occupancy rates. A cluster with a low ratio of edge to area supported a larger population and was more stable than continuous clusters of identical area but with greater irregularity (compare figs. 9J and 9K). A high edge-to-area ratio had a negative impact on demographic stability: the rate of decline in a large, highly irregular cluster was similar to the decline rate of the dispersed cluster system, but it had a lower extinction likelihood.

Source-Sink Dynamics

Previous results demonstrated the impact of reserve shape when each landscape cell was either suitable or unsuitable for breeding. In that case, the breeding population was limited entirely to the suitable habitat. In a landscape containing a gradient of habitat qualities, source locations would produce an excess of individuals, and sink locations would absorb some of the dispersing juveniles from the sources. Consequently, when a possibility exists of nesting in sink locations, populations will occur exterior to the source habitat areas even though vital rates in the sinks do not allow for a self-supporting population (see similar conclusion in Buechner 1987, p. 71). The presence of sink areas adjacent to habitat clusters may adversely affect the stability properties of the clusters. In our simulations, the mean population size of the entire landscape was higher in the source-sink system, but the mean occupancy of the reserve clusters was lower and the variability among the population size trajectories increased with time.

In summary, the landscape model demonstrated that the shape of clusters is nearly as important as their size. As a result, the size of irregularly shaped clusters must be larger to maintain the same mean occupancy rate compared to clusters more circular in shape. Further, model results indicate a possibility that in landscapes exhibiting a gradient of habitat qualities, the presence of sink habitats adjacent to reserves may have opposing effects. Overall population size is increased but projected population sizes are more variable. In terms of persistence likelihoods, however, we believe that increases in population size associated with increases in the amount of sink habitat should

more than compensate for any negative effects associated with increased variability in the sizes of populations within clusters.

Application of the Landscape Model to the Southern California Metapopulation

Constructing the Map

The map, which characterized in a spatially explicit fashion the distribution of owl populations and their habitat islands in southern California, was based on the 1986-91 cumulative spotted owl survey data done primarily on public land (Chapter 3; Stephenson 1991). Each township (6-x-6 miles) in the Southern California Province was characterized according to the estimated number of owl sites it contained (fig. 4C). The collection of sections with owl sites defined the habitat islands and corresponded closely to locations listed in table 9A and shown in figure 9A. Thus, owl locations at a scale of 36 square-mile sections defined the location of suitable owl habitat. Each section, representing about 23,000 acres, was represented by nine hexagonal grid cells. This produced grid cells of about 2,500 acres, roughly corresponding to the size of individual spotted owl home ranges during the breeding season in mixed-conifer forests of the Sierra Nevada (table 6B). If a section had >9 sites, the extra sites were added to an adjacent section. The initial map, as it appears at the beginning of a simulation, is shown in figure 9L.

Imposing a fixed grid-cell size on a species with geographically variable area requirements is problematic. The number of owl sites will be underestimated in those parts of the species' range where its area requirements are smaller. For those habitats in southern California where home ranges are apparently the smallest (riparian/hardwood areas; table 6G), we examined the distribution and spacing among known owl sites. Most were separated by large areas of chaparral, making it unlikely that a single grid cell would contain two or more home ranges. In some cases where a single cell could contain two or more owl sites, we have probably underestimated the number of sites.

Initializing the Map

The map was initialized, in terms of owl pairs, using the estimated number of suitable sites per township (36 square miles) (see fig. 4C). If a township, for example, was estimated to contain six pair sites, then six sites (grid cells) were randomly selected from among the nine sites representing that township on the map. Each simulation was initialized with about 360 pairs of spotted owls.

For most simulations we used only two habitat types—suitable and unsuitable. Suitable habitats were characterized by a λ , slightly >1.0. Unsuitable habitats (the landscape matrix)

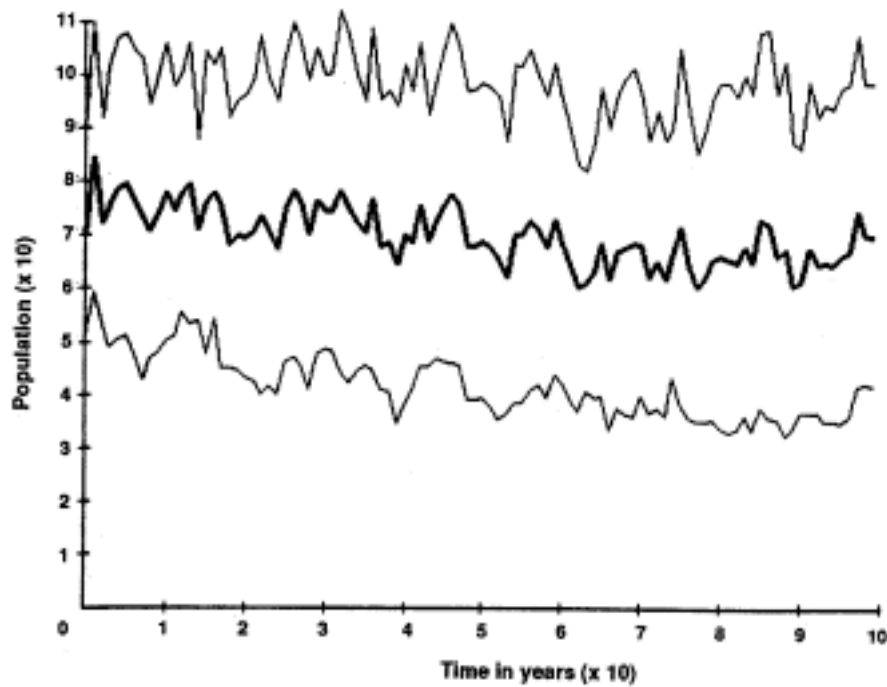
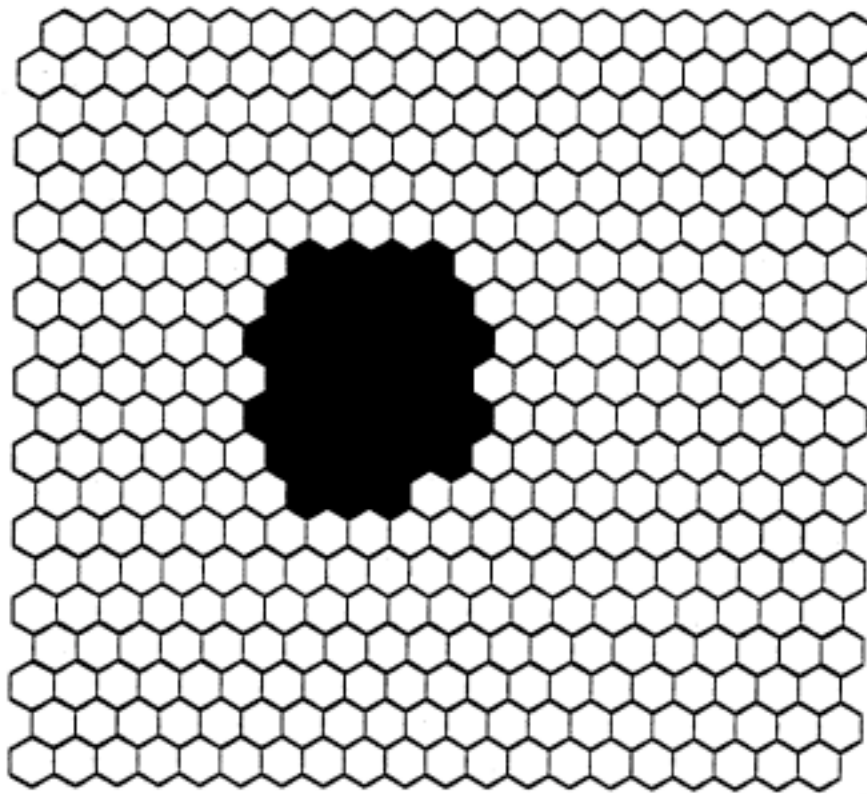


Figure 9J-Landscape model simulation showing simulated landscape with suitable habitat arrayed in one large, regular block. Results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.

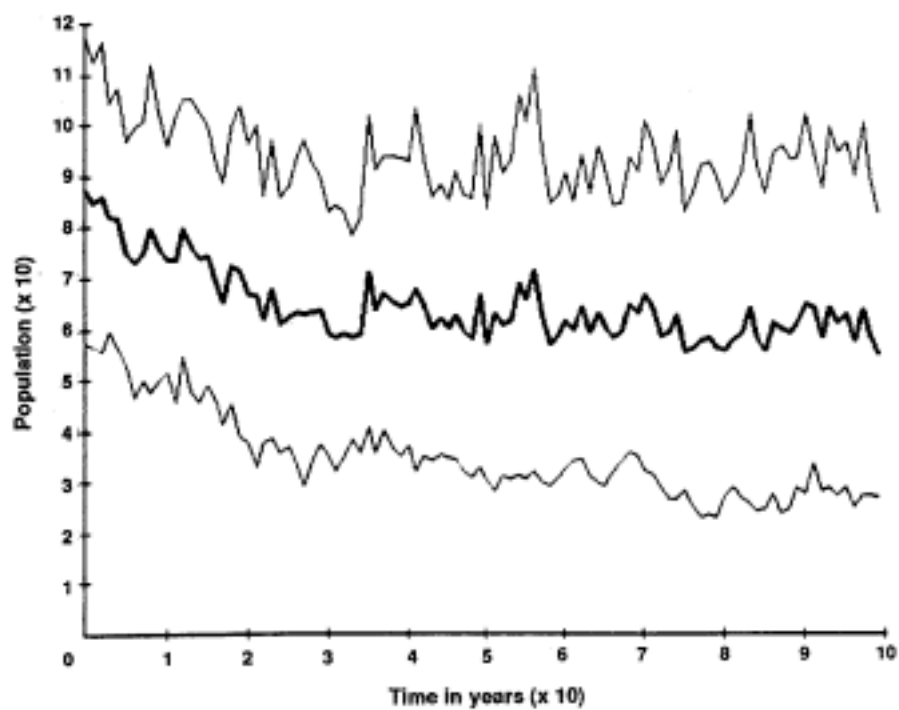
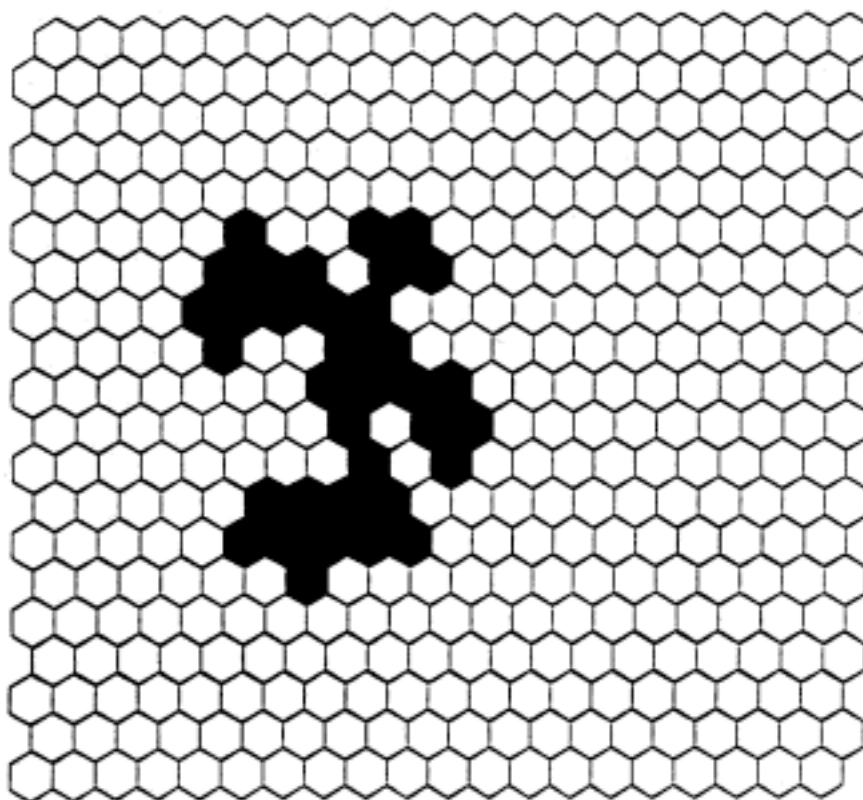


Figure 9K-Landscape model simulation showing simulated landscape with suitable habitat arrayed in one large, irregular block. Results are based on 30 simulations. The heavy line represents the mean population, the thin lines are one standard deviation from the mean.



Figure 9L—The southern California metapopulation "map" used as the initial condition for subsequent simulations based on the landscape model. In this map showing the initial condition, hexagonal cells defining the "islands" were assumed to be suitable habitat. Areas outside of the islands (the matrix) were unsuitable.

were characterized in different ways according to expected survival rates (table 9D), but these sites never supported reproduction. Sink habitat was introduced in a third set of simulations; it had an assumed $\lambda_s = 0.80$.

Simulations

All simulations assumed stochastic fecundity rates, expressing both within- and among-year variation (see above). Survival rates only expressed within-year variation based on binomial sampling probabilities. All owls experienced similar pulses in reproduction—that is, we assumed complete spatial autocorrelation within the metapopulation. Simulations represented 150-year projections and were based on 50 replications. Various assumptions were made about the search capabilities of dispersing juveniles and the degree to which the matrix surrounding habitat islands could support owl survival (table 9D). In general, birds were twice as likely to move to a suitable cell than an unsuitable cell. This had the effect of making it less likely to leave an area of clustered, suitable habitat and more likely to be attracted to such an area. The map was static—after setting initial conditions, there were no changes in the amount or distribution of habitat—for all simulations.

Each suitable site was assumed to contain a pair of owls at the initiation of each simulation. Therefore, the population was effectively above its carrying capacity at time zero (figs. 9L–9P). Even under optimum conditions, a suitable site would have an expected pair occupancy rate <1.0 because of random mortality events. As a result, each simulation showed an initial population

decline. Comparisons of results based on population trajectories should be made over the last 100 years of each simulation.

Interpreting Simulation Results

Results of simulations should not be interpreted as estimates of extinction likelihoods. We believe it is premature to make reliable estimates of extinction likelihoods at this time, as too many uncertainties exist about the long-term values of the vital rates and the dispersal capabilities of juvenile owls. For example, we do not know whether gaps between adjacent habitat islands are total or only partial barriers to dispersal. The most relevant output from the simulations are the maps, which summarize mean occupancy rates for each cell over the 150-year simulation interval. In general, areas of the landscape with very high occupancy rates represent potential source areas. In contrast, areas of the landscape with low occupancy rates represent sink areas. Interpreting the model results in a visual and spatially explicit way allows insights into areas of the landscape that are particularly vulnerable to local extinction events, as well as areas that represent sources for immigrants to other local populations.

Results

All simulations were initialized according to the spatial pattern of suitable habitat shown in fig. 9L. Suitable habitat supported demographic rates, on average, that yielded a λ slightly >1.0 . Differences among the simulations reflect different assumptions about the survival risks experienced by owls moving

Table 9D-Values of the demographic rates in suitable habitat and in the matrix for different model simulations. Risks to dispersing birds and dispersal capability were varied among the different simulations.

Demographic rates	Suitable habitat	Simulation						
						Source reduction	Source/sink	
		A	B	C	D		Matrix	Sink
Juvenile survival	0.358	0.20	0.20	0.18	0.01	0.18	0.18	0.30
Subadult survival	0.903	0.70	0.70	0.45	0.01	0.45	0.45	0.75
Adult survival	0.903	0.80	0.80	0.45	0.01	0.45	0.45	0.75
Fecundity	0.279	0	0	0	0	0	0	0.175
Dispersal capability		22	44	22	22	22	22	22

through the matrix among the habitat islands. Because dispersal abilities are largely unknown, we bracketed a range of possible responses, ranging from very optimistic to an assumption of almost complete isolation of local populations (see table 9D). None of the simulations assumed any absolute barriers to dispersal in any direction, with the exception of the Pacific Ocean, which acted as a reflecting barrier.

Simulations A and B

In these simulations we made optimistic assumptions about the survival risks experienced by dispersing birds. Survival rates were only slightly depressed from values experienced in suitable habitat (table 9D). Simulation A suggested a relatively stable metapopulation structure with areas of high occupancy concentrated in the San Gabriel-San Bernardino Mountain complex (fig. 9M). Smaller and more isolated subpopulations, such as Tecuya Mountain, the South Santa Lucia Mountains, and Palomar Mountain (fig. 9A), had significantly lower mean occupancy rates, indicating frequent turnover within sites with subsequent recolonization at irregular intervals. In general, the lower the mean occupancy rate of a site, the longer the interval to recolonization after a turnover event.

Parameter values for simulation B were identical to A, except that we doubled the search capabilities of dispersing owls (table 9D) and the equilibrium population was about 15 percent higher than observed in simulation A. Results were similar except that occupancy rates were elevated overall, most significantly in the smaller but isolated clusters (for example, in the Los Padres Ranges of Ventura and Santa Barbara counties, and on Mount San Jacinto) (fig. 9A). Thus, sites were being recolonized at a greater rate.

Simulation C: Increasing Dispersal Costs

Assumptions made in the previous simulations about risks to movement in the matrix were very optimistic. In this simulation we relaxed those assumptions somewhat, and assumed that survival rates in the unsuitable matrix habitat were half those in suitable habitat (table 9D). Results indicated that small, remote subpopulations had occupancy rates in suitable sites of only 20-40 percent (fig. 9N). That is, suitable sites in these habitat islands are unoccupied 60-80 percent of the time. Occupancy

rates in the San Gabriel-San Bernardino complex remained high because, having many tightly clustered owl sites, they were effectively immune to costs of dispersal through matrix habitats. Total population size was reduced by about 30 percent, compared to simulation A, but appeared to reach an equilibrium within the last three decades of the simulation (fig. 9N).

Simulation D: Population Isolation

In this simulation, we set movement costs in the matrix very high so that all but the closest clusters were effectively isolated from each other. The effects were dramatic. Overall population size was reduced by about 40 percent, and the population size did not equilibrate until the ninth decade (fig. 9O). High per-site occupancy rates were restricted to relatively large clusters (>40 sites) and with mostly contiguous sites (fig. 9O). In areas with a low density of suitable sites, even habitat islands with about 40 sites, such as the Palomar Mountain/central San Diego County/Cuyamaca/Laguna Mountains complex (fig. 9A), were unstable and had very low occupancy rates (<15 percent). All local populations between the western part of the San Gabriel Mountains and the San Rafael wilderness (Las Padres NF) experienced frequent local extinction events (fig. 9O). The San Gabriel/San Bernardino complex remained the most stable locus of high occupancy within the metapopulation.

Simulation E: Source Reduction

The San Gabriel/San Bernardino complex consistently had the highest occupancy rates and was the key source population for immigrants into other areas of the metapopulation. Therefore, we wanted to investigate its resilience to disturbance and the effect that such disturbance would have on the stability of the rest of the metapopulation. To simulate this scenario, we randomly changed 1/3 of the suitable sites within this complex to unsuitable sites and assumed moderate survival costs to movement through the matrix (table 9D).

The effect of the simulated decline in habitat within the largest population was pronounced. The overall size of the metapopulation was markedly reduced, and an equilibrium size had not been attained even after 150 years (fig. 9P). Comparing figures 9P and 9N suggests that loss of habitat within the largest source population would greatly reduce occupancy rates through

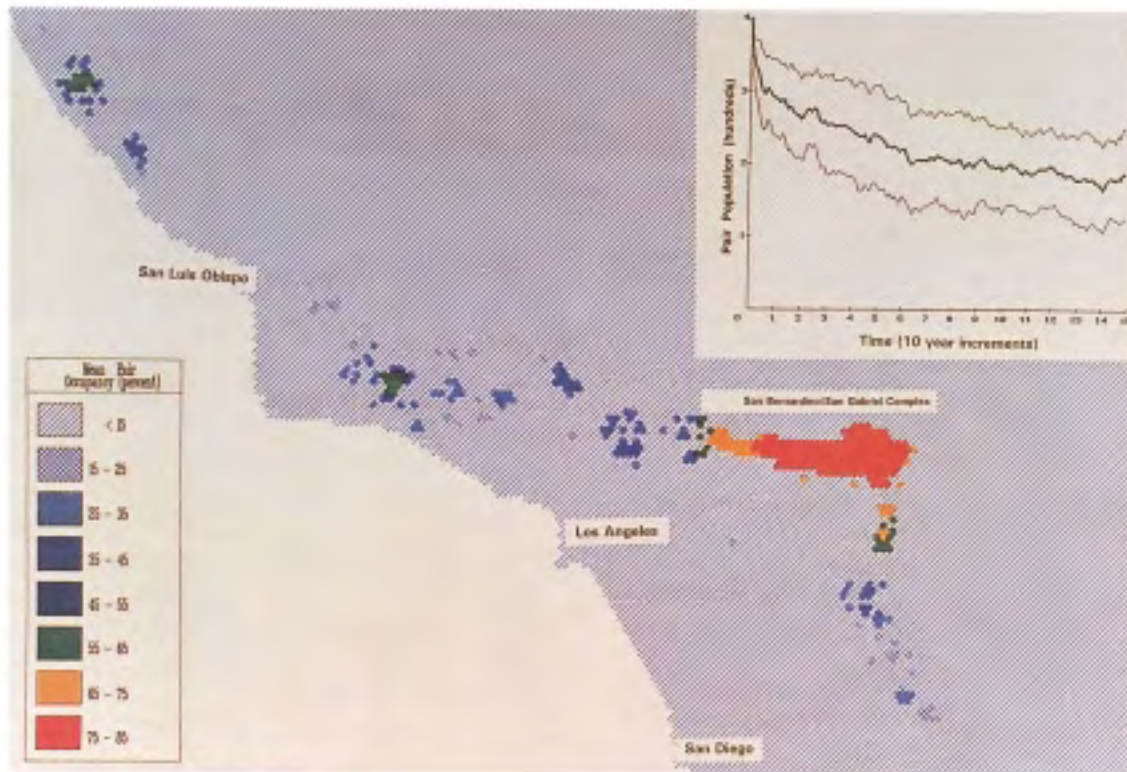


Figure 9M-Landscape model simulation A, showing mean ($\pm$ standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

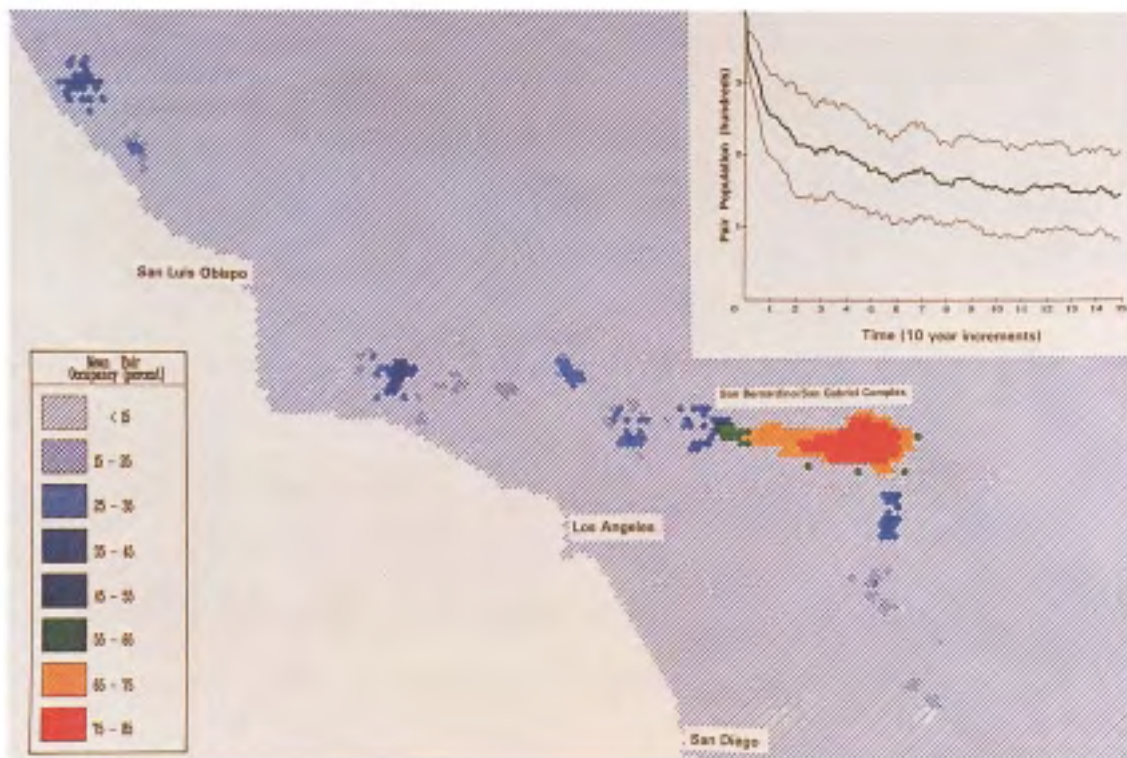


Figure 9N-Landscape model simulation C, showing mean ($\pm$ standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

out the metapopulation. In addition, the small local populations of owls immediately to the west of the complex had gone extinct or had occupancy rates less than 20 percent. Interestingly, the overall size trajectory for the metapopulation in this simulation showed a steeper decline than that for isolation (simulation D) (fig. 9O). That is, decreasing the net production of potential colonists from the major source population within the metapopulation appeared to have more adverse effects than increasing the degree of isolation among local populations. Collectively, these results suggest that, to a large extent, the persistence of much of the southern California metapopulation relies upon maintaining the habitat integrity of the San Gabriel/San Bernardino habitat complex.

Simulation F: Source-Sink Effects

For this simulation we randomly changed 50 percent of the suitable (that is, source) habitat ($\lambda = 1.02$) within the entire metapopulation (fig. 9L) to sink habitat ($\lambda = 0.80$). This simulation thus represented both a source reduction and the introduction of sink habitat. Sink habitat, unlike matrix habitat, supported both survival and reproduction, but at nonreplacement rates (table 9D). We assumed limited ability by the owls to discriminate between source and sink habitats—searching birds were only 10 percent less likely to settle in sink habitat. Simulation results suggested a dramatic, exponential decline to metapopulation extinction within about 100 years (fig. 9Q). Average occupancy rates over the interval were >15 percent only for the San Gabriel/San Bernardino complex. Even this habitat island was unstable, however, and could not sustain its population over the long-term. Given this level of source reduction (50 percent), even greatly increasing the owl's ability to discriminate source from sink habitats did not stabilize the population.

Discussion

Simulation results suggested that the San Gabriel/San Bernardino owl population plays a pivotal role in maintaining the southern California metapopulation. Unfortunately, the resident, territorial population of spotted owls in the San Bernardino Mountains has declined precipitously since 1987 (LaHaye et al. in press; Chapter 8). If the territorial population is in some sort of dynamic balance with a nonterritorial (floater) population, then these sorts of declines may be accommodated over the short-term and pose no long-term threat (see Franklin 1992). If these trends also characterize the other local populations, however, and were to persist for another 5–10 years, we believe the persistence of the entire metapopulation would be at risk.

Several key factors remain unknown. For example, we do not know if these trends characterize the other local populations. If the decline in the territorial population in the San Bernardino Mountains is a response to region-wide, environmentally in-

duced variation, then other local populations may be responding in a synchronous fashion. The degree of environmental correlation within the metapopulation is also unknown. Regional rainfall patterns, however, suggest that the degree of correlation may be high (figs. 8A and 8B). The effects of environmental correlation on persistence among populations depends upon their life histories, including diet switching and changes in prey availability (for example, Horton and Wright 1944, Vogl 1967). Modeling efforts by Harrison and Quinn (1989) suggest that even strong environmental correlation in extinction risks will not have a major effect on persistence time for large vertebrates, except when local populations become very small—but see a counter argument in Stacey and Taper (1992). Our models all assumed a complete correlation among populations in their response to environmentally induced variation in fecundity.

Persistence in metapopulations also depends critically on dispersal capabilities, distances between local populations, and risks involved in moving between habitat islands. The persistence of small, local populations with high turnover rates depends upon rescue by colonists from other populations in the metapopulation. This, too, is an area involving much uncertainty. The dispersal capabilities of California spotted owls and how they move through heterogeneous landscapes are mostly unknown.

Given the uncertainties regarding synchrony of extinction risks among local populations, whether the declines in the size of the territorial population will continue into the future, and the dispersal capabilities of juvenile owls, we believe it is premature to estimate extinction likelihoods. Simple application of the current estimates of the vital rates for the San Bernardino population (table 8G), for example, would show a rapid collapse to extinction. Our approach has been to gain general insights into the management of owl habitat in terms of its quality, amount, and geometry. We did this by viewing population dynamics as emergent reflections of landscape pattern and the distribution of habitat types. The landscape model was particularly valuable because it allowed us to gain insights into the dynamics of individual populations related to specific locations on the landscape.

Simulation results suggest that, in those parts of the species' range where suitable habitat constitutes only a small fraction of the landscape, populations are unstable and have low occupancy rates. The pattern is improved if the metapopulation contains a large source population. This result parallels the individual-territory model and predictions from Lande's (1987) modeling. That is, when the amount of suitable habitat becomes too small a percentage of the landscape, thresholds are encountered and populations may decline to extinction (fig. 9O). This occurs despite the continued presence of suitable habitat at these locations.

The general predictions from the cluster model were also demonstrated by the landscape model. Specifically, when clusters (habitat islands) became too small, or suitable habitat too diffuse, occupancy rates dropped precipitously. Assuming moderate to strong risks to dispersing birds, only those clusters with more than 40 sites and largely contiguous habitat showed high occupancy rates (figs. 9M and 9N). For example, the isolated sites on the western slope of the San Gabriel Mountains dropped to low occupancy rates when dispersal costs were high (fig. 9O).

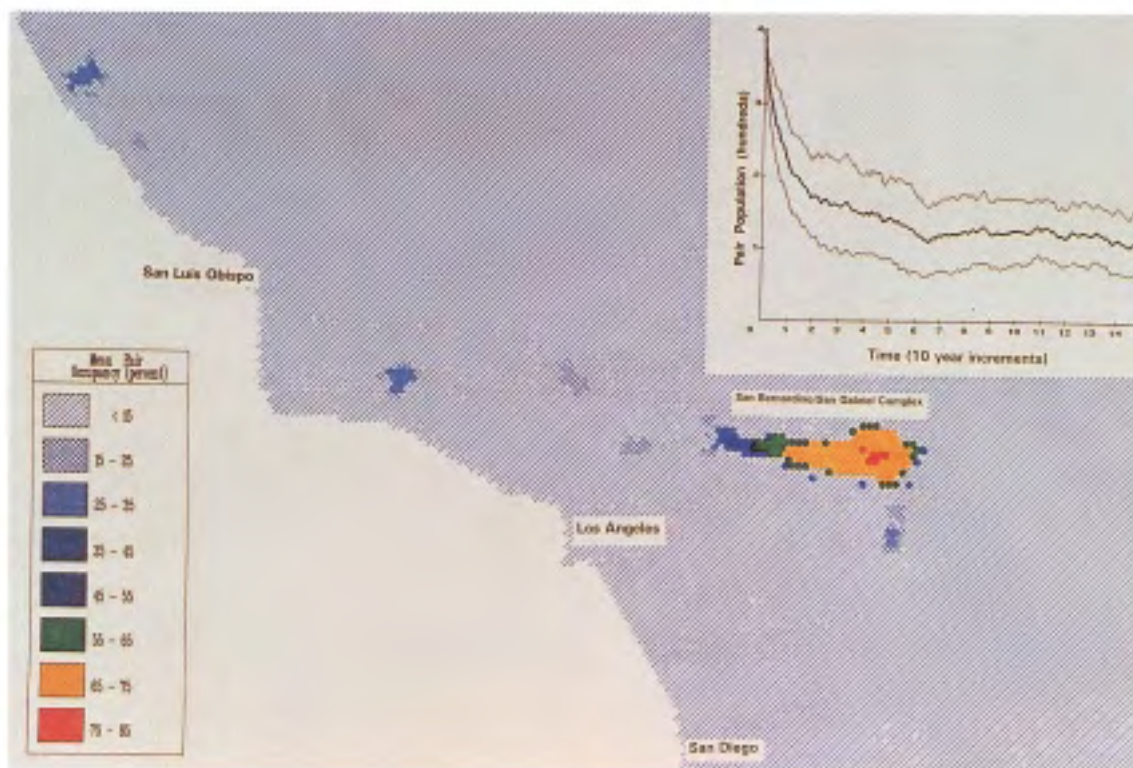


Figure 9O-Landscape model simulation D, showing mean($\pm$ 1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

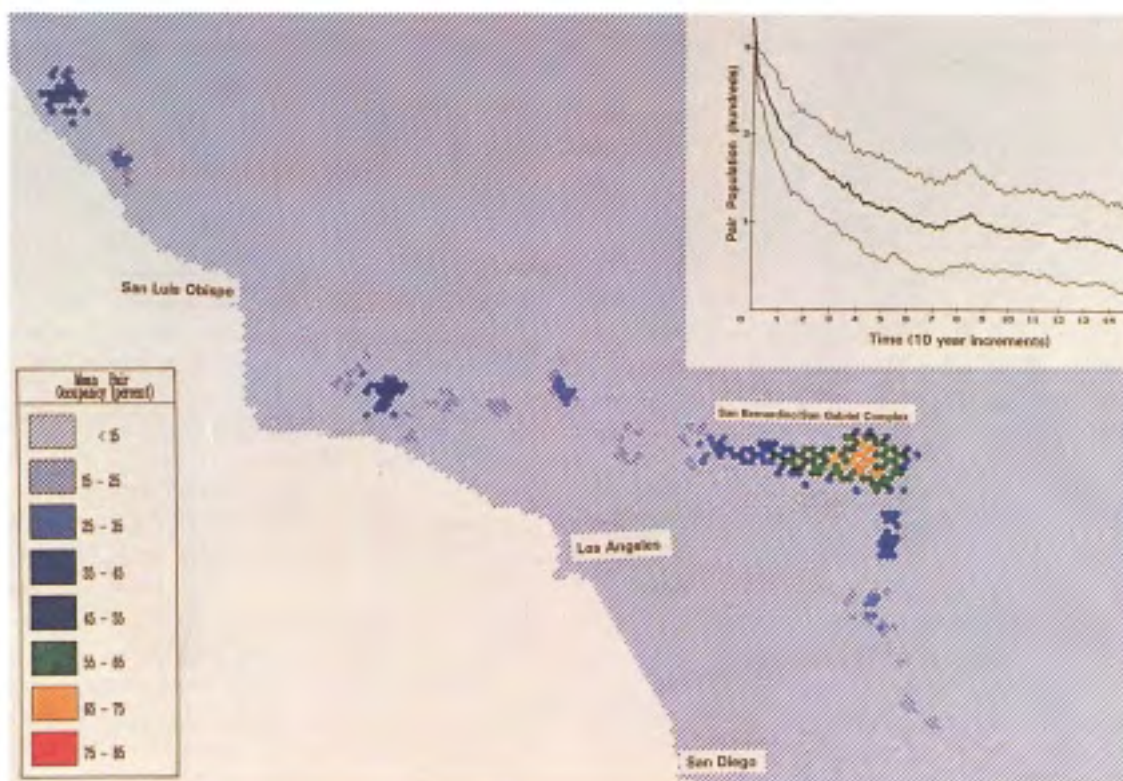


Figure 9P-Landscape model "source reduction" simulation, showing mean ($\pm$ 1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

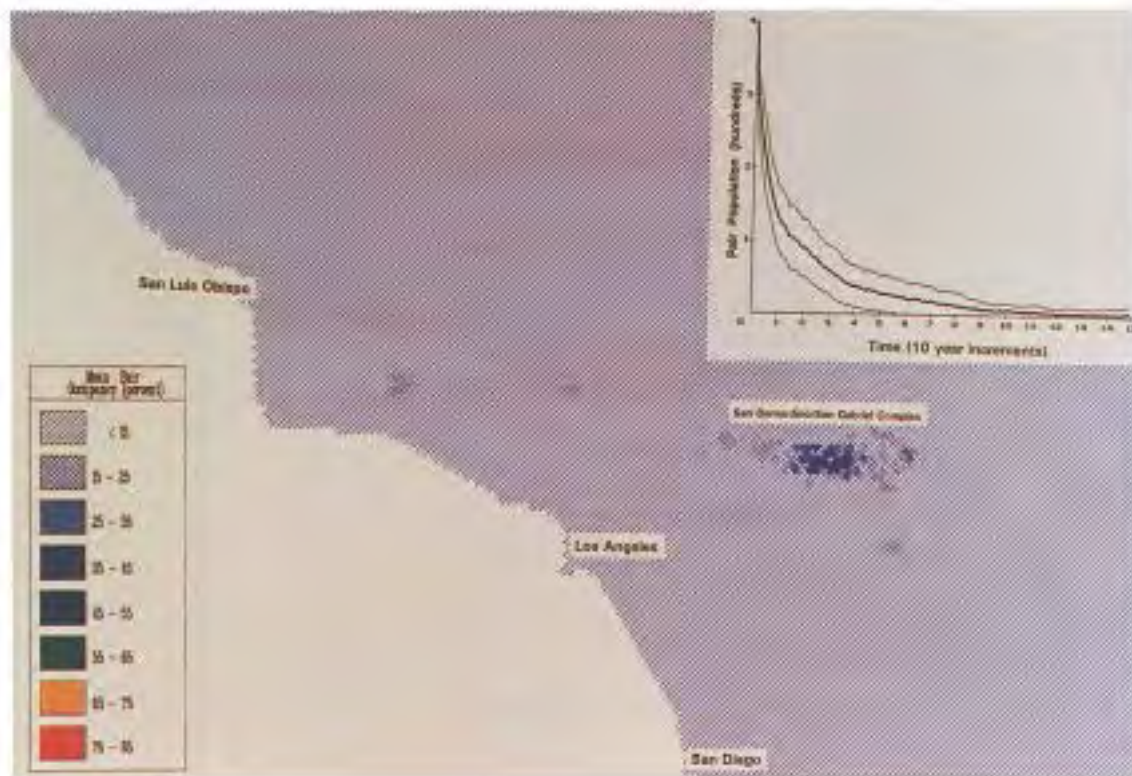


Figure 9Q—Landscape model "source/sink" simulation showing mean (± 1 standard deviation) 150-year trajectory of the metapopulation (inset) and the mean pair occupancy rate of habitat cells (from fig. 9L) averaged across the time interval and based on 50 simulations (parameter values used in the simulation are described in table 9D).

The simulations also illustrated the interaction between size and spacing (fig. 9G). The islands near the San Gabriel/San Bernardino complex retained moderate occupancy rates even though they were small and dispersal risks were high (for example, the San Jacinto Mountains, 11 miles from the southern San Bernardino Mountains). In contrast, the population occupying the Los Padres Ranges, >30 miles from the western edge of the San Gabriel Mountains, declined to <40 percent mean occupancy even though this habitat island supports at least 65 pair sites. In general, the largest clusters with the shortest nearest-neighbor distances (table 9A) were the most stable and had the highest occupancy rates.

A consistent finding from the simulations, and predictable from our simpler models, was the significance of the San Gabriel/San Bernardino population to the dynamics of the entire metapopulation. Simulated declines in the amount of suitable habitat in this complex lowered occupancy rates throughout the entire metapopulation (fig. 9P).

Population declines were particularly pronounced when half of the source habitat was changed to sink habitat and the owl's ability to discriminate among these habitats was limited (fig. 9Q). As the ability to discriminate source from sink habitats increased, the rate of decline of the population became less pronounced, but with a 50 percent reduction in source habitat no positive equilibrium was attained. When selection is imperfect, some owls may settle in sink habitat and reduce the occupancy rate in source habitat. The result is a decline in population size, often with no positive equilibrium. This finding is consistent

with results reported by Pulliam and Danielson (1991) based on a different model formulation.

In some situations the presence of sink habitat may contribute to metapopulation size (Pulliam and Danielson 1991, Howe et al. 1991). Whether sink habitat acts to enhance metapopulation persistence depends critically on the owls ability to discriminate between source and sink habitats. If some owls that would otherwise settle in source habitat, are attracted to, and settle in, sink habitat then the effects can be negative. The extent to which spotted owls can discriminate among habitat types in terms of their expected birth and death rates is unknown. It is unlikely, however, that habitat selection is perfect. Because search is finite, population trend ultimately depends upon the amount and distribution of source habitat, even when selection among source and sink habitats is perfect.

In the case of the California spotted owl, the effects of landscape pattern on survival during dispersal may induce high levels of both spatial and temporal variation in juvenile survival rate. If habitat becomes more fragmented, the uncertainty of successful juvenile dispersal will become progressively more relevant to the likelihood of persistence. Even in a diffuse system with many suitable territories, pair occupancy will be low because of low recolonization rates. As a result, in a highly fragmented system, positive density-dependent growth rates usually associated with low population densities are unlikely. The effects of changes in landscape pattern on demographics are particularly significant if losses occur disproportionately in source habitat (fig. 9P).

Habitat-induced population declines also occur at the scale of the individual pair site or territory. Territories, the basic unit for our models, can be thought of as small islands, each having a maximum of one reproducing pair. They are similar to islands in that (1) they have spatial dimension—they occupy a certain area of the landscape; (2) they have some level of habitat quality; and (3) when they experience local extinction (one or both members of the pair either dies or emigrates), they must be recolonized through immigration from outside the territory or by an existing, nonterritorial floater within the territory.

The concept of territories as individual islands, with habitat quality explicitly defined by the expected values for birth and death rates, is key to understanding the dynamics of the spatial models. In all of the spatial models, search for suitable habitat is a sampling process. In the individual-territory model, the landscape is searched randomly and search success depends on the average density of suitable sites on the map. In the territory-cluster model, random search is confined to the clusters, which vary in the number and adjacency of suitable sites. Search success in this model depends primarily on the density of suitable territories within the cluster and secondarily upon the density of clusters in the landscape. In the landscape model, search success is defined at each time-step and for each owl by the density of suitable habitat in the territories immediately adjacent to the cell ("territory") currently occupied. When three or more habitat types occur, each cell on the map is not only a location, but, in terms of search success, a habitat-quality state with specific transition probabilities controlling movement into alternate states.

In a spatial model with search, a system composed of territorial clusters is more stable than a diffuse system because clusters produce regions where search efficiency is maximized. Circular clusters are the most stable because the density of suitable habitat is locally maximized. All other geometric forms will have lower search efficiency when compared with a circular cluster, unless clusters have strongly reflecting boundaries. In a cluster with a sufficient number of suitable territories, a population can recover from low occupancy because search efficiency will remain high. The key to stable populations within clusters is that they contain a sufficient number of high quality ($=$ suitable) sites ($E[\lambda] \geq 1.0$) to support population large enough to avoid local extinction due to stochastic demographic events. Surprisingly, it is possible that the presence of marginal or sink habitat may actually reduce population size even though some individuals may breed in these habitats (Pulliam and Danielson 1991, McKelvey et al. in press).

Management Recommendations

Our recommendations for the persistence of spotted owls in the Southern California Province focus on the dynamics of its habitat at two spatial scales. First is the landscape scale. The arrangement of owls and owl habitat across the landscape shows that most of the population is concentrated in the San Gabriel/San Bernardino Mountains complex. Every effort should be made to keep this population intact by maintaining the amount and spatial connectivity of suitable habitat there. Current demographic estimates suggest that the resident, territorial population is in significant decline. This population needs to be closely monitored for the foreseeable future, and attempts must be made to better understand the causes of the decline.

Other smaller, local populations do not have the potential to provide a large number of colonists. These populations are important, however, in diminishing the risk that local populations would simultaneously experience adverse impacts (Den Boer 1968, 1981). Advantages are often gained by distributing populations widely across an extensive geographic area (Quinn and Hastings 1987, Gilpin 1990)—the degree of environmental correlation among local populations is reduced, as is the likelihood of simultaneous extinction events (see discussion in Stacey and Taper 1992).

Local populations will continue to function as part of a larger metapopulation only if they remain connected through dispersal. If local populations become increasingly isolated by reduction in the sizes of habitat islands or by the creation of barriers to dispersal, occupancy rates decline because of a decline in the rate of demographic rescue, and the likelihood of extinction increases (table 3K; see discussion of problem areas in Chapter 3). Small, isolated populations will be the first to be lost to extinction, but even the largest, most continuous populations will experience increased risks if the overall size and spatial extent of the metapopulation is decreased.

Options to decrease population isolation through management efforts are severely limited in southern California. Because the current metapopulation structure is largely the natural expression of vegetation patterns resulting from edaphic, topographic, and climatic constraints, little opportunity exists to enhance dispersal habitat between subpopulations. The obvious goal, therefore, is to avoid creating additional barriers to dispersal beyond those not amenable to management.

The second level of concern is at the scale of the individual territory. It may be that the greatest threat to persistence of spotted owl populations is a subtle but continual decline in habitat quality (that is, a gradual conversion of source to sink habitat), on a site-by-site basis. As discussed in Chapter 8, subtle declines in λ will be difficult to detect except in the largest and longest-term demographic studies. Pulliam (1988) and Pulliam and Danielson (1991) concluded that knowledge of habitat-specific

demographic rates is ultimately needed for the effective management of wild populations. We agree. We must be able to target for preservation those habitats needed today for the species' persistence, and learn how to manage for such habitats in the future. Only by understanding the relations between demographic rates and the structure and composition of vegetation at the stand level can we be certain of maintaining habitat that provides for a stable or growing population.

Both scales of research and management-landscape and territory-are equally important, and both must be pursued to address the persistence requirements of spotted owls in southern California.

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Chapter 10

General Biology of Major Prey Species of the California Spotted Owl

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Full understanding of the habitat relations of California spotted owls depends, in part, on knowledge of the habitat relations of their primary prey species. For example, the northern flying squirrel is the primary prey of the owl in conifer forests of the Sierra Nevada, comprising as much as 61 to 77 percent of the total biomass eaten in some localities and seasons (table 4A). The dusky-footed woodrat is the primary prey in lower-elevation forests and woodlands of the Sierra Nevada and throughout all habitats in southern California, making up 74-94 percent of the diet, by weight, in various areas. Current evidence indicates that suitable nest sites and the most common foods of northern flying squirrels are usually found together in mature and older forests, which may help us understand why spotted owls forage more often in such forests. Woodrats are typically associated with shrubfields, especially those dominated by thick-leaved, evergreen species. Spotted owls in the Sierran foothills and in southern California commonly occur in forests and woodlands with a light to moderate shrub understory, or that adjoin more extensive stands of chaparral. In addition, radio-tracking studies of spotted owls in the Sierra NF have shown that their home ranges in Sierran mixed-conifer forests are measured in thousands of acres, but those in foothill riparian/hardwoods are measured in hundreds of acres (Neal et al. 1990). This difference is probably related, at least in part, to the facts (1) that woodrat densities are generally several times higher than flying squirrel densities and (2) that woodrats weigh nearly twice as much as flying squirrels.

Here, to expand a general understanding of spotted owl ecology, we present brief biological descriptions of several species of small to mid-sized mammals that most commonly occur in diets of the California spotted owl (see Chapter 4).

geographic range (see color photo 5-29). They are most numerous where shrub cover is dense, and least abundant in open areas (Fitch 1947). They are one of few small mammal species of chaparral habitats that flourish in old, dense stands (Quinn 1990).

Habitats that are unsuited or poorly suited for dusky-footed woodrats include open grasslands or fallow, weedy ground; sparsely wooded forests; woodlands solely of conifers or with little shrub understory; and pure stands of chamise, manzanita, or ceanothus (Linsdale and Tevis 1951).

In the Sierra Nevada, this woodrat occurs generally below 5,000 feet in elevation (lower in the north-about 3,300 feet at Mt. Lassen and 4,000 feet in Yosemite National Park (NP), and higher to the south-rare at 6,000-6,500 feet in the Kern River drainage). It occupies foothill riparian/hardwoods in the northern San Joaquin Valley. The highest capture rates of woodrats in the foothills of the west-central Sierra Nevada were in chaparral, woodland, and forest communities with a mix of overstory trees and shrubs (table 10A). These results appear to agree with those of Sakai and Noon (1992a), who indicate that dusky-footed woodrats in northwestern California are most abundant in brushy stands of sapling/early-aged poletimber. In the southern Sierra Nevada (Kern County), in a chaparral community of ceanothus and interior live oak between 2,560 and 3,200 feet in elevation, woodrats were most often trapped around patches of rock gooseberries, and their nests were common where gooseberry thickets encircled rock outcrops or dead snags (Lawrence 1966).

In the San Bernardino Mountains, the dusky-footed woodrat occurs on both the Pacific and desert slopes, ranging from about 1,600 feet on the Pacific slope and 3,800 feet on the desert slope up to at least 8,000 feet on both sides, where it is the primary prey species of the spotted owl (LaHaye pers. comm.). Grinnell (1908) found most nests in California scrub oak and pinyon associations and few along willow-lined canyons. They occur in big sagebrush/pinyon-juniper woodlands in the New York-Providence mountain chain in eastern San Bernardino County.

In the San Gabriel Mountains, dusky-footed woodrats occur on both the Pacific and desert slopes, exhibiting the same elevational distribution as in the San Bernardino Mountains. In the coastal sage belt, they are restricted to areas close to intermittent streams supporting tall shrubs or small trees. Nests are built mostly of white sage in isolated clumps of lemonade sumac. Population densities -generally are low in this community (M'Closkey 1972). Higher numbers are found in adjacent canyons on densely vegetated slopes. At higher elevations on the desert side, favored spots for nests are thickets of chokecherries, mountain whitethorn, and currants. In the pinyon-juniper woodlands, both conifer species were used for nest sites; but Califor-

Dusky-Footed Woodrat

Distribution and Habitat

Dusky-footed woodrats occur in the Pacific Coast region from the Oregon side of the Columbia River to northern Baja California. Within the range of the California spotted owl, they inhabit coastal, piedmont, and montane chaparral and forest communities. Evergreen or live oaks and other thick-leaved shrubs are important habitat components throughout this woodrat's

Table 10A-Captures of small mammals in snap traps (Museum Specials and Victor rat traps) in various habitats and seral stages in the western Sierra Nevada, California, based on sampling in Amador, Calaveras, Mariposa, Nevada, Placer, and Tuolumne counties. Values are captures per trap night¹ (adapted from Williams and Johnson 1979).

Habitat and Seral stage	Species captured				
	Dusky-footed woodrat	Brush mouse	California mouse	Deer mouse	Pinyon mouse
Annual grassland	0	0	0	0.0910	0
Chaparral					
Grass/forb	0	0	0	0.2340	0
Light shrub	0.0039	0.0133	0	0.0261	0.0011
Dense shrub	0.0098	0.0031	0	0.016	0.0004
Oak/digger pine					
Seral	0.0007	0	0	0.0074	0
Mature	0.0052	0.0319	0.0007	0.0059	0
Ponderosa pine					
Seral	0.0011	0.0015	0	0	0.0011
Mature	0.0007	0	0	0.0020	0
Mixed-conifer					
Seral	0.0048	0.0045	0	0.0003	0.0003
Mature	0.0030	0.0052	0	0.0015	0
Riparian/hardwood					
Low elevation	0.0044	0.0044	0	0.0022	0.0011
Mid-elevation	0	0	0	0.0007	0

¹ Data from 33 transects; total trap nights = 19,824.

nia scrub oak seemed to be preferred wherever it occurred. They sometimes build no visible nests where talus is available (Vaughan 1954), although careful examination usually reveals clipped branches adjacent to crevice or tunnel entrances (Sakai and Noon 1992a).

In central coastal areas, dusky-footed woodrats appear to prefer closed woods on drier sites, including a high percentage of live oaks with a mixed shrub understory (California coffeeberry and poison oak are the most prevalent shrubs). North-facing slopes meet these conditions best in the area around Hastings Natural History Reservation (hereafter, Hastings Reservation) at about 1,500-2,500 feet in elevation, where intermittent streams with willows also provide high-quality habitat (Linsdale and Tevis 1951). Overhead branches and downed logs often provide woodrats with a means of traveling above ground level; this appears to be an important structural component of the habitat for some populations (as at Hastings Reservation) but not for others.

Woodrats radio-tagged by Sakai and Noon (1992b) sometimes moved in the evenings as far as 165 feet into old-growth forests adjoining their home ranges in shrublands. Sakai and Noon did not determine how long these woodrats remained in the old-growth, or what they did there, but generally they were back in their nests in the shrublands by the following morning. Two radio-tagged woodrats dispersed through old-growth forest from their natal home range into another shrubfield, in one case a distance of at least 650 feet. Such movements by woodrats

would make them more available as prey for species like spotted owls that frequent these older forests.

Patterns of Abundance

Reported densities of dusky-footed woodrats range "from just a few animals to >40 per acre in early pole-timber stages, to perhaps 0.4 to 1.2 per acre in large saw timber and old growth" (Thomas et al. 1990, p. 207). In a corridor of habitat measuring approximately 100 by 1400 feet along an intermittent stream, Linsdale and Tevis (1951) trapped about 30 different individuals per month in one year and about 66 per month in another. These results suggest woodrat "densities" of about 9.3 and 20.6/acre-more than a two-fold difference between years. Densities in undisturbed habitats ranged from 2.1/acre in open woodlands of canyon live oaks and scattered Pacific madrones in the Santa Cruz Mountains, Santa Clara, County (Merritt 1974), to 18.3/acre in a riparian/hardwood forest of red alders, willows, and elderberries in coastal Sonoma County (Wallen 1982, Carraway and Verts 1991). Farther inland in Sonoma County, densities were 8.1/acre in late summer and 5.7/acre in winter in an undisturbed, riparian deciduous woodland dominated by red alder, California boxelder, and willows (Cranford 1977). In a study on the San Dimas Experimental Forest in the San Gabriel Mountains (Horton and Wright 1944), mean densities of woodrat houses were 4.6/acre in an area primarily of chaparral and oak woodland, 1-4/acre in

chamise chaparral, 10/acre in riparian/hardwood communities, and 10/acre in unburned oak/chaparral and mixed chaparral above 4500 feet; a golden oak woodland with nearly complete canopy cover and almost no shrub understory had almost no woodrats. Chew et al. (1959) found 16 dead woodrats per acre in a burned canyon bottom dominated by oaks and California sycamores in south-coastal California.

Various studies have reported effects of habitat change on densities of dusky-footed woodrats. Woodrats declined significantly during a prolonged drought in the Santa Monica Mountains, Los Angeles County (Spevak 1983), and Linsdale and Tevis (1951) reported depressed numbers during a drought at Hastings Reservation. On the other hand, Kelly (1989) reported a dramatic population increase during a serious drought at Hastings Reservation in 1988. He attributed this to a large acorn crop in the autumn of 1987, possibly augmented by mild weather conditions. Removal of poison oak from the understory depressed population density in the Berkeley Hills, Alameda County (Vestal 1938); flood, browsing, and trampling of the understory by ungulates reduced woodrat numbers at Hastings Reservation (Linsdale and Tevis 1956). Following complete removal of shrubs from study plots in chaparral cover in coastal dunes near Morro Bay, San Luis Obispo County, a woodrat population declined sharply in the first 2 years following treatment and disappeared entirely by the third year. Areas undisturbed by fire had higher densities of woodrats than burned areas (Lee 1963, Gambs and Holland 1988). Studies by Wirtz et al. (1988), in an area of montane chaparral that burned in southern California, established that preburn densities of woodrats had not yet been reached 4 years after the burn. Postburn densities were higher in areas of light and normal burn than in areas with hot burns where all plant material was destroyed.

A suspected outbreak of plague in 1966-67 decimated woodrat populations in foothills of the southern Sierra Nevada, the Tehachapi Mountains, and the Coast Range (Murray and Barnes 1969).

Cranford (1977) reported significantly larger home ranges for males than females (0.59 vs 0.48 acre) in a riparian woodland bordered by grasslands and surrounded by redwood forest. Kelly (1989) found the same situation in riparian/hardwoods in Monterey County. Sakai and Noon (1992b) found a similar difference, though not statistically significant, among woodrats in shrubfields dominated by brushy tanoaks with an overstory of Douglas-fir in northwestern California. Depending on the spacing of nest clusters (color photo 5-25), females often shared portions of the same home range; consequently home ranges of breeding males can overlap those of several females.

Diet

The herbivorous dusky-footed woodrat apparently obtains most or all of its water from its food. It eats parts of a wide variety of plant species, but the water-rich leaves of thick-leaved shrubs found throughout the woodrat's range are probably the most important source of food. The bulk of the diet consists of leaves and the terminal shoots of twigs, with seasonally important food sources consisting of flowers, fruits (nuts, seeds, fleshy fruits, and so on) and fungi. Bark, wood, and other organic

materials are also eaten occasionally. Fruits, fungi, and leaves are often cached within nests.

Linsdale and Tevis (1951) found that acorns and fruits of California coffeeberry were most numerous in caches examined at Hastings Reservation. Leaves and other parts of coast and canyon live oaks, California blackberry, chamise, California coffeeberry, buckbrush, and Jim brush were the major plants eaten. Somewhat less common in the diet were valley, blue, and black oaks; California wild rose; toyon; poison oak; Pacific madrone; and mountain whitethorn. Parts of 56 other plant species were consumed (amounting to about 10 percent of the total diet), while 470 plant species (87 percent of the flora at Hastings Reservation) were not found in the diet of this woodrat.

In Joshua Tree National Monument, about 75 percent of the material in food caches in nests consisted of shrub live oak and about 25 percent was California juniper (Cameron 1971). These proportions were the same even where the dusky-footed woodrat occurred together with the desert woodrat. The main foods in southern California coastal sage communities were lemonade sumac (fruit, seeds, vegetative parts), California buckwheat (vegetative parts), white sage (seeds, flowers, vegetative parts), and California scrub oak (leaves, fruits) (Meserve 1974).

Weights

Specimens from the western Sierra Nevada ranged in weight from 7.2 to 8.6 ounces (Grinnell and Storer 1924). Winter and summer weights in samples from foothill areas in San Diego County averaged 7.7 ± 0.7 and 6.5 ± 0.4 ounces, respectively (Stallone 1979). Sakai and Noon (1992b) reported a mean weight of 7.8 ± 0.14 ounces for a pooled sample of both sexes and all ages ($n = 366$) in Humboldt County. Adult males there averaged 10.7 ± 0.14 ounces ($n = 101$), and adult females averaged 8.5 ± 0.09 ounces ($n = 133$). At Hastings Reservation (Linsdale and Tevis 1951), adult males averaged 8.8 ounces (range 7.1-10.6) and adult females averaged 8.4 ounces (6.4-12.5). These rodents exhibit marked individual and seasonal variation in weight (table 10B). Immature woodrats weighing <5.3 ounces were trapped

Table 10B-Weights (mean and range in ounces) of all ages of male dusky footed woodrats captured each month during a year at Hastings Natural History Reservation, Monterey County, California (adapted from Linsdale and Tevis 1951).

Month	<i>n</i>	Mean	Range
January	68	8.9	7.0 - 12.0
February	67	9.3	4.9 - 13.6
March	94	9.2	5.4 - 13.0
April	106	9.0	2.6 - 13.3
May	77	8.5	3.2 - 13.2
June	83	7.8	2.7 - 11.6
July	97	7.0	1.9 - 11.3
August	54	7.1	1.9 - 11.4
September	92	7.9	3.2 - 13.3
October	58	8.0	3.5 - 11.3
November	66	8.6	3.5 - 12.7
December	91	9.0	3.7 - 12.9

only between April and September. Immatures weighing from 3.5 to 7.0 ounces were trapped in all months but were taken most often in June and July.

Nests

Nests of sticks and other woody debris are typically located on the ground, occasionally in trees (color photo 5-23) or dense shrubs where support for the structure is available, and sometimes in rock crevices and abandoned human structures. Linsdale and Tevis (1951) summarized nest locations at Hastings Reservation as follows:

Most often	Bases of coast live oaks, California coffeeberry, willows, poison oak, California buckeye, California-laurel (bay).
Less often	Against logs, in rock outcrops (probably because of a lack of appropriate rocks or insufficient cover plants in areas studied—rocks are important in the San Gabriel Mountains and the southern Sierra Nevada), hollow cavities in trees (perhaps because of rarity and difficulty of detecting such nests), and among limbs of trees (trees with the right configuration of large and small branches to support nests may be preferred over the ground).

The structure of the plant community where nests were located at Hastings Reservation was described by Linsdale and Tevis (1951) as a mixed woodland with a mosaic of dense shrubs and trees, forming a complete and complex (multilayered) canopy:

Most often	Closed woodlands consisting predominately of coast live oaks (59 percent; $n = 100$).
Less often	Dense shrubs (28 percent), especially where California coffeeberry and poison oak were most abundant.
Rare (<10 pct)	Lone coast live oak trees (5 percent); live oak savanna (8 percent) (blue oak and valley oak savannas were not used for nests).

Nests are an important part of woodrat population dynamics. Nest clusters, occupied by related individuals, are common in favored habitats. Females, unlike males, stay in or near their natal area throughout their life, where related females breed in the same vicinity, living close together in kin clusters but in separate houses (Kelly 1989). In addition, individuals tend to cluster in favored habitat patches; consequently, such favored areas tend to become "crowded" over time (Linsdale and Tevis 1951). Vogl (1967) reported one adult per nest, but Sakai and Noon (1992a) have occasionally captured two adults per nest in northwestern California.

Reproduction and Development

Linsdale and Tevis (1951) found that 70 percent of the woodrats in their study area at Hastings Reservation survived less than 1 year, 27 percent survived 2 years, and 3 percent survived at least 3 years. Reproduction occurred in all months at Hastings, with the fewest pregnancies in December and the most in February. The number of juveniles appearing outside the nest

was greatest in July and least (0) in January and February. Females were polyestrous, producing one to five litters per year, with one to four young per litter (mean about 2.5).

Forest Management

Fires, shrub removal, logging, and other human and natural disturbances generally reduce the suitability of woodrat habitat. Selective cutting of trees that opens the canopy and promotes growth of shrubby understory probably enhances habitat after several years, as do other logging techniques that promote successional stages with a complex mix of over- and understory trees and shrubs (Hooven 1959). The short-term effect, however, probably would be to reduce habitat suitability for woodrats. Although studies by Sakai and Noon (1992b) indicate that woodrats sometimes move from shrubfields into the edges of old-growth forests, it cannot be argued that logging to create openings would result in a net benefit for spotted owls in the conifer zone of the Sierra Nevada. First, available data from radio-tracking studies indicate that spotted owls seldom forage in shrubfields (Neal et al. 1989, Sisco 1990, Solis and Gutiérrez 1990, Zabel et al. 1992); and second, dusky-footed woodrats are generally uncommon as high as the mixed-conifer zone in the Sierra Nevada, where most logging currently occurs. Flying squirrels are the dietary staple of spotted owls in forests at these higher elevations, so logging there is more likely to have a negative effect on owl prey (via flying squirrels) than a positive one (via woodrats).

In forests below the Sierran mixed-conifer zone, small-scale logging operations might benefit spotted owls by enhancing woodrat populations. Although this needs further study, smaller sales might benefit spotted owls if done in areas adjacent to forested stands where the owls are known to forage. In such cases, woodrats that occasionally wander from their shrubby home ranges into the adjoining forest could become available as prey for spotted owls.

Woodrats do not survive fire well, especially very hot burns (Wirtz et al. 1988), and they are slow to recolonize burned areas (Longhurst 1978, Wirtz et al. 1988). Consequently, aggressive fuels management programs in chaparral country can benefit woodrat populations, especially in southern California where home ranges of owls in riparian/hardwood forests are closely surrounded by thick stands of chaparral (Chapter 5).

Northern Flying Squirrel

Distribution and Habitat

The northern flying squirrel is a medium-sized, nocturnal rodent that nests in trees in a great variety of forest communities over a broad, continental distribution. In California they occur in the North Coast, Klamath, southern Cascade, Sierra Nevada, and

Transverse Ranges. They are distributed throughout forested regions of the Sierra Nevada but apparently are more common in the mixed-conifer and red fir forests of the Pacific Slope than in the drier forests of the east slope. They are generally found above about 4,000 feet elevation in the Yosemite region and down to about 3,000 feet or lower in the northern Sierra Nevada, and in protected canyons and on north-facing slopes farther south. A single record from Chico is probably exceptional, but it suggests that flying squirrels may sometimes occur near the floor of the Central Valley in riparian/hardwood forests. Isolated populations also occur in the San Bernardino and San Jacinto mountains and probably in the San Gabriel Mountains of southern California.

Unfortunately, little published information is available on habitat associations or population levels of flying squirrels within the range of the California spotted owl. In the Sierra Nevada, common tree species associated with flying squirrels are black oak, white fir, and red fir. In the Lassen area, McKeever (1960) found flying squirrels in stands of ponderosa pine, lodgepole pine, and mixed stands of red and white fir. According to Waters and Zabel (1992), populations of flying squirrels have been located in second-growth stands of white fir at high elevation (about 6,300 feet) in the Lassen NF (color photo 5-1). These squirrels often travel and forage on the ground, so elements of the forest understory also are probably important in determining the suitability of their habitat.

In the San Bernardino Mountains, flying squirrels occur in mixed-conifer forests between about 5,200 and 7,500 feet in elevation (color photo 5-35). White fir and black oak are the principal tree species associated with these squirrels in the San Bernardinos (Grinnell 1908, 1933; Williams 1986). On a ridge south of Big Bear Lake, Summer (1927) caught 22 flying squirrels over the course of several months—all in white firs.

Stand size was an important attribute of suitable flying squirrel habitat in mature mixed-evergreen forests dominated by Douglas-fir on the Six Rivers NF. Northern flying squirrels were found in 60-80 percent of stands larger than 50 acres, on about 15 percent of stands of 25-50 acres, and on <10 percent of stands smaller than 15 acres (Rosenberg and Raphael 1986).

Sites with northern flying squirrels in isolated populations in the southern Appalachians varied markedly in plant community structure and composition (Payne et al. 1989). Occupied sites were commonly on north-facing slopes or in montane islands of conifer forests with cooler, mesic environments. Density of overstory trees varied from 364 to 1336 per acre; density of snags ranged from 11 to 138 per acre; and understory cover ranged from 35 to 86 percent. In a study of the southern flying squirrel in central Virginia, Sonenshine and Levy (1981) concluded that areas with few shrubs or vines as ground cover were unsuitable as habitat. An oak or oak-associated canopy with an understory of dense shrubs was optimal habitat. Presence of the squirrels was strongly correlated with shrub density. Although major differences exist in the distribution and habitats of northern and southern flying squirrels, the study by Sonenshine and Levy suggests that understory may be as important as tree canopy in determining habitat suitability.

Although Doyle (1990) captured similar numbers of flying squirrels in riparian and upland habitats, she concluded that riparian habitats were, nonetheless, superior to upland sites for flying squirrels. Waters and Zabel (1992) have found relatively high densities of flying squirrels in forest stands on the Lassen NF that are not near running water.

Patterns of Abundance

No published data are available on population densities, age structure, or reproduction in the Sierra Nevada or the mountains of southern California. A summary of most available literature indicated that "typical squirrel densities reported for mature and old-growth forests are 0.4 to 1.2 animals per acre" (Thomas et al. 1990, p. 205). Carey et al. (1992) found that flying squirrel density in southwestern Oregon was significantly greater in old-growth Douglas-fir stands (mean density = 0.8/acre) than in managed second-growth stands (mean = 0.4/acre). On the other hand, Rosenberg and Anthony (in press) failed to show significant differences between flying squirrel densities in old-growth (mean = 0.9/acre) and second-growth Douglas-fir stands (mean = 0.8/acre). Waters and Zabel (1992) found that average flying squirrel density was about 43 percent higher in late-seral red fir/white fir stands on the Lassen NF (range = 0.7-1.5/acre) than in red fir/white fir stands that were about 100 years old (range = 0.6-1.0/per acre). They have also found that flying squirrel density is strongly associated with the abundance of truffles-fruiting bodies of underground (hypogeous) fungi.

Diet

The diet of northern flying squirrels, at least as determined in California studies, consists primarily of truffles and arboreal lichens (McKeever 1960, Hall 1991, Waters and Zabel 1992), although they are known to eat a variety of other foods including seeds, nuts, insects, bird eggs and nestlings, and tree sap (Wells-Gosling and Heaney 1984). Maser et al. (1985) found that 90 percent or more of foods eaten in Oregon were fungi and lichens-hypogeous fungi accounted for more than 80 percent of the summer diet, and lichens comprised more than 50 percent of the diet year-round in northeastern Oregon. At Sagehen Creek, in the eastern Sierra Nevada, Hall (1991) found that spores of hypogeous fungi were the most common items found in feces and stomach samples year-round, but suspected that samples taken during deep snow cover indicated that the squirrels may store hypogeous fungi for consumption during winter months. Lichens and gill fungi were most prevalent during periods when snow covered the ground at Sagehen Creek. Hall considered arboreal lichens to be a very important winter food source for flying squirrels in areas with much snowfall (also see McKeever 1960). From studies of captive-reared animals, Laurance and Reynolds (1984) determined that winter diets consisting almost wholly of lichens may be more a matter of necessity than of preference for northern flying squirrels. The captives selected pine seeds over lichens, moss, algae, and cones and branch tips from ponderosa pine.

Weights

Size varies significantly in a north-south cline along the Pacific Coast (Wells-Gosling and Heaney 1984), with the largest individuals in Alaska and British Columbia and the smallest in California. Weights of flying squirrels captured in Yosemite NP ranged from 3.62 to 5.76 ounces (Grinnell and Storer 1924). Juveniles captured in August and September in the Lassen NF averaged 2.89 ounces, and adults averaged 4.34 ounces (Waters and Zabel 1992). In a study by Witt (1991) in Douglas County, Oregon, the mean weight of adults captured between September 1983 and June 1984 was 4.7 ± 0.1 ounces (range = 3.7-6.5 ounces, $n = 164$). Generally the mean weight of adults was highest in January (mean = 5.0 ounces), dropping steadily to April, remaining stable from April through August (mean = 4.4 ounces), and increasing again through December.

Nests

Northern flying squirrels use several den sites; Carey (1991) found individuals in Oregon that used as many as seven. Two types of nests or dens are common—those located among branches of trees (for example, stick nests built by birds or other tree squirrels, clumps of dwarf mistletoe, and moss), and those located in natural cavities in trees and snags or abandoned woodpecker holes (Wells-Gosling and Heaney 1984). In Oregon, live conifers with cavity nests averaged 49 inches in d.b.h.; snags with cavity nests averaged 35 inches in d.b.h. (Carey 1991). Nests in such cavities are probably important in areas with cold winters (Cowan 1936, Weigl 1978), although Waters and Zabel (1992) have found populations of flying squirrels in high-elevation (about 6,300 feet) stands of second-growth white fir where few snags or cavities occurred. We do not know how commonly flying squirrels build their own nests.

Reproduction and Development

Litters commonly consist of two to four young, rarely one to six (Wells-Gosling and Heaney 1984). In Yosemite NP, females with two to four embryos were found in June (Grinnell and Storer 1924). Young are born between mid-June and mid-August in Oregon (Carey 1991). Weaning occurs at an age of about 60 days. Carey reported that young in an Oregon study were not weaned until mid-October to mid-November; they either dispersed in autumn or spent the winter in the nest with their mother. Young can walk and begin to leave the nest when about 40 days old. Most yearling females did not breed, and about 25 percent of the adult females did not breed in a given year. Although several authors have suggested that more than one litter is produced per year (Grinnell and Storer 1924, Witt 1991), a single litter is probably more common, at least throughout the Sierra Nevada (Waters and Zabel 1992). In the Sierra Nevada, two "half-grown" young were captured on 31 October, and a "quarter-grown" young was found on 16 September (Grinnell and Storer 1924, p. 214).

Forest Management

Habitat features that most strongly influence flying squirrel abundance include: sufficient trees to enable efficient locomotion; nest and den site substrates (cavity-bearing trees and snags), and truffle and arboreal lichen biomass. Although flying squirrels can glide at least 155 feet (Mowrey and Zasada 1984, J. R. Waters pers. observ.), forestry practices that create openings wider than about 120 feet probably have a negative effect on flying squirrel locomotion. Tree height is also important. Flying squirrels cannot glide as far from small trees as they can from tall ones.

As cavities provide important nest and den sites, efforts should be made to leave cavity-bearing trees and snags. In areas lacking potential nest sites, it may be possible to increase flying squirrel populations by adding nest boxes.

Truffles and arboreal lichens are the most important food types for flying squirrels throughout California and in the Pacific Northwest. Arboreal lichens are especially important as a winter food resource. Forest practices that reduce truffle and lichen biomass will probably negatively impact flying squirrel abundance. Ongoing research by Waters and Zabel (1992) indicates that truffle biomass is strongly associated with the presence of a well-developed soil organic layer and the volume of decaying logs (color photos 5-7, 5-18, and 5-34). Forest practices that negatively impact those parameters, such as broadcast burning and bulldozer piling after logging (Harvey et al. 1980), will reduce the capability of the forest to sustain flying squirrels. Data from Waters and Zabel (1992) also show that arboreal lichens (in the genera *Letharia* and *Bryoria*) commonly eaten by flying squirrels are much more abundant in older red fir/white fir forests than in younger forests.

Management of conifer forests in the Sierra Nevada for flying squirrels should emphasize retention of large snags and older trees, and nonintensive site-preparation techniques.

Pocket Gophers

Distribution and Habitat

Two species of pocket gophers occur within the main geographic range of the California spotted owl. Mountain pocket gophers range from the Mt. Shasta Region southward in the Sierra Nevada to at least the northern boundary of Tulare County (Hall 1981). They generally occur from above 6,900 feet in the Sierra NF (5,600 feet in the Stanislaus NF and Yosemite NP) to slightly above timberline (Grinnell and Storer 1924; D. F. Williams, pers. observ.). They are found throughout subalpine areas of both Sequoia and Kings Canyon NPs (Graber, pers. comm.), generally at elevations above 8,500 or 9,000 feet that are not frequented by spotted owls. They are most common in deeper, drier soils around meadow margins, but they occur everywhere

except on bare rock and within closed-canopied, mature and older forests with little or no herbaceous ground cover (Ingles 1952).

Southwestern pocket gophers occur in the western Sierra Nevada at elevations below the mountain pocket gopher, and in the lowlands, mountains, and deserts of western and southern California and northern Baja California. They probably range to timberline in the southern Sierra Nevada, from Tulare County southward. Distribution records of pocket gophers above 6,900 feet in the southern Sierra Nevada are unavailable, although one or the other species surely is found there (Hall 1981). Southwestern pocket gophers are most common on open ground with well-drained soils supporting grasses and forbs, but they can be found everywhere except on bare rock and in closed-canopied, mature and older forests.

Great Basin pocket gophers occur on the eastern slopes of the Sierra Nevada and on the Modoc Plateau. We do not discuss them in detail here because they probably occur mostly outside the breeding range of the California spotted owl, and because features of their population dynamics, habitat, and diet that are of importance to spotted owls probably do not differ from those of other pocket gophers. Generally, the ranges of these three species of pocket gophers do not overlap.

Patterns of Abundance

Mean density of mountain pocket gophers in favored meadow habitats was estimated at 10/acre in autumn over a 4-year period (Ingles 1952). The lowest estimates were in summer and autumn 1950 (4/acre), the highest in summer 1949 (19/acre). Biomass of mountain pocket gophers fluctuated from a low of 27.7 ounces/acre in spring 1948 to a high of 46.3 ounces/acre in summer 1949; this had dropped to an estimated 11.8 ounces/acre by the following summer.

In favored habitat at the San Joaquin Experimental Range (SJER), Madera County, the density of breeding adult southwestern pocket gophers averaged about 2.0/acre over five breeding seasons. Numbers of young produced by these adults averaged 2.3/acre over four breeding seasons (estimates from figures in Howard and Childs 1959, p. 340). Near Bass Lake, Madera County, in a Sierran mixed-conifer forest (about 4,500 feet), the density on a plot that included cutover forest and meadows was 4.6/acre, but Storer et al. (1944) believed this to be only half or less of the actual population.

General Life History Features

Pocket gophers are solitary and territorial, normally not ranging beyond the boundaries of their territories. They are most active early in the morning and late in the day, near sundown; at the highest elevations, most activities occur in late afternoon and evening. They are fossorial creatures, digging and living in underground tunnels, and creating many shallow, foraging tunnels about 5 inches below ground level. Their burrow entrances are plugged with dirt except when the gophers are pushing dirt from excavations to the surface, foraging on plants around the

burrow entrance, or searching for mates. During excavation and while foraging on plants at the surface, they usually expose no more than the anterior half of their body at the burrow entrance.

Most burrowing activities occur during the cooler, wetter months in western California. At lower elevations, little or no burrowing occurs during the dry summer period, when gophers retreat to their few, deeper tunnels and plug the shallow ones. They may subsist mainly or entirely on cached food during this period. At higher elevations, when snow covers the ground, pocket gophers come to the surface and burrow through the snow to reach food plants, often packing these tunnels with dirt from underground excavations.

Burrow systems of neighbors typically are discrete. Any interconnections that may be accidentally established apparently are kept plugged with dirt. Hearing may play a role in preventing encroachment by neighbors (Ingles 1952).

Soil, plant cover, and seasonal flooding are the principal factors determining habitat suitability and density of these pocket gophers. Areas with waterlogged soil and sites of seasonal flooding are unsuitable as permanent habitat. At SJER, at an elevation of about 1,000-2,000 feet in the western foothills of the Sierra Nevada, the strongest correlation with abundance of pocket gophers was soil depth (Howard and Childs 1959). Gophers were not found living in soils shallower than about 12 inches, and were most abundant in soils at least 24 inches deep. Areas with the deepest soils showed the highest above-ground productivity of herbaceous plants.

Mean weights of female pocket gophers were greater in sites with deep soils compared to sites with shallow soils, but differences were not statistically significant. Pocket gophers living in irrigated fields are significantly larger and heavier than their genetically identical neighbors in natural communities (Howard and Childs 1959, Patton and Brylski 1987). Areas supporting an abundance of grasses and forbs, especially species forming underground rhizomes, corms, tubers, bulbs, and other storage organs, provide the greatest habitat values for food. Areas with dense or complete canopy cover of woody shrubs and trees provide the poorest habitats for pocket gophers.

Diet

Pocket gophers eat a variety of plants, favoring herbaceous over woody material. Food not immediately consumed is cached in underground larders. Much of the information on diet comes from examination of these caches. Most species of grasses and forbs known to occur in a foothill oak-pine savanna at SJER were found in caches of southwestern pocket gophers. Seeds, tubers, bulbs, rhizomes, and acorns also were found in the caches (Howard and Childs 1959). Mountain pocket gophers near Huntington Lake, on the Sierra NF, also ate a wide variety of plants. During snowless months, caches of corms and roots of meadow bitterroot and golden brodiaea were found in caches. In winter, mountain pocket gophers cached mountain whitethorn leaves in snow tunnels, and the parts of willow stems covered with snow were frequently gnawed (Ingles 1952).

Weights

Microgeographic, seasonal, and annual variations occur in weights of adult pocket gophers. Season, sexual activity, and habitat quality have major influences on size and mass of adults (Howard and Childs 1959, Daly and Patton 1986, Patton and Brylski 1987). Mean weights of mountain pocket gophers in a Sierra Nevada meadow ranged from 2.2 (lowest summer average) to 3.1 ounces (highest spring average). Nonbreeding animals in autumn averaged from 2.2 to 3.0 ounces in different years (Ingles 1952). Weights of southwestern pocket gophers at SJER varied as follows (Howard and Childs 1959, fig. 11).

Females 8-10 months of age--mean = 2.2 ounces (range 1.8-2.6).

Females 20-22 months of age--mean = 2.6 ounces (range 2.2-3.1).

Males 8-10 months of age--mean = 3.2 ounces (range 2.3-8.8).

Males 20-22 months of age--mean = 4.3 ounces (range 3.9-4.7).

Mean weights of trapped animals were highest in spring and lowest in summer and autumn.

At Hastings Reservation, modal weights of trapped males were between 4.0 and 4.4 ounces, with a range of about 2.1 (juveniles) to 7.7 ounces (largest adults). Modal weights of trapped females were between 3.2 and 3.9 ounces, with a range from about 1.9 (juveniles) to 4.7 ounces (largest adults) (Daly and Patton 1986, fig. 3).

Reproduction and Development

Mountain pocket gophers begin breeding in May or June and young are born in June to August. Only one litter of three or four young per year is the norm. From about mid-July to early September, young disperse over the ground surface until a suitable site is found (Ingles 1952). Often burrow systems established by dispersers are in marginal or unsuitable habitats, such as shallow, sterile, granitic soils, or in small plots of higher ground surrounded by waterlogged soil. Some adults and young of the previous year apparently disperse in winter through snow tunnels. Dispersing adults are predominately males.

Based on studies by Howard and Childs (1959), southwestern pocket gophers at SJER commenced breeding in January, considerably earlier than is the case with the mountain pocket gopher. Most females were first pregnant the last 2 weeks of February; mean litter size there was 4.6. The young dispersed from March to May, although both young and adults occasionally moved over the ground at other periods of the year. Females born in January sometimes produced litters in April or early May of the same year. Most females produced only one litter per year, but a few had two. Between 50 and 75 percent of the females in January 1950-1954 were young of the previous breeding season (9-11 months old).

In a mixed-conifer forest at an elevation of about 4,500 feet, near Bass Lake, Madera County, scanty data suggest that young are born in early July and that some females may have two litters, similar to populations of this same species at lower elevations (Storer et al. 1944).

In a montane woodland community at Hastings Reservation, southwestern pocket gophers began breeding after onset of

the winter rainy season, usually by January (Daly and Patton 1986). The breeding population was composed of animals at least 7-8 months old. Most females probably had only a single litter.

The breeding season of southwestern pocket gophers in the San Bernardino Mountains, at an elevation of about 7,500 feet near Bear Lake, is probably similar to that of mountain pocket gophers in the Sierra Nevada (Grinnell 1908).

Estimated survival of southwestern pocket gophers to 1 year of age ranged from about 5 to 40 percent for males and 15 to 50 percent for females between 1949 and 1953 (Howard and Childs 1959). Less is known about mountain pocket gophers, but 34 percent of the individuals in autumn populations in the Sierra NF were young of the year, and little turnover was detected in the spring breeding populations of 1949 and 1950 (Ingles 1952).

Forest Management

Generally, actions that tend to benefit pocket gophers would tend to lessen overall habitat suitability for spotted owls, so we would not recommend any active management to increase the amount of suitable habitat for gophers. Natural and man-made openings in the forest will undoubtedly occur with sufficient regularity to assure that these burrowing mammals will continue to be available as prey for California spotted owls.

White-Footed Mice

Distribution and Habitat

Five species of white-footed mice (genus *Peromyscus*) occur within the range of the California spotted owl. Indeed, white-footed mice are nearly ubiquitous in terrestrial habitats and often one or another species in this group is the most abundant small mammal. They exhibit considerable geographic variation in habitat associations, so results of studies on a given species in one locality should not be too broadly applied. Because of its marginal occurrence with the California spotted owl, we do not include the cactus mouse in this review.

Brush Mouse

Brush mice range throughout most of the area inhabited by California spotted owls, although they are absent from most of the inner coastal ranges (Diablo Range) of central California south of Suisun Bay and north of the Transverse Ranges in Kern and Santa Barbara Counties. They are relatively scarce above 3,500 feet in the northern portion of the western Sierra Nevada (Grinnell et al. 1930), but may occur higher in chaparral and other shrub associations on south-facing slopes (Jameson 1951). They occur up to about 5,100 feet at the level of the Sierra NF. On the Pacific slopes of the San Gabriel Mountains, brush mice

occur mainly between 1,600 and 6,000 feet, where they show decided preferences for rocky sites in oak woodlands, riparian/hardwood communities, and mixed-species chaparral (Vaughan 1954). Brush mice climb readily and are often seen or captured in trees. They are not known to hibernate or to enter torpor.

Brush mice may construct nests in hollows in trees or in ground burrows. They are closely associated with oaks and rocky sites. At Pinnacles National Monument in the Gabilan Range, Monterey County, brush mice comprised only 5 percent of the white-footed mice captured in a complex mix of woodland, chaparral, and grassland communities. They were significantly associated with poison oak and medium-sized rocks (10-50 inches), and they showed a significant negative association with grass (Fellers and Arnold 1988). Elsewhere they are typically the most common white-footed mouse where rocks and oaks occur together in oak woodlands and forest communities below the mixed-conifer zone. In the central Sierra Nevada (Yosemite NP), oaks and proximity to water were commonly associated with brush mice (Grinnell and Storer 1924). Other researchers have not verified a dependence on surface water; possibly exposed rocks in canyon bottoms and shrubby growth along streams provide suitable habitat in otherwise inhospitable surroundings. At SJER, an area with no permanent streams, brush mice were the most common species of white-footed mouse, preferring rocky areas sheltered by oaks (Quast 1954). They were also the most common species in the La Panza Range of San Luis Obispo County, with nearly equal abundance in blue oak woodland, mixed chaparral (chamise, ceanothus, and scrub live oak), and the ecotone between these communities along canyon bottoms (Murray 1957).

California Mouse

California mice occupy chaparral and woodland communities in western California and northern Baja California, south of San Francisco Bay on the Coast, and from Mariposa County southward in the Sierra Nevada foothills. Their elevational distribution in the Sierra Nevada is generally from the lower half of the ponderosa pine forest downslope to the mid-elevation, oak-pine woodlands and chaparral. Elevational limits in the mountains of southern California are generally below about 4,900 feet, with an exceptional record at 7,900 feet in the San Jacinto Mountains (Grinnell 1933). California mice climb readily and are frequently captured in traps set in shrubs and trees (Meserve 1976a, 1977). They may become torpid on a diurnal cycle when deprived of food (Hudson 1967).

California mice have more specialized habitat requirements than brush and pinyon mice, preferring broadleaved woodlands and mixed chaparral and being more limited in their elevational and latitudinal distributions. Within their geographic range, they are closely associated with the distribution of both dusky-footed woodrats and California-laurel (bay), although both associates occur much farther north than California mice (Merritt 1974). Plant communities inhabited include valley foothill hardwood and oak-pine woodlands, various chaparral associations, and riparian deciduous. Within preferred habitat, California mice are often the most abundant small mammal species. At Pinnacles National Monument, California mice accounted for 10 percent

of all captures of white-footed mice. They were absent from areas of extensive grass and large patches of chamise chaparral. Variables most strongly associated with the presence of this species were hollyleaf cherry, medium-sized rocks, and Chinese nests (a wildflower) (Fellers and Arnold 1988). They are among the commonest rodent species in mixed-chaparral communities in the San Gabriel Mountains below about 4,900 feet (Vaughan 1954, Wirtz et al. 1988). In coastal sage communities, they are generally limited to thickets of large shrubs and small trees in riparian/hardwood stands (Vaughan 1954). M'Closkey (1972) captured only six residents in coastal sage scrub and their mean duration on plots was less than half that of cactus and deer mice. He believed their occurrence on the study plot was due to previous flooding of their preferred habitat along washes where trees and large shrubs were found.

California mice often nest in abandoned or occupied stick nests of dusky-footed woodrats. They also may nest in hollows in trees, snags, or logs, and they construct stick nests of their own, often under fallen logs and smaller downed woody material (Merritt 1978). They apparently do not burrow readily; many researchers have proposed that their distribution and abundance are limited by availability of suitable nesting sites (Merritt 1974, 1978).

Deer Mouse

Deer mice occur throughout the range of the California spotted owl, and in most plant communities, from marshes and grasslands at or below sea level, through woodlands and forests, to above timberline in the mountains. Within this broad area, however, they are generally common only in riparian/hardwood and grassland communities at lower elevations, and riparian, forest, and meadow communities from the mid-elevation mixed-conifer zone upslope through lodgepole and subalpine pine forests. Deer mice probably are the most terrestrial of the white-footed mice considered here (King 1968; Meserve 1976a, 1977). Meserve (1977) seldom found them in shrubs or trees in a southern California community of coastal sage, even though they can climb readily and are taken in traps set in brush and trees. Torpor under natural conditions is unknown for deer mice.

Deer mice typically nest in ground burrows, hollow logs, or talus. Nests are less frequently located in hollows of trees and snags. They are generally much less common than brush and pinyon mice in ponderosa pine, oak-pine woodlands, foothill and montane hardwood forests, and chaparral on the western slopes of the Sierra Nevada (for example, tables 10A and 10C; Quast 1954), in the coast ranges, and in mountains of southern California. Within these communities, they are most often found in riparian deciduous associations, wet and dry meadows, and grass/forb seral stages. In the northern Sierra Nevada, deer mice were significantly more abundant in forested than in shrub stages of mixed-conifer forest (Jameson 1951). In coastal woodland and chaparral communities, deer mice are uncommon and usually associated closely with riparian/hardwood communities or large openings dominated by annual grasses and forbs. At Pinnacles National Monument, deer mice comprised 20 percent of the white-footed mice captured in a complex of grassland, oak, pine, and chaparral communities. Most captures were on burned

Table 10C-Captures of small rodents that may be prey of California spotted owls, by successional stage (after Verner and Boss 1980)¹ in forest communities of the western Sierra Nevada, Sierra NF (D. F. Williams pers. observ.). Total adjusted sampling effort was 18,200 trap days (one trap day = one pitfall trap set for 24 hours). Trapping was simultaneous in all forests and successional stages. Values are actual captures, except "catch rate," which is the number captured per trap day. Captures were standardized to represent equal sampling effort in the various habitat types. (Most habitat types/stages were sampled on two transects of 10 traps each, set for 7 days in 1980 and 28 days in 1982. LTB in ponderosa pine, GF in mixed-conifer, and LTC in red fir forests were sampled only on single transects, so numbers of actual captures there were doubled.)

Forest community and mammal species	Habitat type/stage										Catch rate
	GF	SSS	PMA	PMB	PMC	LTA	LTB	LTC	RH	Total	
Ponderosa pine											
Southwestern pocket gopher	1	1	2	0	0	2	0	--	1	7	0.0013
Deer mouse	12	0	0	0	1	1	2	--	1	11	0.0020
Brush mouse	3	2	3	0	0	1	8	--	10	27	0.0048
Pinyon mouse	0	6	4	6	13	13	0	--	0	42	0.0075
California vole	2	0	0	0	1	0	0	--	1	4	0.0007
Total	18	9	9	6	15	17	10	--	13	91	0.0188
Mixed-conifer											
Southwestern pocket gopher	0	0	1	1	0	0	0	0	0	2	0.0003
Deer mouse	2	21	14	3	6	7	12	11	29	105	0.0167
Brush mouse	0	0	0	0	1	0	0	1	2	4	0.0006
Pinyon mouse	0	0	1	2	0	0	0	0	0	3	0.0005
Long-tailed vole	0	12	4	1	0	0	1	0	7	25	0.0040
Total	2	33	20	7	7	7	13	12	38	138	0.0221
Red Fir											
Mountain pocket gopher	6	1	1	0	0	0	0	2	4	15	0.0024
Deer mouse	40	30	9	15	12	14	15	10	42	187	0.0300
Long-tailed vole	5	6	0	5	1	1	5	0	40	63	0.0100
Total	51	37	10	20	13	15	20	12	86	265	0.0424

¹ GF = grass/forb; SSS = shrub/seedling/sapling; PMA = pole-medium tree with <40 percent canopy cover; PMB = pole-medium tree with 40-69 percent canopy cover; PMC = pole-medium tree with >69 percent canopy cover; LTA = large tree with <40 percent canopy cover; LTB = large tree with 40-69 percent canopy cover; LTC = large tree with >69 percent canopy cover; RH = riparian/hardwood community in corresponding forest zone.

areas and in a grassy field. Variables positively associated with their occurrence were chamise and bird's foot trefoil (together), and yerba-santa. Percent cover of oak leaf litter was negatively associated with deer mice (Fellers and Arnold 1988).

In the San Bernardino Mountains, brush mice outnumbered deer mice on mixed-conifer plots at elevations between 5,800 and 7,000 feet, but deer mice were more abundant on mixed-conifer plots at 7,600 feet (Kolb and White 1974). Grinnell (1908) found deer mice common only in big sagebrush on the desert slopes and high ridges, and in montane forests above 6,900 feet. Deer mice were not captured by Spevak (1983) at four sites in the Santa Monica Mountains, Los Angeles County, in chaparral, riparian, and coastal sage associations. Yet Price and Kramer (1984) caught small numbers in a variety of microhabitats in a coastal sage community in Riverside County. M'Closkey (1972) also captured deer mice in a coastal sage community in Orange County and noted that they were the most general in habitat preference, being found along the moisture gradient from grasslands to woodlands. In mixed montane-chaparral communities of the Pacific slopes of the San Gabriel Mountains, deer mice were absent from chaparral that had not been burned for several years but were present on all burned plots, with peak numbers occurring 2 years after burns (Wirtz et al. 1988).

Pinyon Mouse

Pinyon mice also occur throughout the area inhabited by California spotted owls, but generally range below the mixed-conifer forests on the western slopes of the Sierra Nevada. They are associated with oak-pine woodlands and chaparral communities, usually with one or more species of conifers such as juniper, pinyon pine, or digger pine. They are less common in ponderosa pine habitats, where they most often occur on hotter, drier slopes in association with chaparral or in more mature stages of forest. In southern California they are generally uncommon or only locally distributed on the Pacific slopes of the mountains. Vaughan (1954) found none on the Pacific side of the San Gabriel Mountains. In the San Bernardino Mountains, Grinnell (1908) captured them only at two localities on the Pacific side. One was a south-facing slope at 6,500 feet vegetated with Coulter pine, chamise, deer brush, curleaf mountain mahogany, and California scrub oak-plants typical of the upper-elevation chaparral of the Pacific side, and pinyon pine and western serviceberry-plants more typical of the desert side. The other was a south-facing slope where pinyon mice were taken between 5,100 and 5,500 feet among a mix of plants of upper-elevation chaparral and lower-elevation forest (ponderosa pine, white fir, and black and canyon live oaks). Chaparral plants

predominated. Pinyon mice readily climb and are frequently taken in traps set in shrubs and pygmy conifers (for example, juniper, pinyon pine, digger pine, Coulter pine).

Pinyon mice nest in ground burrows or hollows in trees. They apparently do not become torpid. In the central coastal chaparral, woodland, and forest communities, they are common wherever shrub or tree cover is found, especially with one or more species of pygmy conifers or dense stands of chamise or ceanothus chaparral (or a mix of these and other shrubs). Pinyon mice were the most abundant small mammal trapped in chamise chaparral at Hastings Reservation (Bradford 1976). At Pinnacles National Monument, pinyon mice accounted for about 66 percent of the white-footed mice captured in a variety of oak, pine, grass, and chaparral associations. They were found in all community types but grassland. Large rocks and various shrub species were significantly associated with occurrence of pinyon mice. Grasses and forbs indicated the poorest habitats (Fellers and Arnold 1988). In the Sierra Nevada, they are mostly limited to areas with dense brush or tree cover below about 4,600 feet, and are usually abundant only where oaks do not dominate. At SJER, pinyon mice were commonly associated with moderate to dense stands of brush, particularly buckbrush, and rocks. Likewise, in the southern Sierra Nevada (Kern County), pinyon mice preferred stands of buckbrush and rock outcrops (Lawrence 1966). In the La Panza Range of San Luis Obispo County, they were more than four times as common in a chaparral community of chamise, buckbrush, and coast live oaks as they were in a blue oak/digger pine woodland (Murray 1957). None was taken in chaparral communities in over a decade of studies on the San Dimas Experimental Forest, on the Pacific slope of the San Gabriel Mountains (Wirtz et al. 1988).

Patterns of Abundance

Results of trapping suggest some differences in habitat affinities of white-footed mice in the western Sierra Nevada (tables 10A and 10C). Deer mice were captured in most habitat types and seral stages, exhibiting apparent specialization at low elevations (where brush and pinyon mice co-occur) in sites dominated by grasses and forbs. Their habitat associations increase markedly with increasing elevation to the point that they are ubiquitous in the red fir zone, where no other species of white-footed mice occur. Pinyon mice were generally confined to sites with shrubs, mixtures of shrubs and small trees, or shrubs and widely scattered trees in all habitats sampled except the oak/digger pine type, yet other studies (Quast 1954, Block et al. 1988) found them to be common in this woodland type, where they were associated with shrubs. Brush mice were relatively uncommon in most habitats, except those at lower elevations that had large trees in the canopy. California mice were essentially missing from the sample, although study sites were either too far north for this species or generally in habitat types where we would not expect to find them.

Any interpretation of habitat use reported in tables 10A and 10C should note differences in elevation and forest composition. Sierran mixed-conifer sites reported in table 10A, for example,

were mostly on north-facing slopes of canyons 2,000-3,900 feet in elevation, where Douglas-fir occurred with ponderosa pine, sugar pine, incense-cedar, or black oak. Studies reported in table 10C were farther south, at elevations of 5,200-6,500 feet. Douglas-fir was rare there, and most sites had white fir mixed with the other species listed above.

Densities of white-footed mice within the range of the California spotted owl generally fluctuate between lows in December and January to highs in July and August. At higher elevations in mixed-conifer and fir forests, annual peaks in densities may be delayed into August or September. Densities of different species vary from <1 to >30 mice/acre. Various density estimates have been reported in the literature; these are summarized below (animals/acre), but readers should be mindful of the problems with estimating densities of small mammals and the variety of methods used.

Brush mice-1.0-15.3 (Zeiner et al. 1990); 3.0-15.2 (Sierran mixed-conifer, Bass Lake area, Storer et al. 1944); 1.3 (Lake Tahoe area, Storer et al. 1944).

California mice-31.2 (xeric chaparral, central California, Merritt 1974); 37.2 (mesic oak-laurel forest, central California, Merritt 1974); 0.1-0.8 and <0.8 (southern California coastal-sage scrub, MacMillen 1964 and M'Closkey 1972, respectively).

Deer mice-4.0-10.0 (White et al. 1980); 4.9-14.2 (mixed-conifer forest, Sierra Nevada, Bass Lake area, Storer et al. 1944); 19.1 (Lake Tahoe area, Storer et al. 1944), <0.4-1.6 (southern California coastal sage, M'Closkey 1972).

Pinyon mice-1.0 (oak-laurel forest, central California, Merritt 1974); 34.8 (xeric chaparral, Merritt 1974).

General Life History Features

White-footed mice are nocturnal and active throughout the year. Some species become torpid under food or water deprivation, but others do not. They nest in ground burrows, talus, hollow logs, and in hollows in trees. They readily climb in brush and trees (scansorial). Arboreal tendencies differ among species, however, with brush and California mice being the most scansorial of the species occurring in California, and deer mice the least. White-footed mice are not highly territorial except near their nest, but territoriality differs among species. The California mouse is the most territorial species, living in male-female pairs with nearly nonoverlapping home ranges (Ribble and Salvioni 1990).

Diet

White-footed mice are omnivorous, feeding on seeds, fruits, fungi, flowers, foliage, insects and other arthropods, carrion, and other animal matter (Zeiner et al. 1990). Specific studies suggest that the four species considered here are largely opportunistic in choice of diet, although differences are seen where species' ranges overlap (for example, Jameson 1952; Meserve 1976a, 1976b). Insects (especially larvae and pupae), seeds, fruits, and fungi probably comprise the bulk of their diets. California mice

eat large quantities of California-laurel seeds, the thick, hard coats of which cannot be cracked by pinyon mice (Merritt 1974). In a coastal sage community, California mice ate mostly shrub fruits, seeds, and flowers and smaller quantities of grass seeds (Meserve 1976a).

Reproduction and Development

Reproduction varies geographically, altitudinally, and annually. Females appear to be seasonally polyestrous, with most births occurring between March and October, but some females may be pregnant in any month. The most prolonged reproductive seasons are found in populations at or near sea level and on the lower slopes of coastal ranges. The shortest reproductive seasons occur at the highest elevations in montane communities.

The breeding season of brush mice peaks in April and May; a secondary peak in June to August seems to depend upon the previous crop of acorns. Litters average three to four young; females probably average near two litters per year, although they can have four. Females born in spring can breed in the summer of their first year.

Although California mice may breed year-round in coastal areas, most breed between March and September. Litter size averages two to three (MacMillen 1964, Merritt 1978), with up to three to four litters per year. Females born early in the year breed late in the reproductive season of the same year, although California mice mature more slowly than the other white-footed mice considered here.

Deer mice may breed year-round, depending upon climate, but most reproduce between March and October. Litters are larger at higher elevations and latitudes, but probably average four to six for populations within the range of the California spotted owl. Numbers of embryos for 46 females from the Sierra NF, most captured between mid-June and mid-August in mixed-conifer and red fir forests, averaged 5.2 ± 1.43 (range = 2-9). Mean litter size for 11 females in a southern California coastal-sage community was 4.3 ± 1.3 (MacMillen 1964). Females may have two to four litters during the breeding season-fewer at higher elevations and latitudes. Young born in spring breed later in the same summer or autumn.

Pinyon mice breed mainly from May to September, averaging two to three young per litter. Females may breed when 3 months old.

Little information is available on dispersal by these species within the geographic range of the California spotted owl. Dispersal probably commences soon after weaning, but individuals may leave their natal homes over a protracted period, depending upon circumstances such as survival of the mother, population density, and food abundance. Time to weaning varies geographically and by species. For brush and deer mice, weaning probably averages about 25 days (range of reported values, 22-37 days, summarized by Zeiner et al. 1990). California mice are weaned in an average of 35 days, although some litters may not be weaned until 44 days (McCabe and Blanchard 1950, Merritt 1974). Clark (1938) reported 50 days as the period before weaning in pinyon mice, although other studies found considerably

shorter periods-about 25 (McCabe and Blanchard 1950) or 30 days (Douglas 1969).

Weights

The deer mouse is the smallest of the four species considered here. Adults (excluding pregnant females) weigh about 0.53-0.91 ounces (Layne 1968); the mean for a Sierra Nevada sample was 0.70 ± 0.01 ounces, n = 144. Grinnell and Storer (1924) listed a range of 0.45-0.74 ounces for deer mice caught in the central Sierra Nevada.

Adult brush mice ranged in weight from about 0.77 to 1.19 ounces in the Yosemite region (Grinnell and Storer 1924). The mean of a mixed-age sample of brush mice in the Sierra NF varied from about 0.74 to 0.95 ounces (table 1013).

Breeding adult pinyon mice from central coastal California averaged 1.19 ± 0.11 ounces (Merritt 1974). The range of weights in the Yosemite region was 0.82-1.44 ounces (Grinnell and Storer 1924). Samples of breeding adults from the Sierra NF averaged about 0.98-1.09 ounces.

California mice are the largest of the white-footed mice in California. Most reported adult weights range from about 1.33-1.75 ounces (Grinnell and Storer 1924, Layne 1968, Jameson and Peters 1988). Merritt (1974) reported mean weights of breeding adults as 2.0 ± 0.28 ounces in central coastal California. A population mean for all ages and sexes captured year-round in a coastal-sage community in southern California was 1.20 ounces (MacMillen 1964).

Table 10D-Variation in weights (in ounces, mean ± SD, with range and sample size below) of three species of white footed mice during summer (June-August, Sierra National Forest, Fresno County) and winter (January, San Joaquin Experimental Range) (D. F. Williams pers. observ.).

Season	Sample	Brush mouse	Deer mouse	Pinyon mouse
Summer	Adults	0.99 ± 0.11 (0.74 - 1.33) n = 39	0.74 ± 0.13 (0.46 - 1.12) n = 208	1.00 ± 0.07 (0.77 - 1.30) n = 31
		0.51 ± 0.08 (0.41 - 0.63) n = 5	0.43 ± 0.09 (0.21 - 0.56) n = 113	0.54 ± 0.12 (0.39 - 0.77) n = 12
		0.93 ± 0.18 (0.42 - 1.33) n = 44	0.63 ± 0.19 (0.21 - 1.12) n = 321	0.87 ± 0.24 (0.39 - 1.30) n = 43
	Young	0.78 ± 0.07 (0.67 - 0.95) n = 31	0.54 ± 0.07 (0.39 - 0.70) n = 14	0.90 ± 0.13 (0.70 - 1.09) n = 9
		0.61 ± 0.03 (0.56 - 0.67) n = 12	0.49 ± 0.07 (0.35 - 0.60) n = 13	0.57 ± 0.08 (0.49 - 0.67) n = 5
		0.73 ± 0.10 (0.56 - 0.95) n = 43	0.51 ± 0.08 (0.35 - 0.70) n = 27	0.78 ± 0.20 (0.45 - 1.09) n = 14

Management

Clearcutting or similar tree harvest and brush thinning or removal generally result in increased numbers of deer mice. Wildfires and controlled burns that reduce shrubs and small trees and increase cover of grasses and forbs also enhance populations of deer mice in woodland, forest, and chaparral communities (Jameson 1951, Quast 1954, Lawrence 1966, Spevak 1983, Fellers and Arnold 1988, Wirtz et al. 1988) (also see table 10C). On the other hand, numbers of other species of white-footed mice in lower-elevation mixed-conifer, ponderosa pine, oak-pine woodland, and various hardwood and chaparral communities would be reduced or eliminated by clearcutting, brush removal, or fire. Management that promotes increased abundance of oaks would increase numbers of brush mice. In the San Gabriel Mountains, in mixed-chaparral communities on the San Dimas Experimental Forest, brush mice were rare on plots in chaparral that had not been burned for 28 years, but increased in abundance after burns. Brush mice increased to six times their preburn density on areas with normal burns and 14 times on areas with hot burns. Brush mice recolonized burned areas sooner than California mice (Wirtz et al. 1988). In coastal northern California (Hopland Field Station, Univ. of California), both brush and pinyon mice were adversely affected by converting chaparral to grassland, but positively affected by converting old, decadent chaparral to young- and intermediate-aged stands (Longhurst 1978). California mice were the only common *Peromyscus* in the mature montane chaparral at San Dimas Experimental Forest. They were the slowest of the white-footed mice to recolonize mixed montane-chaparral communities in the San Gabriel Mountains after burns. Captures after burns were greater on normal burns than hot burns, and postfire densities were generally greater than preburn densities (Wirtz et al. 1988). Management that promotes increased cover and vertical complexity of chaparral and woodlands, increased abundance of California-laurel and dusky-footed woodrats, and increased numbers of potential nests would enhance populations of California mice.

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Chapter 11

Historical Perspectives on Forests of the Sierra Nevada and the Transverse Ranges of Southern California: Forest Conditions at the Turn of the Century

Kevin S. McKelvey and James D. Johnston

Preface

Let me say a word of thanks to the members of the forestry force who acted as my escort. I wish to thank other gentlemen also, but particularly the members of the forestry force. I am, as you gentlemen probably know, exceedingly interested in the question of forest preservation. I think our people are growing more and more to understand that in reference to the forests and the wild creatures of the wilderness our aim should be not to destroy them simply for the selfish pleasure of one generation, but to keep them for our children and our children's children. I wish you, the Forest Rangers and also all the others, to protect the game and wild creatures and of course in California, where the water supply is a matter of such vital moment, the preservation of the forests for the merely utilitarian side is of the utmost, of the highest possible consequence; and there are no members of our body politic who are doing better work than those who are engaged in the preservation of the forests, keeping nature as it is for the sake of its use and of its beauty.

Theodore Roosevelt, 9 May 1903.

The Sierra Nevada has been impacted by western civilization for more than 150 years and heavily impacted for at least the past 100 years. Impacts include mining, logging, the grazing by both sheep and cattle, and changes in fire patterns—notably fire suppression in the twentieth century. Site-specific data from the 1800s are scattered and not comprehensive, but several events occurred around the turn of the century that led to reasonably detailed and quantitative accounts of the condition of the land and forests. General Grant, Sequoia, and Yosemite National Parks (NPs) were established in 1890. Forest reserves were set aside between 1891 and 1909 and renamed as National Forests (NFs) in 1907. After creation of the forest reserve system, the United States Geologic Survey (USGS) initiated the first systematic surveys of the forest reserves as part of a series of annual reports. For a brief period, from about 1897 to 1902, these surveys were very thorough and often included maps of topography, timber volume, logging intensity, and species distribution. Surveys covering most of what is now the Eldorado and Stanislaus NFs and Yosemite NP were published in 1900 (Fitch 1900a, 1900b; Marshall 1900; Sudworth 1900a). Similar inventories were done by Leiberg (1902), mainly in what is now the Tahoe and Plumas NFs. Additional information concerning what are now the Sierra and Sequoia NFs and Sequoia/Kings Canyon NPs was obtained by analyzing Sudworth's (1900b) unpublished field notes.

Areas in southern California were also surveyed around the turn of the century. Leiberg (1899a, 1899b, 1899c) examined the

San Jacinto, San Bernardino, and San Gabriel reserves in 1897. The San Jacinto Quadrangle was reexamined in 1900 and Barnard (1900) produced a 30-minute topographic map (fig. 11A).

This chapter is largely an analysis of these USGS survey efforts, with ancillary data from other sources. The men involved with the surveys were professionals whose job it was to assess the condition of the newly created reserves. Their studies appear to be reliable and accurate, providing quantitative assessments of forest stands that are of great historic interest and importance today.

Sierran Forests at the Turn of the Century

Nonaboriginal Human Impacts

Logging in the Middle and Southern Sierra Nevada

Logging was used mainly to support local markets, including the growing towns and communities of the Sacramento and San Joaquin Valleys (Ayers 1958). All major towns were associated with mines, and nearly all timber cut supported the mines—for housing employees, timbers to keep tunnels from collapsing, processing ore, and transporting processed ore to market by rail (Sudworth 1900a). "Large mines" consumed between 2,000 and 3,500 cords annually (fig. 11B). Fuel needs of stamp mills—machines or mills for pulverizing ore—were impressive. The Empire Mine, for instance, had a 30-stamp mill that consumed 11 cords of wood in a 10-hour period (Bohakel 1968) or, assuming constant operation, 9,600 cords a year.

Most logging before 1900 occurred at low elevations on lands adjacent to mines, because wagons were the chief means for transporting timber (Sudworth 1900a, Leiberg 1902) (fig. 11C). Sudworth mapped cut-over and partially cut regions (fig. 11D, table 11A). With the exception of a large area of cutting that extended up the American River, Forest Service (FS) lands and many higher-elevation private lands had not been logged (fig. 11E). Laudenslayer and Darr (1990) provided an analysis of cutting during that period by the Michigan-California Timber Company.

The partially cut lands, especially those more distant from Placerville, were largely exploited for the shake market (Sudworth

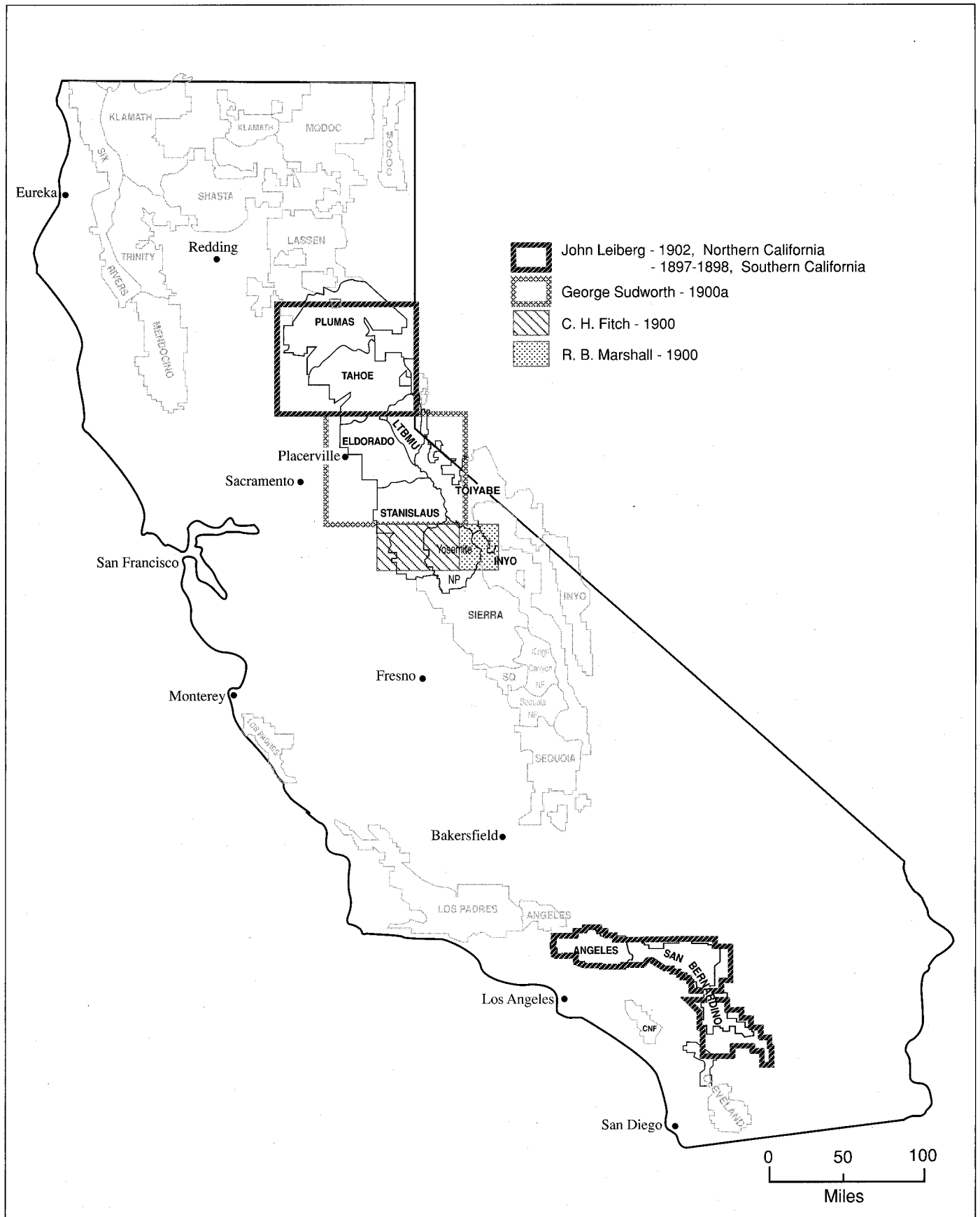


Figure 11A--Areas surveyed by Leiberg (1899a, 1899b, 1899c, 1902), Marshall (1900), Fitch (1900a, 1900b), and Sudworth (1900a).

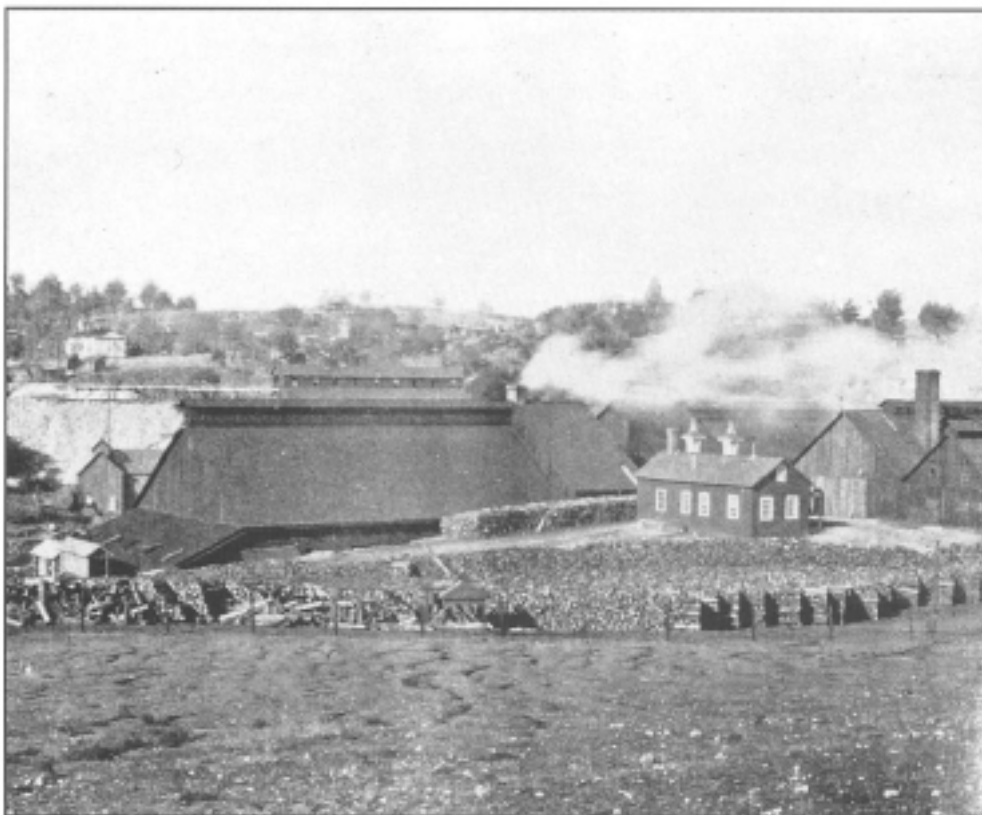


Figure 11B--Large mining plant at Angels Camp, where great quantities of yellow pine cord wood were consumed. Thousands of cords of this 4-foot cordwood were needed to keep each mill going throughout the year. Hundreds of mills operated up and down the Sierra Nevada during this era, processing ore for gold and other minerals. Wood also was the primary fuel for heating and cooking in homes and businesses, as well as providing energy to run the steam engines, which powered winches, sawmills, and locomotives.

Location: -----In foothills just below the Stanislaus National Forest, central Sierra Nevada.

Elevation:-----About 2,000 feet

Date: -----Probably 1899

Source:-----Sudworth 1990a

Photo-grapher: ----Unknown

Figure 11C--A common method of hauling yellow pine logs to mills was by horse and wagon. Before railroads entered the area, transportation of raw logs and lumber had definite limitations. Mills, which remained close to the timber source, tended to be smaller and more mobile. When the local timber was used up, the mill was disassembled and moved to another area.

Location:-----Stanislaus National Forest, central Sierra Nevada

Elevation: ----About 4,000 feet

Date: -----Probably 1899

Source: -----Sudworth 1990a

Photo-grapher: ----Unknown



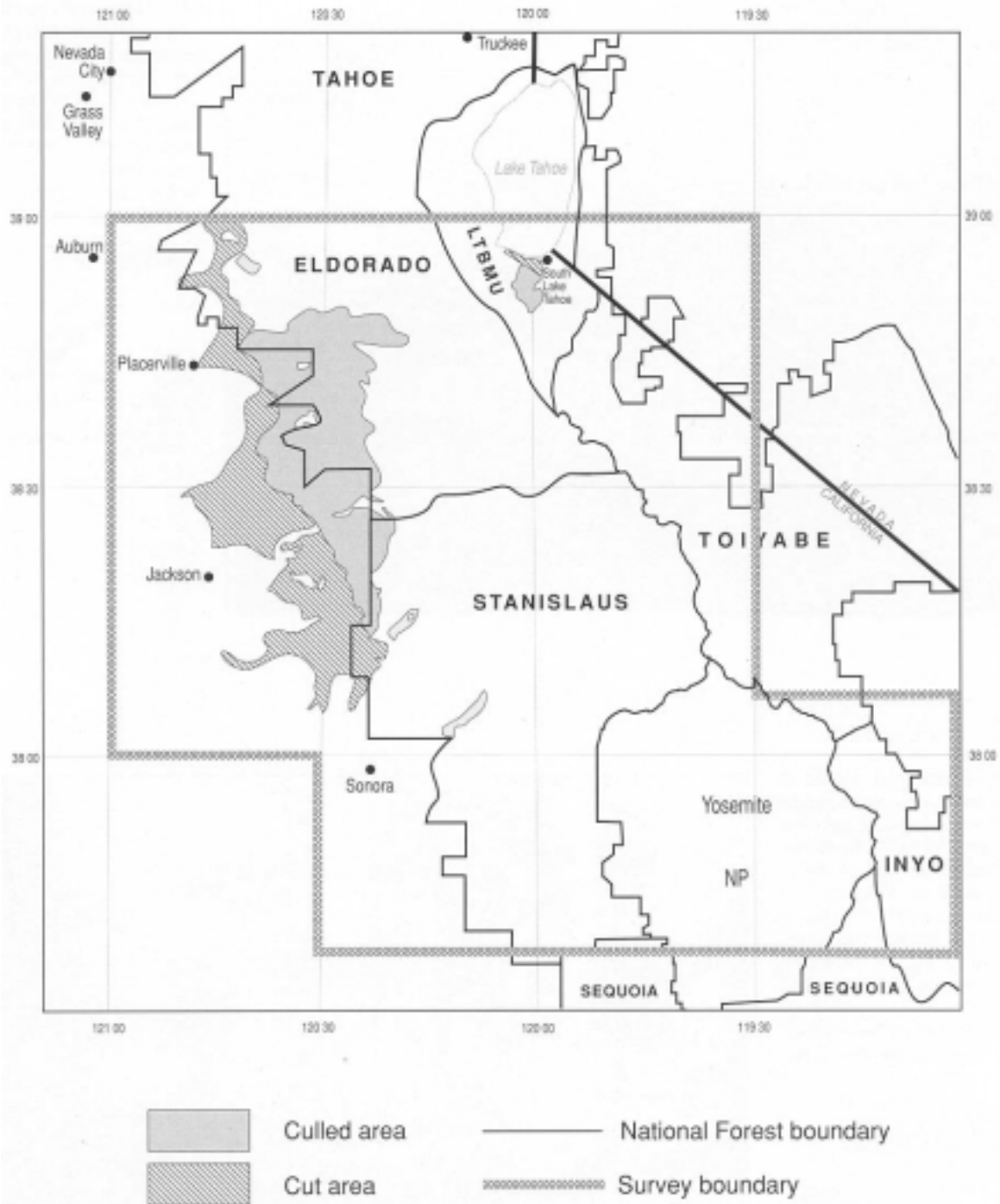


Figure 11D--Areas of logging activity from maps by Marshall (1900), Fitch (1900a), and Sudworth (1900a). Culled areas were selectively logged. Most of the cutting in this area was associated with the town of Placerville.

Table 11A--Areas sampled by Sudworth in the Sierra Nevada at the turn of this century (Sudworth 1900a) (see figs. 11A and 11D).

Areas	Area (square miles)		
	Logged	Culled ¹	Virgin ²
Thirty-minute quadrangles			
Placerville	122	162	152
Jackson	175	18	0
Pyramid Peak	0	148	642
Big Trees	89	104	564
Markleeville	0	0	322
Dardanelles	0	0	659
Forest Reserves			
Stanislaus	0	0	641
Tahoe	0	3	130
Total	386	435	3,190
Percent of total	10	11	79

¹ Culled areas were selectively logged.

² Lands listed as grazing or nonforest were omitted.

1900a). Shakes were the most valuable product at the time, maintaining a market value well above dimension lumber into the twentieth century. On the Stanislaus NF in 1912, for instance, shake prices were \$5.00 to \$7.50 per thousand (Graves 1912), approximately the same price reported by Sudworth.. Shakes were produced only from the choicest sugar pines, and only from select portions of the bole--no more than 40 percent, according to Sudworth. For this reason, shake cutting always resulted in partial removal of standing timber, and it always left much waste. Following a similar pattern, giant sequoias were split to produce grape-stakes (fig. 11F).

Logging in the Northern Sierra Nevada

Ore deposits extended into higher elevations in the northern Sierra Nevada than in the middle and southern parts. Consequently, placer and hard-rock mining and logging were more extensive there than to the south. In particular, areas north of Nevada City and the Truckee Basin were heavily cut (fig. 11G). Again, access was key and the presence of the Southern Pacific Railroad allowed transportation to more distant markets. Lake

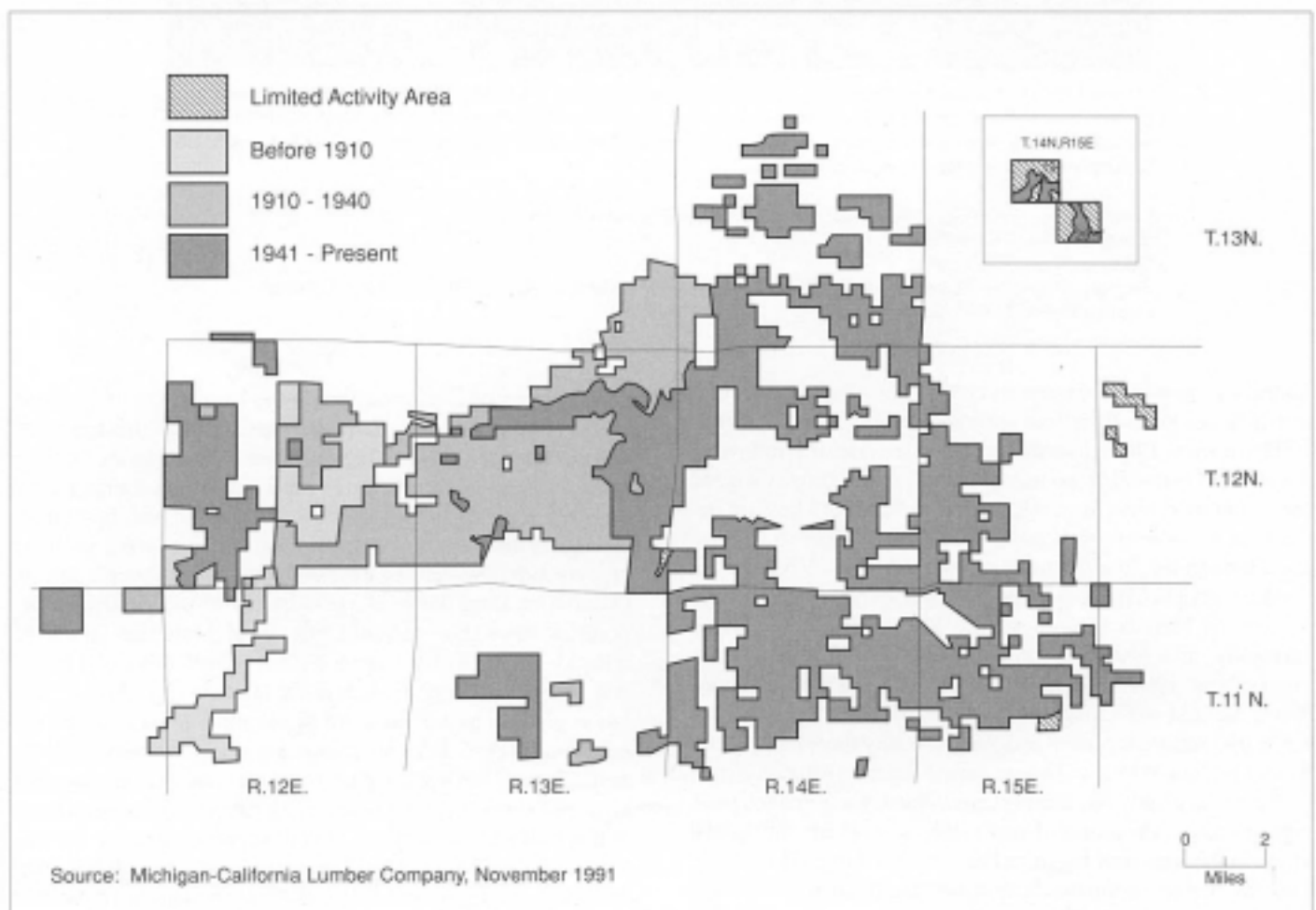


Figure 11E--Chronology of cutting on lands of the Michigan-California Timber Company. These lands lie within the area surveyed by Sudworth in 1900. Cutting prior to 1910 occurred within a very limited acreage.



Figure 11F--This ancient giant sequoia, named the Mark Twain Tree in 1888, sprouted in 550 A.D.; it was 1,341 years old and 90 feet around the base at the time of this photo. Smith Comstock erected a sawmill just 250 yards west of this tree. Giant sequoia wood made poor lumber, so it was split into grapestakes (center) and posts (left) to supply California's rapidly expanding vineyards.

Location: -----Big Stump, Sequoia/Kings Canyon National Parks

Elevation: -----5,760 feet

Date: -----1891

Source: -----Steve Anderson Collection, Hume Lake Ranger District, Sequoia National Forest

Photographer: -----C. C. Curtis

Tahoe also provided convenient access, allowing large quantities of timber to be taken from areas adjacent to the lake (Leiberg 1902, McKeon 1984). In addition, a 4-mile-wide strip following the railroad between Reno and Sacramento was heavily logged for locomotive fuel (fig. 11G; Palmer 1992). Gold-bearing deposits at mid-elevations (Clark 1966) caused mines to be scattered throughout forests of the region. The Yuba River Basin, north of Nevada City, was logged to supply large mines at Grass Valley and Nevada City (elevations 2,400 and 2,600 feet, respectively) as well as at Sierra City (elevation 4,200 feet).

Leiberg (1902) reported that 1,386,890 acres in the northern Sierra Nevada were logged between 1850 and 1902, and that 2,337,930 acres were uncut. Logging intensity there varied from 5 to 99 percent of total volume removed. Leiberg estimated that, on the average, only 50 percent of the volume was removed from logged stands. He provided two means to evaluate the spatial extent and intensity of logging. The maps used to prepare figure 11G gave volume estimates, both in the "culled" areas and in areas that were not entered. Those maps were supported by detailed written descriptions of the forest on a drainage-by-drainage basis.

Analysis of cutting patterns in the North and Middle Forks of the Feather River, for instance, clearly shows that most cutting occurred at elevations below current FS boundaries. Oroville was the primary destination of lumber from these drainages, and the only method for transporting the timber was by wagon, restricting the trip to 40 miles or less (Leiberg 1902). Most cut areas reported by Leiberg were within 20 miles, straight-line, of Oroville or along lower slopes adjacent to the Central Valley north of there. For example, Big Bend Mountain (about 15 miles) was heavily cut over and Chino Creek (about 20 miles) was reportedly logged. According to Leiberg (1902, p. 58), however, in an area of about 15 square miles immediately north of Chino Creek "...lies a block of heavy forest, the heaviest in the basin. It is of the yellow-pine type, but contains an unusually large proportion of sugar pine... Both the yellow and sugar pine in this heavy block of timber are of exceptionally large size and of old growth. Much of the sugar pine runs above 5 feet basal diameter, with clear trunks 40 to 60 feet in height." This block of timber was clearly desirable but just beyond reach of the wagon-based logging of 1902. For this reason, cutting in these

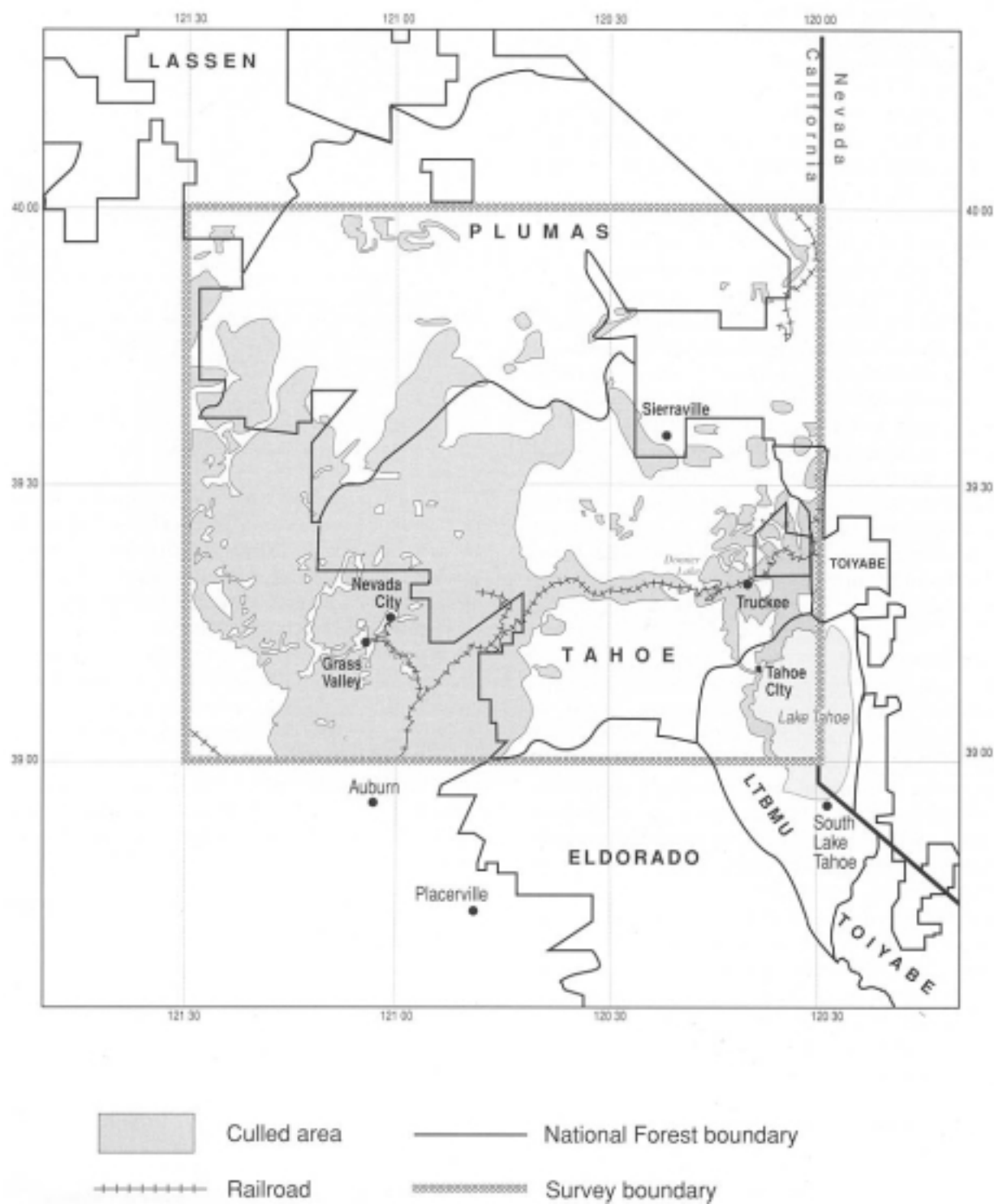


Figure 11G--Areas of logging activity from maps by Leiberg (1902). Leiberg did not, as did Sudworth (1900a), differentiate between cut-over lands and culled lands. In many areas cutting appears to have been very light.

drainages did not extend far into what is now the Plumas NF (fig. 11G). Areas of NF land that were entered tended to be at extreme limits of the transportation capabilities and would therefore have been subjected primarily to high-grading of sugar pines. This assertion is supported by an inventory done by the Plumas NF in 1910, which estimated that 870,506 acres of the Plumas were in a forested condition but only 11,983 acres (1.3 percent) had been "cut over" (Moore 1913).

On the other hand, 57 percent of the Yuba river drainage was described as being cut. In areas adjacent to towns or major rivers, Leiberg stated that most trees were removed. On other lands, cutting was much more selective.

Results of inventories by Leiberg and Sudworth, supported by the Plumas NF plan of 1913 and records of the Michigan-California Timber Company, show that cutting at the turn of the century was spatially limited to areas near population centers and major transportation routes. With notable exceptions of the Truckee Basin, Yuba River Basin, and lands immediately adjacent to the Southern Pacific Railroad, logging occurred at low elevations with relatively little within NF boundaries in the Sierra Nevada prior to the turn of this century. Limited by transportation capabilities, much of the logging on what are now NF lands was reduced to light high-grading of the most valuable trees. The NF most heavily impacted was the Tahoe. There the railroad, combined with mining at higher elevations, caused significant logging in what is now FS land. Even in the Tahoe NF, however, about half of the forest had not been entered at the turn of the century.

Grazing by Sheep

Unlike logging, which impacted limited acreage in the Sierra Nevada prior to 1900, the entire Sierran range appears to have been intensely overgrazed for decades, beginning in the early 1860s when a severe drought killed most of the cattle in California (Vankat 1970, Ratliff 1985, Ewing et al. 1988). According to Ratliff, not only did the drought cause a shift from cattle to sheep, but it also initiated the practice of summer grazing in alpine meadows of the Sierra Nevada (fig. 11H). In 1862, California ranges supported 3 million sheep, about 40 percent of which grazed the Central Valley. Grazing peaked in 1876, when more than 6 million sheep grazed state-wide (Ratliff 1985, Ewing et al. 1988). Sheep grazing was still intense in 1900, when an estimated 200,000 animals grazed during summer and fall in the Sierra Reserve (Vankat 1970). Descriptions of the impact of grazing on vegetation are particularly intense in much of the literature of that period:

There are practically no grasses or other herbaceous plants. The forest floor is clean. The writer can attest the inconvenience of this total lack of grass forage for in traveling over nearly 3,000,000 acres not a single day's feed for saddle and pack animals was secured on the open range... Barrenness is, however, not an original sin. From a study of long-protected forest land in the same region and from the statements of old settlers, it is evident that formerly there was an abundance of perennial forage grasses throughout the forests of this territory... It would seem that this bare condition of the surface in the open range has been produced only through years of excessive grazing by millions of sheep—a constant overstocking of the range (Sudworth 1900a, p. 554-555).

The trampling of thousands of sheep pastured on these slopes during the summer and fall reduces the soil, to a depth of 6 or 8 inches, to the consistency of dust. Rain washes this dust into creeks and rivers, and heavy winds lift it up and carry it away (Leiberg 1902, p. 15, concerning the red fir type).

The great obstacle to the explorer is not the danger of crag or chasm, but the starvation threatening his animals, through the destruction of the fine natural meadow pasturage by sheep (Russell Dudley 1898, professor of botany, as quoted by Vankat 1970, p. 20).

The soil being denuded of grass is broken up by thousands of sheep tracks, and when the rains come this loose soil is washed down the mountainsides into the valleys, covering up the swamps and meadows, destroying these natural reservoirs (1894 report by Acting Superintendent of Sequoia and General Grant NPs, as quoted by Vankat 1970, p. 20).

The Kern River drainage was ...almost impassable to the traveler, to such an extent is every living thing eaten off the face of the earth and trampled underfoot by the hundreds of thousands of sheep which each year roam over that territory (1893 report by Acting Superintendent of Sequoia and General Grant NPs, as quoted by Vankat 1970, p. 29).

Clean surface; sheep grazed and burned. No reproduction. 10,000 feet elevation (Sudworth 1900b, p. 10).

The last quote above, referring to an area at the headwaters of the Kings River, now in Sequoia/Kings Canyon NPs, was typical of site-specific examples in Sudworth's notes. The seasonal migration of sheep from the Central Valley up to alpine meadows in mid-summer meant that even very remote locations experienced the impact of overgrazing.

Recurrent themes typify the writings of different observers. Grazing at an intensity that produced significant soil erosion was noted in both the northern and southern Sierra. Removal of all grass was repeatedly mentioned in the context of travel being inconvenient because pack animals could not graze. In many cases, this was contrasted with the contention that grasses were abundant in forests prior to grazing. Although we suspect that many early writers harbored an anti-sheep bias, the numbers of sheep mentioned casually (hundreds of thousands, millions) appear to be accurate.

Burning by Sheep Herders

Sheep herders also burned extensively to encourage growth of grasses and forbs and to remove fuel and young trees from the forest floor. All accounts mention this, but we cannot be certain about the extent to which sheep-related fires contributed to overall fire frequency. John Muir, writing in 1877, felt that 90 percent of fires were caused by sheep herders, but his estimate was probably exaggerated (Vankat 1970). It is clear, however, that the pattern and intent of fires set by sheep herders differed from those set by Native Americans. The intent was to improve grazing on high-altitude pasturage and to remove obstacles that impeded movement by sheep. Consequently, sheep herders gave special attention to burning large, downed fuels (Sudworth 1900a, Vankat 1970) and to burning mesic areas to stimulate forage production.

We consider it likely that this intensity of grazing, combined with repeated burning by sheep herders, had a severe impact on herbaceous vegetation and on patterns of forest regeneration in the



Figure 11H--Sheep grazing in the Sierra Nevada.

Location: -----Northside of Crabtree Meadow, Sequoia National Park

Elevation: -----10,400 feet

Date: -----29 July 1890

Source:-----Vankat (1970) Photographer: -----Unknown

Sierra Nevada. In the absence of competing vegetation, regeneration was rapid and dense when sheep and fires ignited by sheep herders were no longer prevalent in montane forests. According to Leiberger (1902, p. 15), such areas were common

...varying from 1 acre to 3 or 4 acres, scattered along the ridges from Webber Peak to the Rubicon River, on which the grass and weeds have been so thoroughly eaten out that even the sheep have abandoned them. On such tracts, left undisturbed for four or five years, Shasta firs [red fir] cover the ground to the number of 10,000 to 15,000 trees to the acre.

Leiberger (1902, p. 43) also reported that stands freed from burning for 15 years

...may be seen in the Mohawk Valley, on areas in the central portions of the basin of the West Fork of Feather River and in the northern portion of the Truckee Basin. These sapling stands, composed of yellow pine, red [Douglas-] and white fir, and incense cedar, singly or combined, are so dense that a man can with difficulty force his way through.

Sudworth (1900a, p. 553) found a "general lack of herbaceous growth and irregular reproduction of timber species [and a] general absence of small-sized timber intermediate between seedlings and the large timber" in unfenced forests. In "fenced and otherwise protected forests," he found "uniform abundance of herbaceous growth," "plentiful reproduction of timber species," and "presence of intermediate sizes of small timber."

Vankat (1970) measured the ages of numerous trees in Sequoia NP, finding that a major regeneration pulse occurred at approximately the time sheep were removed from the Park (fig. 11I). Vankat also found that particular areas (for example, meadows) and species (for example, big sagebrush) had not recovered from grazing by the late 1960s. We can reasonably infer that the intensity of sheep grazing for nearly 40 years in the Sierra Nevada impacted stand structure and regeneration patterns, producing lasting changes in mixed communities of grasses, forbs, and shrubs.

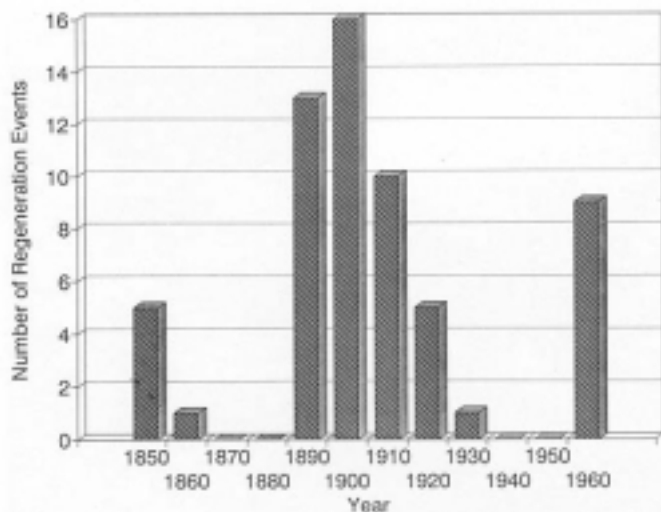


Figure 11I--Periods of significant regeneration on sites within Sequoia National Park. This graph was generated by combining tables found in the appendices of Vankat (1970).

Stand Structure

The best data on stand structures at the turn of this century came from a set of 1/4-acre plots measured by Sudworth (1900a, 1900b). Data from 22 plots were presented in his formal document (1900a) for the USGS on the Stanislaus and Tahoe reserves, and data from 26 additional plots were included in his notes on the Sierra Reserve (1900b). Here we report analyses of all plots in the USGS report but only 20 of the 26 plots in Sudworth's notes. Four of those not analyzed were in groves of giant sequoias (Sudworth was particularly interested in the big trees), and two were at high elevation and contained large components of foxtail pine. These plots represented uncommon forest types and were not considered of general interest. Sudworth did not describe the methods he used to select plots, but their primary purpose was to support the maps he created. His maps, a standard product in USGS surveys of that period, subdivided the entire area surveyed (about 3,000,000 acres) into subunits based on similarity in timber volumes. Sudworth often referred to his plots as being "representative" of a particular area. He probably used scattered plots to calibrate ocular estimates. He reported only trees 11 inches or more in diameter at breast height (d.b.h.) in the USGS report and only 12 inches or more in d.b.h. in his notes. He mentioned regeneration in his notes, but the meaning of the term was not quantified.

Several uncertainties are associated with analyses of data from the turn of the century. In particular, estimates of volume per acre, either at the stand level or derived from plot data, should be viewed with caution. At a stand level, volumes were calculated using scaling rules based on the limits of merchantability. Because small trees (for some species defined as trees <16 in d.b.h.) and tops were not used, and because saw kerfs were wider than today, the volume reported on a per-acre basis in 1900 would, therefore, be considerably less than if the same acreage were cruised today. This underestimation (by current standards) was significant. For the San Jacinto Reserve, for instance, Leiberg (1899a, p. 356) estimated the total volume at

98 million board feet (MMBF). He noted, however, that "The sawmills in the reserve... handle the timber in the most economical manner possible, utilizing the trees far up in the crown, where the diameter dwindles to 8 inches or less. Worked up in this manner, the quantity of available merchantable timber would amount to at least 200,000,000 feet..."--a full doubling of the volume estimate.

Volume estimates based on the plots could be derived directly from the data, but this too is risky because the criteria used for plot selection are unknown, and volume appears to have been very heterogeneously distributed in the forest. Fitch (1900a) noted that volume averaged 80-140 thousand board feet (MBF) per acre in selected areas of the Yosemite Quadrangle, but the overall average was between 30 and 40 MBF. Given the small number of plots available for analysis, coupled with the highly variable stocking levels present at the time, use of volume statistics derived from plot data to infer volume-per-acre for the forest system is not justified. For this reason, we have not used volume estimates to compare current and historical forest conditions. Instead we have used the proportions of stems in particular diameter classes, or the proportions of basal area by species.

Diameter Distribution

Stands described by Sudworth (1900a) were very large and very old. The average yellow pine, for instance, was reportedly 150-180 feet tall, 3-4 feet in d.b.h., and 250-350 years old. Although Sudworth did not measure trees less than 11 inches in d.b.h., available evidence indicates that trees in those smaller classes were uncommon, though patches of very small regeneration appear to have been present, based on photos and text in Sudworth's report and on discussion by Leiberg (1902) of regeneration following removal of sheep. Most stems exceeded 25 inches in d.b.h., and many extremely large specimens were measured (fig. 11J). Of the major timber species, sugar pine, Douglas-fir, and white fir occurred only as very large trees (fig. 11K). Sugar pines were a minor stand component, but most of them were in the very large diameter classes. A comparison of that distribution with the largest diameter stands in Sierran for-

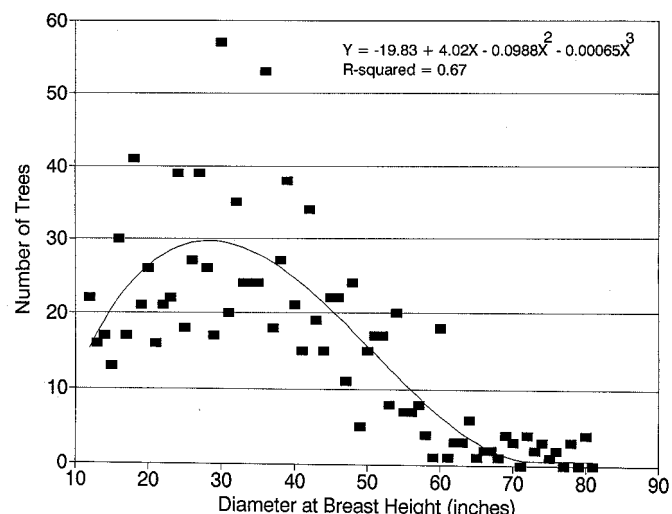


Figure 11J--Distribution of trees in forests of the Sierra Nevada in 1900. All species were lumped by diameter class and all of the plot information (Sudworth 1900a, 1900b) was combined. Many of the trees with diameters at breast height <15 inches were lodgepole pines.

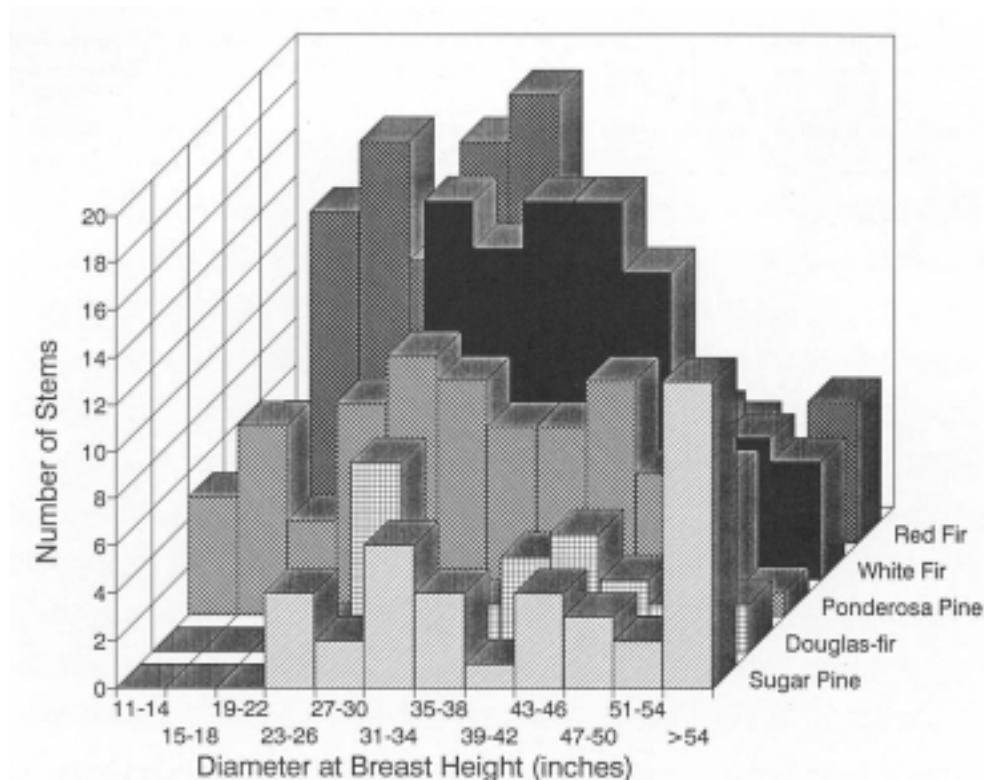


Figure 11K--Diameter distribution of trees in the Sierra Nevada, by species, for published plot data (Sudworth 1900a). Sugar pine, Douglas-fir, and white fir were present only in very large diameter classes.

ests today shows that far more of the stand basal area in the forests of 1900 was concentrated in very large trees (fig. 11L).

Species Composition

Species composition was apparently mixed at the turn of the century, with all major timber species represented. White fir and incense-cedar were widely distributed and present in large numbers (table 11B, fig. 11M). Pines did not dominate the forests, either in number or in volume. Volume estimates by species at about the turn of the century, available from several sources (table 11C), supported the plot-level data of Sudworth (1900a, 1900b). Note that many estimates made at that time underestimated the volume in true fir, because those trees were not considered merchantable unless they were at least 16 inches in d.b.h., whereas pines were merchantable when 12 inches or more in d.b.h. (Leiberg 1902). For his part, Sudworth did not give forest-wide volume estimates, but noted that the elevational range of white fir was between 3,800 and 7,500 feet, and that it formed 30-45 percent of the stand in areas where it was most abundant.

When compared with the current species composition in Sierran forests, the composition at the turn of the century was reasonably similar (compare fig. 11N and table 11C). Comparing the forest-wide estimates made by the Plumas NF in 1913 (Moore 1913) with current estimates from mixed-conifer timber strata (timber strata codes are defined in table 1C and in Appendix B), it appears that true fir and incense-cedar have increased and that pines have decreased (fig. 11O). This is probably an overestimate of the shift, however, because other strata, such as

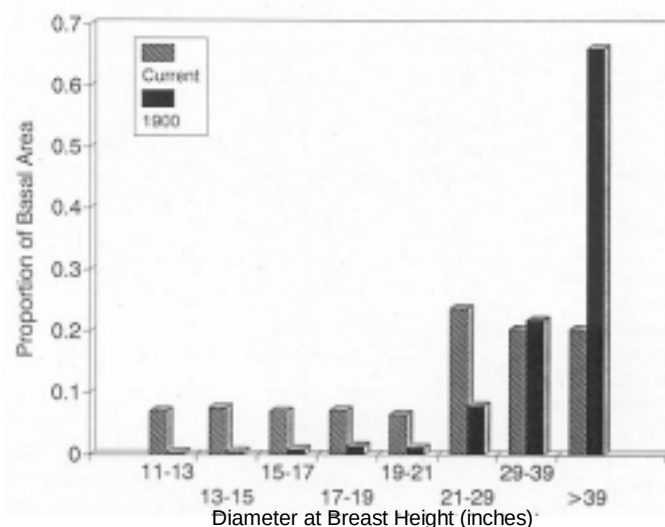


Figure 11L--Basal-area distributions of trees in forests of the Sierra Nevada for 1900 and current stands. The 1900 distribution was based on information presented in figure 11J; the current distribution was based on Forest Service Region 5 inventory data from timber strata for the largest size-classes (4, 5, and 6).

Table 11B—Species composition matrix (stems per quarter acre) for Sierran forests in 1900 (data from Sudworth (1900a)). Timber strata are our professional judgments about which current classes Sudworth's plots fit (E = eastside pine; M = mixed-conifer; P = ponderosa pine; W = white fir; R = red fir; L = lodgepole pine).

Plot	Sugar pine	Ponderosa pine	Western white pine	Lodgepole pine	Jeffrey pine	Incense-cedar	White fir	Red fir	Douglas-fir	Black oak	Mountain hemlock	Total	Timber strata
1					6		15					21	E
2	2	2				11	3					18	M
3		19				4						23	P
4	16					2	5					23	M
5		8				12				7		27	P
6							20	11				31	W
7				14								14	L
8	4					4	8					16	M
9								47				47	R
10	2				1	3	20	4				30	M
11					9							9	E
12			11					41			15	67	R
13					10		8					18	E
14	4				3	5	4					16	M
15	2					2	6		13			23	M
16			4	28				16				48	R
17	3	4				3	15		2			27	M
18	4	19				6				1		30	P
19		4				2			7	2		15	M
20	1	17				9				1		28	P
21		13				5						18	P
22	1					5	3		12			21	M
Total	39	86	15	42	29	73	107	119	34	11	15	570	
Percent	6.8	15.1	2.6	7.4	5.1	12.8	18.8	20.9	6.0	1.9	2.6		
Frequency	0.46	0.36	0.09	0.09	0.23	0.64	0.50	0.23	0.18	0.18	0.05		

Table 11C—Estimates of the proportional volumes of conifers at various times and locations in the Sierra Nevada.

Species	Yellow pine ¹ type, turn of this century	Shasta fir type, turn of this century	Plumas NF, 1913	M4G strata, ² 1980-1990
Sugar pine	20	0	16	12
Yellow pine	38	21	39	15
Incense-cedar	0	0	29	13
Douglas-fir	21	0	14	16
White fir	19	0	24	44
Red fir	12	75	18	0
Western white pine	0	3	0	0
Mountain hemlock	0	2	0	0

¹ Yellow pine and Shasta fir types from Leiberg (1902). These data were for standing "mill timber" cruised using "Michigan practice"—trees >8 inches in d.b.h. and having ≥10 feet of clear lumber in the trunk. Both incense-cedar and lodgepole pine were listed as being present in the stands, but they were not included in the mill estimates of timber volume. "Yellow pine" is either Jeffrey or ponderosa pine.

² Values shown for M4G strata were averaged over all Sierran National Forests. M4G strata were mixed-conifer stands, with trees ≥24 inches in diameter at breast height, and >69 percent canopy closure (see table 1C).

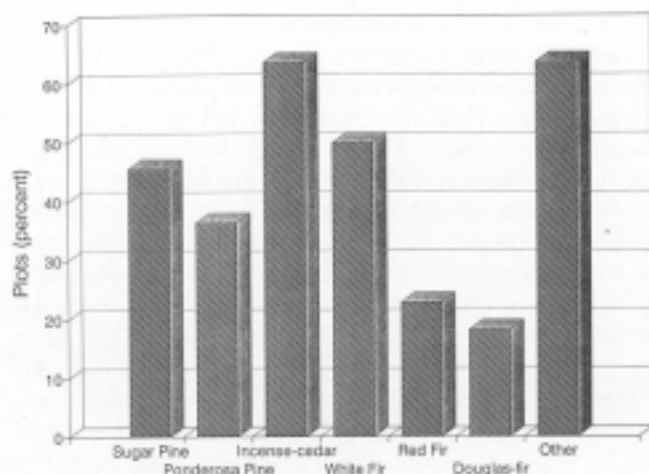
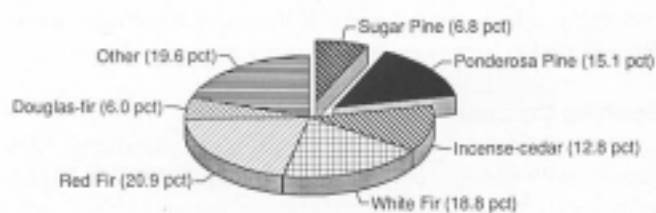


Figure 11M—Proportions of individuals and frequencies of occurrence among plots of tree species, based on plot data from Sudworth (1900a).

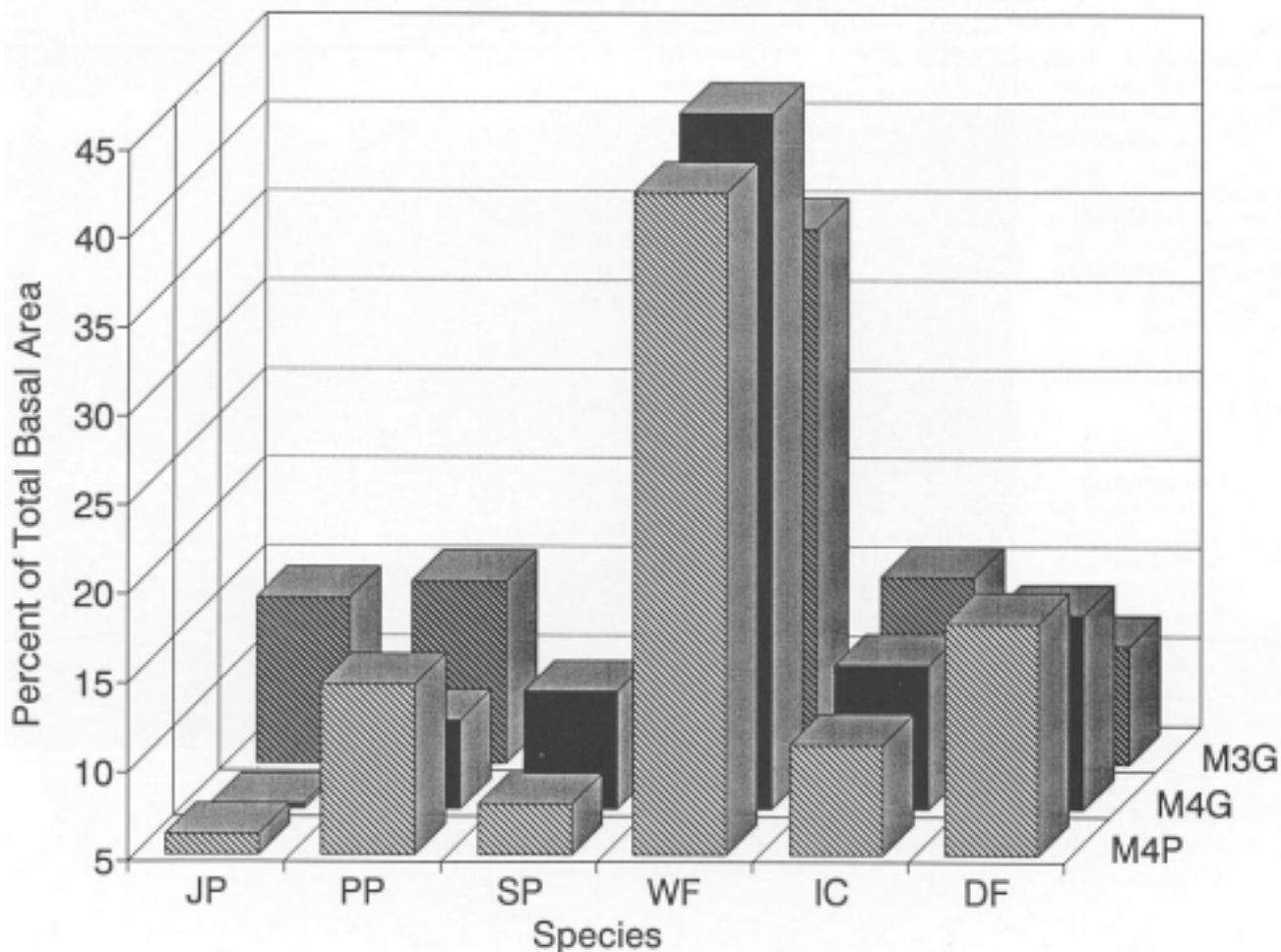


Figure 11N--Species composition (1980-1990) in the most widespread mixed-conifer strata (JP =Jeffrey pine, PP = ponderosa pine, SP = sugar pine, WF = white fir, IC = incense-cedar, and DF = Douglas-fir). For the strata labels, M = mixed-conifer forest, "3" means that the dominant tree diameter-class lies between 12 and 24 inches; "4" indicates that it lies between 24 and 40 inches. "P" indicates poor stocking--canopy closure 0-39 percent; "G" indicates good stocking--canopy closure >69 percent. These data were derived from Forest Service Region 5 inventory data.

the ponderosa pine type, have far fewer firs and a greater percentage of yellow pine. It is reasonable, however, to infer from these data that the proportion of fir (basal area or volume) has increased by perhaps 10-20 percent, while the proportion of yellow and sugar pines has decreased by a similar amount. We are surprised that this trend has not been stronger, given the preference for logging yellow and sugar pine and the expected successional patterns of the forest. The stand structure at the turn of the century was often quite open, and became more scattered subsequent to heavy logging (figs. 11P and 11Q). These open stand conditions may have favored pine regeneration and helped to produce the species composition we see today (figs. 11R and 11S). Compare figures 11P and 11Q with figures 11R and 11S to observe these changes. The trend toward the more shade-tolerant fir will be enhanced by selective removal of other species, by fire suppression, and by maintenance of the very dense stand conditions that exist in many areas of the Sierra Nevada today. The trend will, to a certain extent, be counteracted by infestations of the fir engraver beetle, to which these stands appear to be very susceptible.

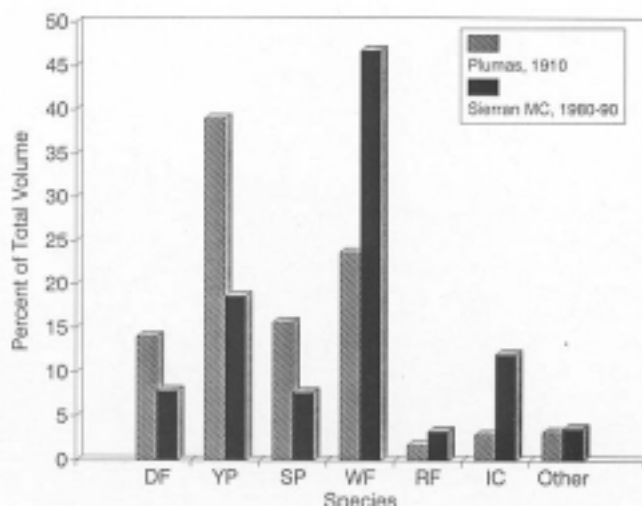


Figure 11O--Volume estimates, by species, in the Plumas National Forest in 1910 (Moore 1913) and from current inventory data. Mixed-conifer (MC) strata M3G, M4P, and M4G were combined for this analysis. See figure 11 N for species codes and a description of the timber strata classifications.

Figure 11P--Left half of two-photo historic panorama. Between 1924 and 1930, this area was owned and intensively logged by the Yosemite Lumber Company, then either sold to or exchanged with the Stanislaus National Forest. Typical of railroad logging days, about 70 percent of the timber was removed and about 30 percent left. An ample number of snags, cull logs, tops, and limbs were left scattered to decay naturally.

Location: ----Looking west from the railroad grade, 1 mile south of Camp 16, into Moss Creek Canyon, Stanislaus National Forest

Elevation:-----6,257 feet

Date: -----1930

Source: -----USDA Forest Service, Regional Photo Archives, San Francisco, CA

Photo-grapher: ---Unknown



Figure 11Q--Right half of two-photo historic panorama. This photo was labeled "old" cutting (1929) on the left background, and "new" cutting (1930) on the right foreground. Note the area left-center (arrows) where soils were intensively impacted by skidding. Today this area still has mostly brush and young black oaks (fig. 11S). Other areas, where some residual conifers were left and skidding had less impact, show a more rapid natural regeneration.

Location: --Looking northwest from the railroad grade over an unnamed tributary to Moss Creek, Stanislaus National Forest

Elevation: --6,257 feet

Date: -----1930

Source:-----USDA Forest Service, Regional Photo Archives, San Francisco, CA

Photo-grapher: -Unknown



Figure 11R-Left half of 1991 comparative photo. Today the area shown in figure 11P shows a dense mixed-conifer forest of white fir, ponderosa pine, incense-cedar, sugar pine, and scattered black oaks. This regeneration is all natural. It has been classified as owl foraging habitat.

Location: ----Same as previous historic photo (fig. 11P), but looking more to the right.

Elevation: ----6,257 feet

Date: -----December 1991

Photo-grapher: ----John S. Senser

Figure 11S-Right half of 1991 comparative photo. Arrows denote the same general areas seen in figure 11Q. Crane Flat Lookout (on the upper right peak) and the railroad grade are hidden by dense second growth. The light vegetation on the background slopes and left foreground is black oak in autumn foliage. Insect kills dominate the patch of gray conifers.

Location: ----Almost the exact perspective as figure 11Q

Elevation: ----6,257 feet

Date: -----December 1991

Photo-grapher: ----John S. Senser



Cutting History in the Sierra Nevada

The rate of volume removal, in general terms, serves as an index of the level of logging disturbance on the land. We developed a cutting history for the Sierra Nevada from 1869-1990 (fig. 11T). This was based largely on county records from 1947-1990 available from the California Department of Forestry and Fire Protection (1947-78) and the California State Board of Equalization (1979-90), and from statewide totals by species prior to 1947 (May 1953). Prior to 1947, therefore, we assumed that all volume generated by species common in the Sierra Nevada was taken only from the Sierra Nevada. That species group included ponderosa and sugar pines, incense-cedar, and white fir. Volume estimates from the early period were probably inaccurate for several reasons. The assumption that the state's entire harvest of sugar and ponderosa pine came from the Sierra Nevada would tend to bias these estimates high. On the other hand, the volume estimates do not accurately account for fuelwood, shake production, and extensive wastage left in the woods (May 1953, Laudenslayer and Darr 1990); all of those factors would tend to bias the volume estimate low. We do not know the extent to which these contrasting biases would tend to offset each other.

By 1913, logging contracts were similar to those used today by the FS. Maximum stump height was 18 inches, and the merchantable top was set at 8-10 inches in diameter. The planned rotation period in the Plumas NF was set at 200 years, and the maximum cut was set at 132 MMBF (Moore 1913). Local use of wood for fuel apparently declined in the early part of the twentieth century. The proposed cut for the Stanislaus NF in 1912 allocated only 164 MBF for "free use" (Graves 1912). Because

of these restrictions, the market volume after 1910 probably reflected the actual cut reasonably well.

Logging in the Sierra Nevada increased until about 1950, with a significant dip during the Great Depression. Logging levels declined slightly after 1950, remained fairly constant until the 1982 recession, then increased again to the point that 1990 levels were near the historic peak. This pattern differs from that in north-coastal California, where the rate of logging increased dramatically after World War 11 and then declined (fig. 11U).

Prescriptions used to cut timber in the Sierra Nevada have also differed from those of the coast. Logging in the Sierra Nevada prior to the 1980s seldom used a clearcutting prescription. If a tree had no market value, it was simply left standing. Even through the 1970s, when a policy shift toward clearcutting occurred, it accounted for most of the volume taken only from 1983 to 1987 (fig. 11V). By the end of the decade, cutting was increasingly concentrated in salvage operations (fig. 11W). Because early cutting, even the relatively heavy cutting done on private lands, seldom involved clearcuts (figs. 11P-11S), disturbance patterns in the Sierra Nevada are very different today from those that have characterized the habitat of the northern spotted owl. In most of the lands occupied by the northern spotted owl, heavy clearcutting in recent years has generated a patchwork of uncut "old growth" and new plantations—a spatially heterogeneous system. In the Sierra Nevada, virtually all stands have been entered and trees have been selectively removed. Both private (Laudenslayer and Darr 1990) and public owners tended to apply similar harvest rules on large blocks of land. Because tree removal has targeted larger stems, and because these large trees appear to have been unevenly distributed on the landscape, forming groves (Fitch 1900b), it is likely that their removal caused a decrease rather than an increase in landscape-level forest heterogeneity.

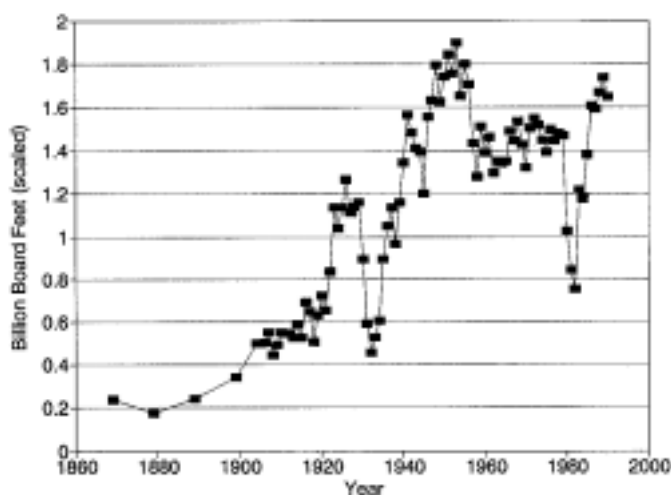


Figure 11T—Market volume of timber from the Sierra Nevada. Volume before 1947 was based on data supplied by May (1953); volumes for 1947-1990 were based on records kept by the California Department of Forestry and Fire Protection (1947-78) and the California State Board of Equalization (1979-90).

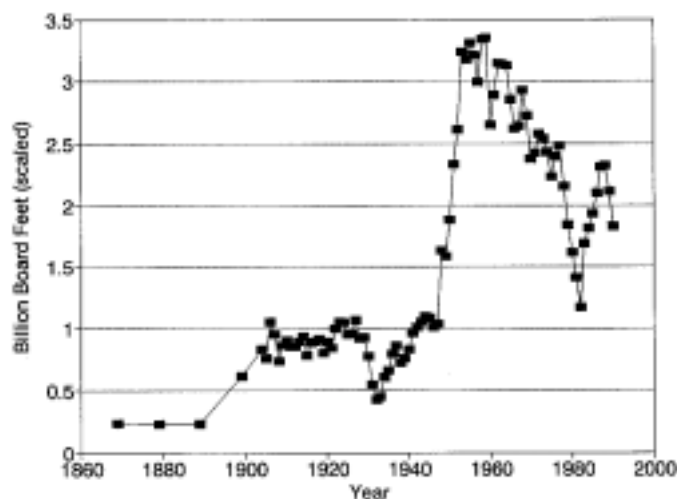


Figure 11U—Market volume of timber from California's North Coast. Volumes were derived from the same sources as those in figure 11T. Volume before 1947 was based on state-wide totals, assuming that all redwood and Douglas-fir came from coastal forests.

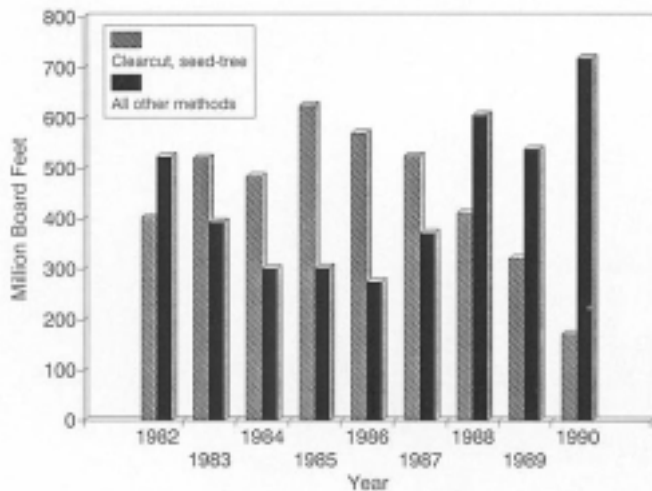


Figure 11V—Logging patterns by prescription for National Forests in the Sierra Nevada, 1982-1990 (from sold-sale records, Forest Service Region 5).

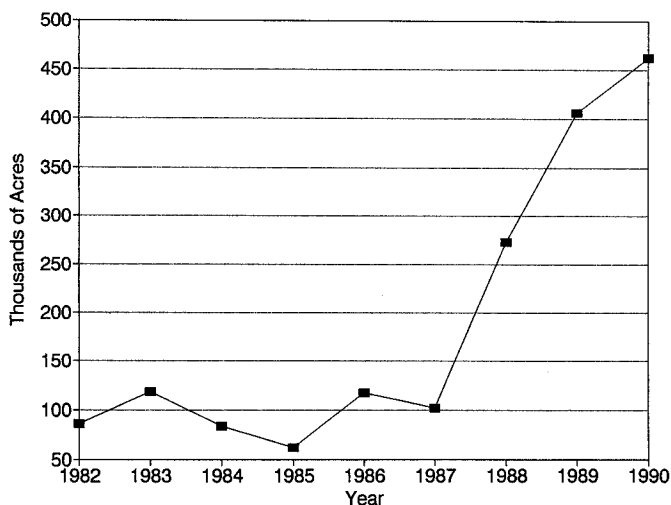


Figure 11W—Acres entered for sanitation-salvage logging on National Forests in the Sierra Nevada, 1982-1990 (from sold-sale records, Forest Service Region 5).

Discussion of Sierran Forest Conditions

Because grazing and burning occurred simultaneously and in the same areas, we cannot separate their effects. As Sudworth (1900a) noted, however, destruction of a perennial grass community did not likely result from fire alone. The ability of intense grazing to interfere with regeneration is well known, and was documented by both Sudworth (1900a) and Leiberg (1902). The bare soils prevalent at the turn of the century probably provided an excellent seed bed for abundant tree regeneration, a process discussed by both Sudworth and Leiberg and supported by

Vankat (1970). The pattern of burning by Native Americans probably differed from that of sheep herders, because their goals differed. Both groups sought short-term and long-term alteration of the forest. Native Americans probably used fire to herd game and to improve wild food crops (Vankat 1970, Lewis 1973, Anderson 1991). Sheep herders, on the other hand, sought to improve grazing and to remove obstacles to the passage of sheep.

We do not expect, therefore, that the forest described at the turn of the century was in any sense pristine. Although most current FS lands were uncut then, the forest floor and regeneration structure were impacted repeatedly by intense grazing. Moreover, even if that forest were relatively untouched, it would not necessarily have looked like a pristine forest that would exist today. Many of the trees in older forests in 1900 were established in the 1600s or before, and grew during a period characterized by extended droughts. The periods from 1750 to 1820 and from 1860 to 1880 were very dry in California (fig. 11X) (Fritts and Gordon 1980, Fritts 1991). The forest that Sudworth (1900a) described was largely established before those droughts began.

Drought, combined with grazing and fire, created a forest dominated by very large, old trees and with very little ground cover. We believe the forests described at the turn of this century were less heterogeneous than the forests influenced by aboriginal and lightning fires. The latter were probably typified by heavily stocked areas on more mesic sites, more trees in intermediate size-classes, and more large-diameter logs and other woody materials on the ground (sheep herders specifically targeted large woody debris for burning).

Cutting in the Sierra Nevada increased steadily over time, reaching a peak after World War II. Since then, with the exception of the 1982 recession, cutting has remained at fairly constant levels. The pattern of partial cutting that typically removed only the largest and oldest trees from a stand, coupled with abundant regeneration that followed removal of sheep from the forests and the initiation of fire suppression, resulted in a shift in diameter distribution of trees between the forests of 1900 and 1990. Available evidence suggests that species composition, measured as basal area or volume, has not yet been substantially altered by these practices, but observation suggests that much of the current regeneration consists of true fir and incense-cedar.

The mixed-conifer zone of the Sierra Nevada, therefore, has few or no stands remaining that can be described as natural or pristine. To various degrees, the forest system has been changed from one dominated by large, old, widely spaced trees to one characterized by dense, fairly even-aged stands in which most of the larger trees are 80-100 years old. This forest appears to be unstable. It is highly susceptible to drought-induced mortality, as competition for water weakens trees on drier sites. It is impacted by massive bark beetle infestations. And it is very flammable (Chapter 12). Its trajectory into the future is largely unknown, but stand structure can be expected to change markedly over the next 100 years.

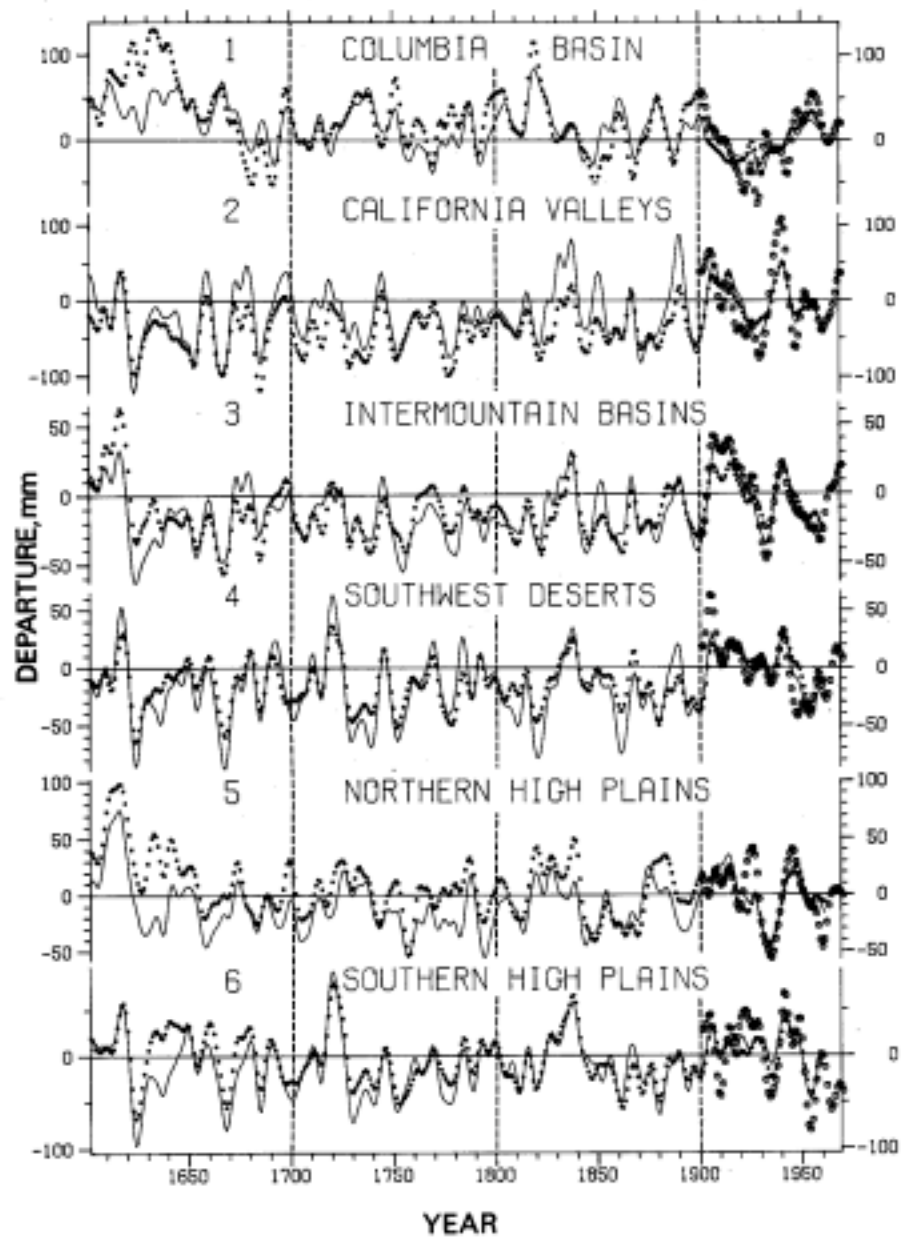


Figure 11X—Patterns of precipitation in the western United States from 1600 to 1970 (Fritts 1991, figure 7.4), based on tree-ring analyses. The solid line is based on data from the western United States, the small dots are based on data from a larger grid covering the entire United States, and the large dots in the twentieth century are based on measured precipitation data.

Southern California Forests at the Turn of the Century

The Forest Reserve system in southern California consisted in 1897 of the San Bernardino, San Gabriel, San Jacinto, and Trabuco Canyon reserves. Today, the San Bernardino NF includes parts of the San Bernardino, San Jacinto, and San Gabriel (eastern edge) reserves. The Angeles NF contains most of the San Gabriel Reserve, and the Trabuco Canyon Reserve, which covered a portion of the Santa Ana Mountains, has been largely incorporated into the Cleveland NF. Leiberg (1899x, 1899b, 1899c) surveyed the first three reserves in 1897, and Bamard (1900) resurveyed the 30-minute San Jacinto Quadrangle in 1900 and provided a map similar to those created by Sudworth and Leiberg for the Sierra Nevada.

Surveys included acreage outside of current FS boundaries. The San Bernardino and San Jacinto reserves, for instance, included many areas that are now privately owned, managed by the Bureau of Land Management, or incorporated into Indian Reservations. For this reason, total acreages are larger and the proportions of reserves listed in a nonforested condition are greater than would be indicated by current inventories. Most of the timbered acreage has, however, been retained by the FS, so statistics associated with forested lands at the turn of the century can be compared with those derived from modern inventories (table 11D). Given the differences in classification methods, the forested acreage statistics are remarkably similar.

Table 11D-*Acres of forested lands in southern California, as estimated in 1899 and in 1987 and 1988.*

Reserve	Year of estimate	
	1899 ¹	1987 and 1988 ²
San Gabriel		
Forested	100,000	145,438
Productive ³	25,000	26,687
Total acres	650,000	651,874
San Bernardino and San Jacinto		
Forested	441,000	389,892
Productive ³	122,500	160,631
Total acres	1,474,000	649,900

¹ San Bernardino Reserve (Leiberg 1899a); San Jacinto Reserve (Leiberg 1899b); San Gabriel Reserve (Leiberg 1899c). Leiberg did not know the exact boundaries of the reserves.

² Data from the Angeles National Forest correspond to the San Gabriel Reserve (USDA Forest Service 1987); data from the San Bernardino National Forest correspond to the San Bernardino and San Jacinto Reserves (USDA Forest Service 1988).

³ Productive lands were defined as Class 1 lands (both accessible and capable of producing timber) by Leiberg, and lands capable of producing >20 cubic feet/acre/year for estimates by the USDA Forest Service (1987).

Species Composition in 1897

Leiberg (1899a, p. 356) estimated species composition in the three reserves that he surveyed (figs. 11Y, 11Z, and 11AA). The methods used to obtain these data were not stated in detail, but Leiberg wrote: "These estimates were based on the customary method of scaling standing timber," suggesting that his estimates were based, at least in part, on measured plot data. The survey effort in 1897, however, appears to have been less intense than in 1900 or 1902. Because less time was spent in the area, the extent to which vegetation patterns were derived from inference, instead of direct observation, would increase. Therefore, tree species that are heterogeneously distributed-especially minor species-easily could be either over- or under-represented.

The general pattern in 1900 was one of low-elevation forests dominated by either ponderosa pine or bigcone Douglas-fir, with white fir entering as a major stand component above 6,000 feet. Lodgepole pine was present in quantities only above 8,500 feet.

Nonaboriginal Human Disturbance by 1900

Logging occurred in the San Bernardino Mountains as early as 1865 (Leiberg 1899b), but was limited in extent. By 1897, logging was still limited to an area north of San Bernardino; it did not extend appreciably into the eastern or northern portions of the San Bernardino Reserve. Logged areas mapped in the San Jacinto Reserve were very small, lying primarily in the upper basin of the North Fork of the San Jacinto River and in an area adjacent to the town of Idyllwild, in the Strawberry Creek drainage. The total area logged in the San Jacinto covered "not more than 1 square mile" (Barnard 1900, p. 575). No extensive timber cutting had occurred in the San Gabriel Reserve by the end of last century (Leiberg 1899c).

Little evidence exists of extensive grazing in the forests of southern California at the turn of the century. Leiberg (1899b, p. 360) estimated that no more than "a few hundred head of stock" were regularly pastured in the San Bernardino Reserve, although several thousand head were grazed there in 1897 because of a drought. Leiberg did not state exactly what a "head of stock" was but, judging from his comments on the San Jacinto Reserve, he probably meant cattle. In the San Jacinto, he stated that "An unknown number of cattle and horses-probably 1,500-2,000 head-graze in the reserve" (Leiberg 1899a, p. 354). Grazing was not discussed for the San Gabriel Reserve. There is, however, evidence of extensive grazing by sheep in the San Bernardino and San Jacinto Mountains in the late 1800s. Minnich (1988) reported that sheep grazing occurred over much of the San Bernardino Mountains during the period from 1860 to 1898, to such an extent that many areas were grazed to a bare-earth condition. In particular, as many as 30,000 sheep were grazed in the area around Little Bear Valley and an additional 30,000 were grazed in the Santa Ana River drainage (Minnich 1988, p. 39-40). As with reports of grazing in the Sierra Nevada, the extent of destruction that resulted from sheep grazing may have been exaggerated because of the biases of early observers.

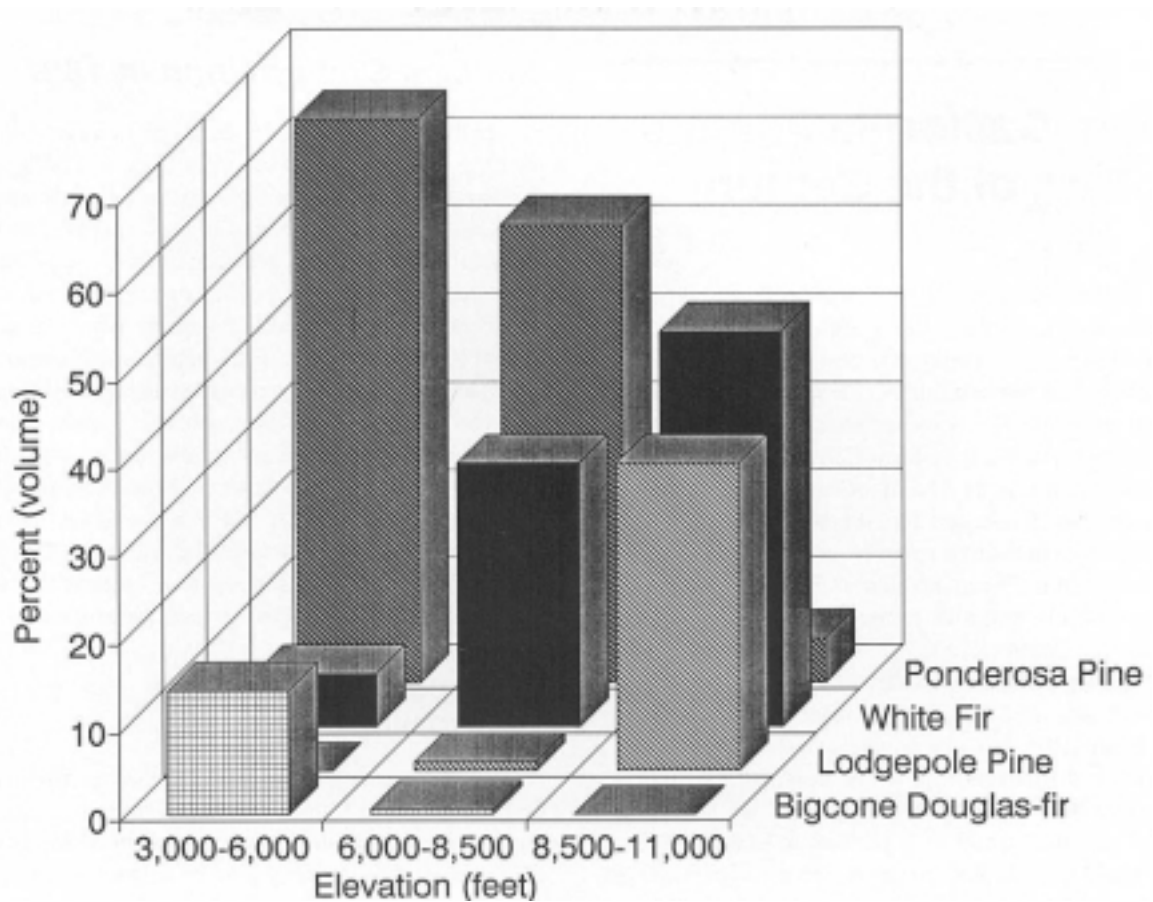


Figure 11Y--Species composition in the San Bernardino Forest Reserve in 1897 (Leiberg 1899b). Hardwood species, with the exception of oaks, were not used when Leiberg calculated percent contribution, by species.

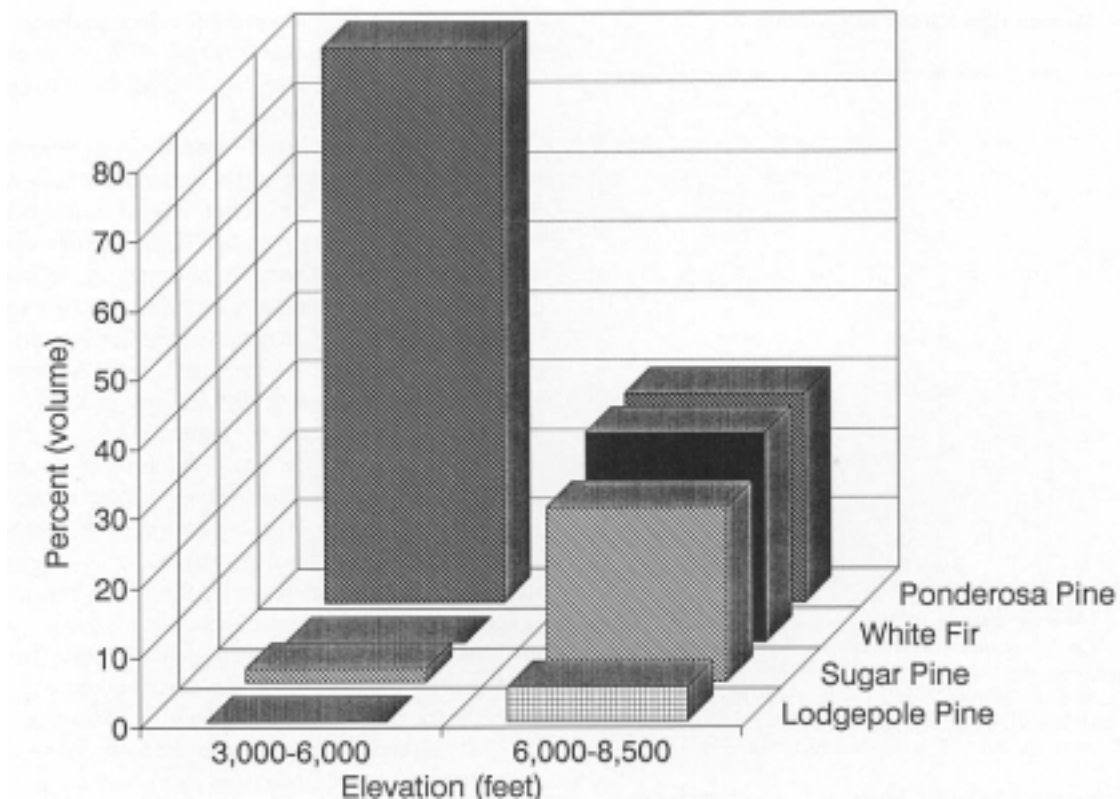


Figure 11Z--Species composition in the San Jacinto Forest Reserve in 1897 (Leiberg 1899a). Hardwood species, with the exception of oaks, were not used when Leiberg calculated percent contribution, by species.

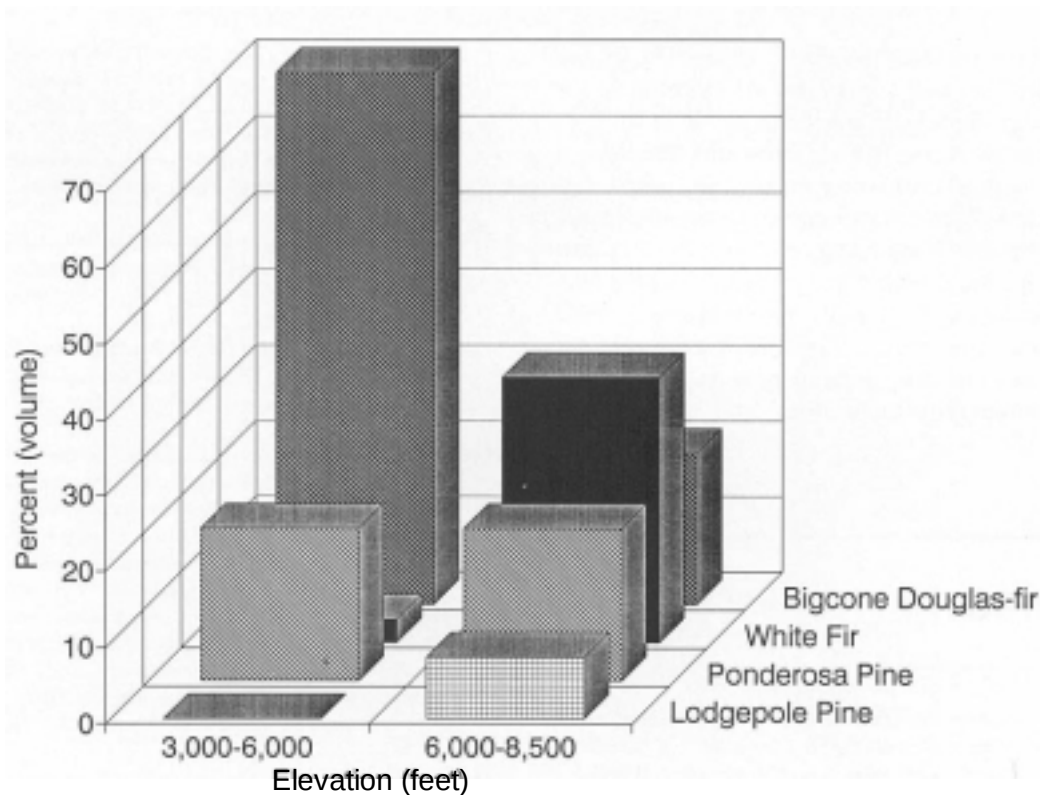


Figure 11AA--Species composition in the San Gabriel Forest Reserve in 1897 (Leiberg 1899c). Hardwood species, with the exception of oaks, were not used when Leiberg calculated percent contribution, by species.

The San Gabriel Mountains are extremely steep, so they were not logged or grazed extensively. They were (and still are) very susceptible to burning, however. In particular Leiberg (1897c, p. 369) noted the destruction of bigcone Douglas-fir stands by fire:

Among the non-commercial species of trees the bigcone fir has suffered the most. Large tracts once covered by it have been totally laid waste and much of what remains is partially burned or scarred... It is not improbable that a considerable

portion of the areas now grown up in brush were in the past covered with a forest of bigcone fir. The very numerous small groves and individual trees of the species rising from the sea of chaparral would lead one to infer that they represent remnants of a more extensive forest. It is also noteworthy that the worst-burnt areas in the three reserves examined are to be found in the San Gabriel Reserve in the region of the most extensive mining operations.

Cutting History in Southern California

We have reconstructed the history of the removal of timber volume from San Bernardino and Los Angeles counties. Volume removed from 1947 to 1990 was based on data from the California Department of Forestry and Fire Protection (1947-78) and the California State Board of Equalization (1979-90). The San Bernardino NF had a very active timber program after World War II, cutting 27.4 MMBF in 1963 alone (fig. 11AB). Altogether, 362.3 MMBF of timber have been removed from these counties since 1947.

Discussion

Changes induced by nonaboriginal man in the southern California forests appear to have been slight by the turn of the century. Some logging and grazing had occurred by then. Leiberg described fires as being widespread but, with the exception of bigcone Douglas-fir stands in the San Gabriel Mountains, he apparently did not believe that forest structure or the balance

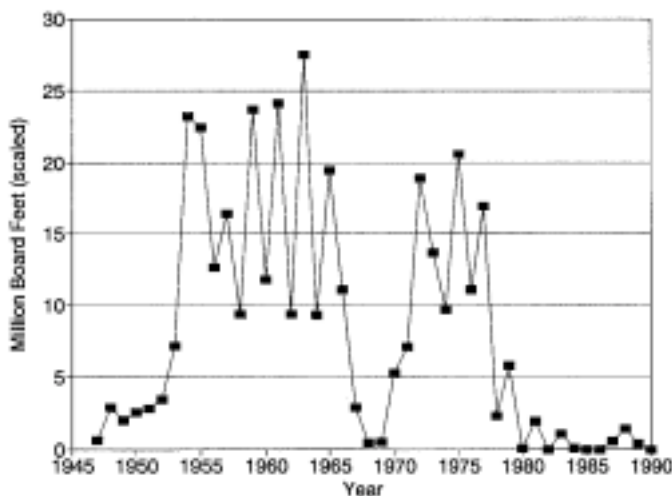


Figure 11AB--Logging intensity in San Bernardino and Los Angeles Counties, 1947-1990 (California Department of Forestry and Fire Protection 1947-78, California State Board of Equalization 1979-90).

between brush and conifer forests was being changed by the fire patterns. Leiberg had no way to ascertain the extent to which burning patterns at that time were unnatural.

In the period after World War II, forest structures would have been significantly altered where timber was logged. Because logging would have been concentrated on sites with higher productivity, it undoubtedly impacted spotted owl habitat, though we cannot determine the extent of that impact. In general, the proportion of the area supporting conifer forests appears to have been reasonably static over the last 90 years. No evidence supports the idea of either spreading or shrinking acreage of chaparral in southern California over that period.

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Fire and Fuels Management in Relation to Owl Habitat in Forests of the Sierra Nevada and Southern California

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Over the millennia, fire has influenced the structure and function of most forested ecosystems and, consequently, most spotted owl habitat in California. Fire is a force that we must understand and attempt to deal with--as a shaper of ecosystems, as a tool, and as a potential destroyer of habitat-if we are to manage intelligently for the California spotted owl. In this chapter we discuss some fire management considerations related to protecting and possibly enhancing owl habitat. We concentrate on Sierran mixed-conifer forests--the most important and extensive habitat type statewide for the spotted owl, and on live oak/bigcone Douglas-fir forests--one of the most important habitat types in southern California (table 1B). We include brief discussions of three additional types-Sierran red fir and southern California mixed-conifer and riparian/hardwood.

Sierran Mixed-Conifer

Sierran mixed-conifer forests contain an estimated 62 percent of all California spotted owl sites in California (table 1B). They are characterized by mixtures of white fir, ponderosa pine, sugar pine, incense-cedar, black oak, Douglas-fir, and giant sequoia. The forest type occurs throughout middle elevations of the Sierra Nevada (Tappeiner 1980; table 1B).

An appreciation of the concept of fire regimes is helpful in understanding the role of fire in mixed-conifer forests. A fire regime is an expression of the frequency, severity, and extent of fires occurring in an area (Agee 1990). It is a function of the frequency with which fuels are dry and continuous enough to carry fire at a time when ignition sources are available, and thus is strongly related to climate. In general, the longer the fire-free interval, the more severe the fire that follows, because more fuels have accumulated in the interim.

Prior to European settlement in the mid-1800s, Sierran mixed-conifer forests were characterized by a short-interval, low- to moderate-severity fire regime. As a result of human activities since the mid-1800s (Chapter 11), including a policy of fire suppression initiated soon after the beginning of the twentieth century, this fire regime has been changed to one of less frequent but substantially more severe fires.

Presettlement Fire Regimes

Several studies have shown that mixed-conifer forests burned rather frequently during the centuries preceding European settlement. Lightning and, in many areas, Native Americans provided the ignition sources. The most comprehensive body of work on fire history in the Sierra Nevada has been done in the giant sequoia groves (Swetnam et al. 1991, Swetnam pers. comm.). These studies documented fire occurrence for 1,500 years and indicated a mean fire interval of 5 to 10 years since 1300 AD for the five groves studied. Maximum fire intervals recorded were 20 years. Other studies (Kotok 1933, Wagener 1961, Kilgore and Taylor 1979, Warner 1980, Skinner 1991) suggested that the mixed-conifer type had a mean fire interval in the range of 5 to 30 years. Mean fire intervals varied in response to site and environmental factors that affected ignition source, fuel accumulation, fuel moisture, and burning conditions. Thus, more mesic sites (for example, moist canyon bottoms, northerly slopes, and higher elevations) and sites protected from winds burned less often than relatively xeric and/or exposed sites (Kilgore and Taylor 1979, Teensma 1987). (The relatively mesic sites may tend to be more closely associated with nesting and roosting habitat used by the spotted owl.) Furthermore, climatic fluctuations on a time scale of centuries (fig. 11X) were reflected in more frequent fires during drier periods (Swetnam et al. 1991).

Frequent fires in the mixed-conifer type maintained surface fuels at fairly low levels, and kept understories relatively free of trees and other vegetation that could form fuel ladders to carry surface fires into the main canopy. This effect of frequent fires, together with widespread, heavy grazing by sheep after the mid-1800s (Chapter 11), probably accounts for the common reports by early observers that forests of the Sierra Nevada were open and parklike (Sudworth 1900, Biswell 1989). Because fuel accumulation was limited, most fires were of low to moderate severity (Sudworth 1900, Kilgore 1973, Biswell 1989). High-severity crown fires usually could not be sustained over large areas (Show and Kotok 1924, Kilgore 1973, Kilgore and Taylor 1979). On the other hand, crown fires that affected small areas (ranging in size from a single tree, to groups of trees, to perhaps several acres) probably were relatively common and an important influence on stand structure. These patches of high fire severity, interspersed within a "matrix" of low-severity fires (Stephenson et al. 1991), occurred in areas with heavy fuel accumulations, sometimes reinforced by steep slopes or extreme weather conditions. This complex fire regime, along with other agents of disturbance (for example, group kills of trees by bark beetles), produced a variable, irregular patchwork of even-aged

groups, most from less than an acre to several acres in size (Show and Kotok 1924; Rundel et al. 1977; Bonnicksen and Stone 1981, 1982; Biswell 1989). Consequently, a relatively fine-grained pattern of variability, modified by topography, existed at a landscape scale.

Openings created by fires and other disturbances provided conditions favorable for regeneration and growth of shade-intolerant and relatively fire-resistant trees and other plants. These species include ponderosa pine, giant sequoia, and California black oak, which is only moderately resistant to top-kill by fire but sprouts vigorously. They were able to regenerate successfully in the presence of frequent fires because of the fuel dynamics of openings in which they became established: A typical scenario may have begun with the death of a small group of trees by bark beetles, locally-intense fire, or other causes. The resulting concentration of fuel was reduced by one or more fires. Mineral soil was exposed, and competing vegetation (including reserves of dormant seeds stored in duff and soil) was reduced. Given a good cone crop and favorable soil moisture and other conditions, seedlings became established. Subsequent fires in the vicinity burned only lightly, if at all, through the opening because of the local lack of an overstory to provide sufficient litter to carry the fire. By the time the new regeneration produced enough litter to carry a fire of appreciable intensity through the opening, some of the young trees were large enough to survive the fire (Kilgore 1973, Biswell 1989). Fire-resistant species would have comprised a disproportionate number of the survivors.

The more shade-tolerant and fire-sensitive species (white fir and incense-cedar) regenerated beneath overstory trees as well as in openings. Periodic fires, however, kept their numbers relatively low, especially in the understory. The more mesic sites generally experienced longer fire intervals and thus permitted more individuals of fire-sensitive species to survive and grow (Kilgore and Taylor 1979).

Twentieth Century Fire Regimes

Twentieth century fire regimes bear little resemblance to those of presettlement times, largely because of human activities since the mid-1800s. One marked difference has been in the annual acreage burned. For example, using a conservative mean fire interval of 20 years for the 586,000-acre Eldorado National Forest (NF), we would expect a mean of 29,000 acres to burn annually. In fact, 13,944 acres burned during the entire period from 1970 through 1990—an average of only 664 acres per year. On the 1,168,500-acre Plumas NF, 85,000 acres burned in the same 21-year period—an average of 4,048 acres per year, although about 58,000 acres would be expected to burn there each year with a mean fire interval of 20 years.

We must get beyond the number of ignitions and acres burned, however, to evaluate relations of wildfires to spotted owl habitat. A study of lightning fires by vegetation type in Yosemite National Park (NP) showed that over 50 percent of the 2,000 fires ignited between 1930 and 1983 occurred in the mixed-conifer zone (van Wagtenonk 1986). Forest Service

statistics do not categorize fires according to vegetation types. Most NFs, however, do have maps that can provide useful information about the spatial and temporal distribution of fires during the twentieth century. Figures 12A and 12B, for example, show the distribution of all lightning fires and all large fires (100+ acres) on the Lassen NF since 1900. Lightning-caused ignitions were scattered over the entire forest. Fires that escaped initial attack and grew large, however, were not evenly distributed. Large fires were grouped in Sierran foothill areas and on the east side of the crest. Similar patterns occurred farther south in the Sierra Nevada. In the 1920s and 1930s, many fires occurred in Sierran foothills and at lower elevations in the mixed-conifer belt—the same general areas where early timber operations (Chapter 11) and widespread burning for range improvement were concentrated. Fires east of the Sierran crest accounted for much of the balance of the large fires this century. Over 50 percent of the nearly 85,000 acres of forested land burned on the Plumas NF since 1970, for example, have burned east of the crest. Within these two broad zones that dominate forest fire statistics in the Sierra Nevada, owls use significant portions of the lower-elevation forests on the western slopes, at least down through the ponderosa pine/hardwood type to the upper digger pine/blue oak type, but they are rare in the eastside forests. In these two zones, fires more often move rapidly beyond the initiating stage and defy initial attack because of flashy fuels, drier conditions, and exposure to high winds.

By comparison, success of initial attack on wildfires evidently is greater in areas of owl habitat within the Sierran mixed-conifer type. Countryman's (1955) description of fuel conditions within old-growth stands applies in large measure to fuel conditions within many mixed-conifer stands used by the California spotted owl. These stands are less flammable under most conditions, because the dense canopies maintain higher relative humidities within the stands and reduce heating and drying of surface fuels by solar radiation and wind. The reduction of wind velocity within closed stands discussed by Countryman is supported by wind reduction factors identified by Rothermel (1983) for stands with closed canopies. Windspeed at mid-flame height for fires burning in surface fuels is approximately one-tenth of the windspeed 20 feet above the stand canopy.

As fuels accumulate, however, fires that do escape initial attack—usually those burning under severe conditions—are increasingly likely to become large and damaging. Success in excluding fire from large areas that were once regulated by frequent, low- to moderate-severity fires has simply shifted the fire regime to one of long-interval, high-severity, stand-replacing fires (van Wagtenonk 1974, Kilgore 1973, Parsons and DeBenedetti 1979, Agee and Edmonds 1992). Forests where owls are found more often than expected (Chapter 5) satisfy the structural requirements outlined by Rothermel (1991) for the propagation and spread of crown fires—heavy accumulations of dead-and-downed fuels, conifer reproduction and other ladder fuels, and continuous forests of conifer trees. Crown fires occur when these features are combined with dry fuels, low humidities, high temperatures, steep slopes, strong winds, and unstable atmosphere.

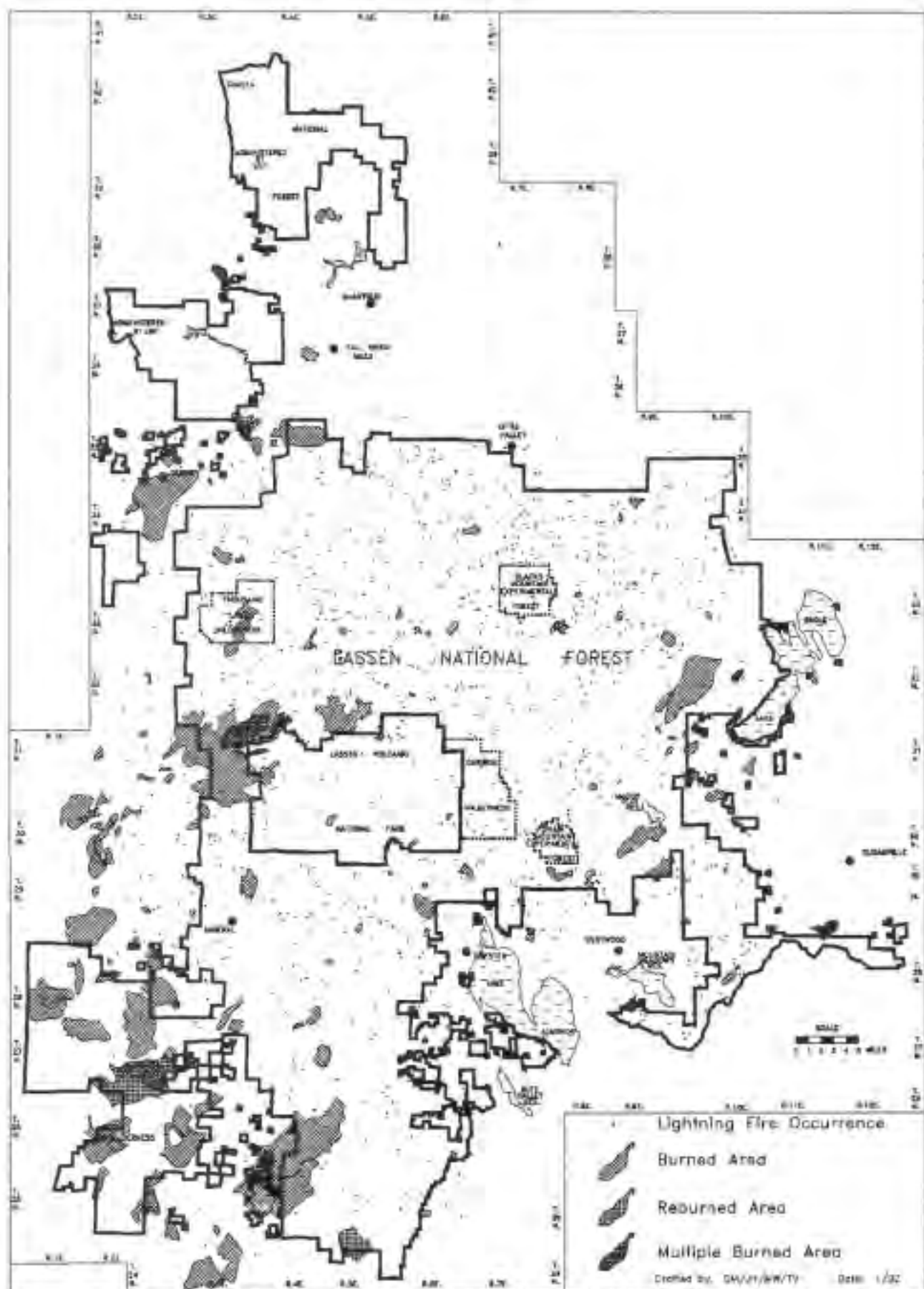


Figure 12A--Fire history of the Lassen National Forest from 1900 through 1939.

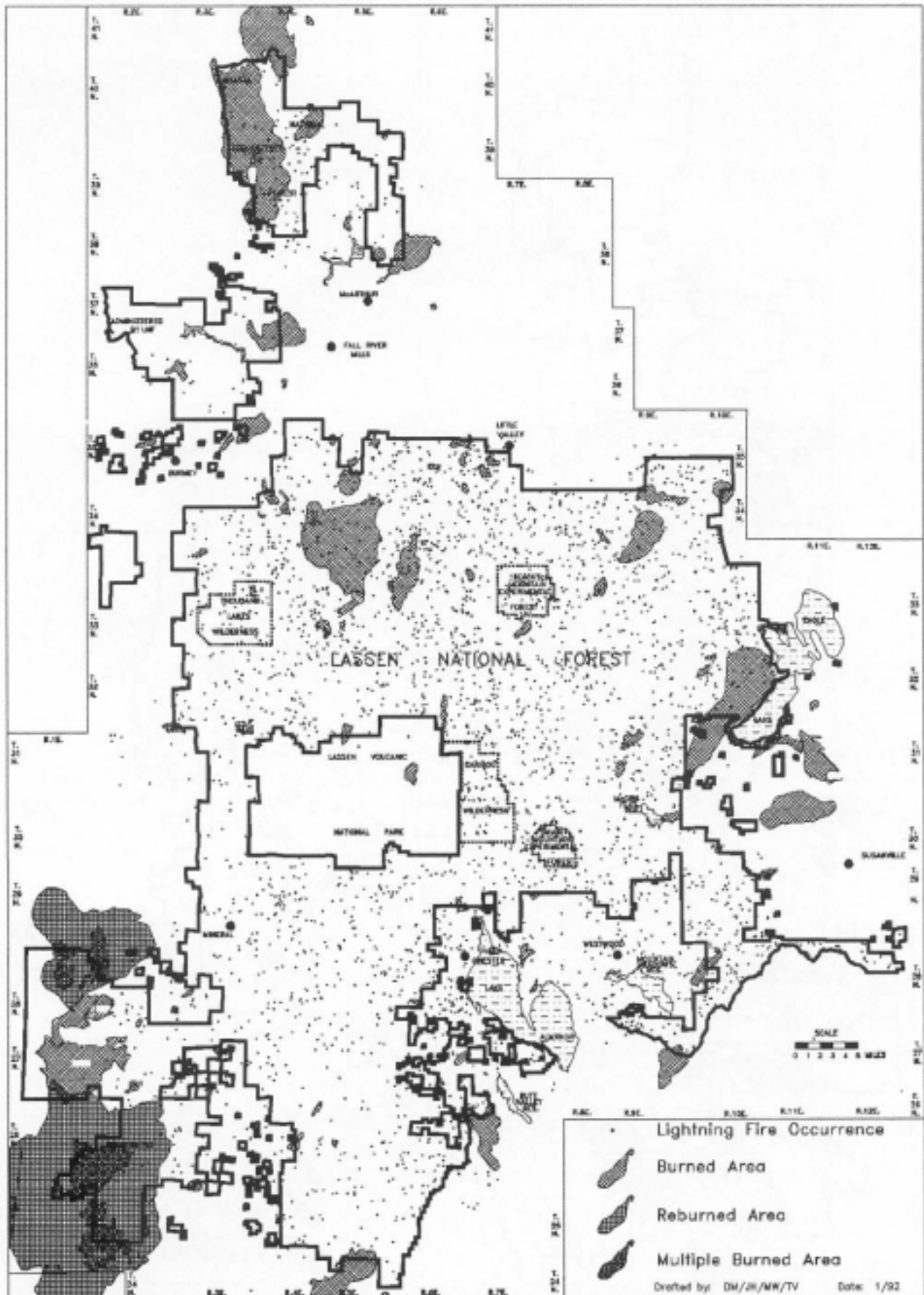


Figure 12B--Fire history of the Lassen National Forest from 1940 through 1990.

Two recent examples of severe, stand-replacing wildfires in owl habitat in the mixed-conifer type were the Stanislaus Complex (1987) on the Stanislaus NF and the Stormy Fire (1990) on the Sequoia NF. Both of these fires burned areas with known owl sites. Numerous other large fires have burned in the general elevational band where owl habitat is found. Although these areas had not been surveyed for owls prior to burning, we assert that they were also home to owls prior to fire. Based on such fires, we suggest three scenarios for severe wildfires in Sierran or southern California mixed-conifer types:

Scenario 1: A fire initiates low on the slope, typically in brushfields, and spreads into the mixed-conifer zone. The fire does not drop to the forest floor because heavy fuel accumulations and fuel ladders, combined with steep slopes, promote either spread through crowns or widespread torching of trees. This is the expected model for areas of mixed-conifer forest lying directly upslope from large brushfields and for imbedded habitat in brushfields in southern California forests. Such fires burn for one to several burning periods (see glossary). Fire behavior is controlled by topography and fuels. Generally the fire is contained within one or several drainages. Control lines are constructed at the break in slope. Regular occurrence of this type of fire results in gradual loss of habitat.

Scenario 2: Many lightning fires are ignited simultaneously and fire-fighting resources are quickly exhausted. All resources are devoted to initial attack or to protection of structures and communities threatened by fires that escape initial attack. Fires become large and burn under changing weather and fuel conditions, until enough resources can be gathered and organized to effect control. In such cases fires burning in uniform fuels become so large that suppression remains unsuccessful until weather conditions moderate, spread ceases, and firelines can be constructed around the entire perimeter. Groups of lightning fires in 1977 and 1987 were examples of this scenario. Weatherspoon and Skinner (1992) found that the effects of such unconstrained fires depended on the fuel conditions they burned through, and corresponded well with prior management actions, including fuel treatments.

Scenario 3: A human-caused fire starts under severe fire weather conditions. Fire spread continues through the duration of the wind event. Examples of synoptic weather patterns associated with such events are detailed by Schroeder et al. (1964). Examples are east winds in the northern Sierra Nevada and Santa Ana conditions in southern California.

A study of lightning fires and spotted owl territories in Yosemite NP showed that owls can and do exist with extensive fires of varying intensities where forest structure has been affected relatively little by human activities. Fifty-six owl sites were confirmed in the Park during surveys in 1988 and 1989 (Gould pers. comm.), and an additional 45 locations were identified as probable owl sites in unsurveyed areas of the Park where the habitat appears to be suitable for the owls (Steger pers. comm.). Among the 56 confirmed sites, six had been burned by prescribed natural fires during the 8 years prior to the surveys when owls were located there (fig. 12C). Over 800 acres of habitat within a 1,200-foot radius of confirmed owl sites had been burned, and an additional 1,300

acres had been burned within a 2,000-foot radius. Crown fires were extensive in one case, although the nest site itself was under-burned. The remaining fires were primarily low to moderate in intensity, with only occasional torched areas.

Effects of Fire Suppression

The structure and composition of Sierran mixed-conifer forests have been affected profoundly by fire suppression policies begun in the early 1900s. This and other forest types with short-interval fire regimes have been changed more by suppression than types with longer fire intervals because more cycles of fire and associated fire effects have been excluded in the short-interval regimes.

As frequent fires of low to moderate severity ceased to be a dominant ecological force, shade-tolerant and fire-sensitive tree species (especially white fir) increased dramatically in abundance, particularly in small to medium size classes. Previously much less common except in the cool and moist extremes of the type, multiple-canopied stands consisting largely of these shade-tolerant species are now common (Parsons and DeBenedetti 1979, Bonnicksen and Stone 1982, van Wagtenonk 1985). Regeneration of pines, black oak, and other shade-intolerant species has declined, except in areas opened by wildfires or management activities. "Selective" cutting has reinforced the changes in stand structure and composition brought about by fire exclusion (color photo 5-10). The patchwork of small, even-aged aggregations that characterized the mixed-conifer type before 1900 has become less distinct (Bonnicksen and Stone 1982). Consequently, stands have become more complex when viewed vertically, but less complex and more homogeneous in terms of areal arrangement.

With fire suppression, fuels on the forest floor (including coarse woody debris) have accumulated far beyond their normal levels (Parsons and DeBenedetti 1979). The increased prevalence of white fir in the understory has created hazardous fuel ladders, linking surface fuels to upper canopy layers (color photos 5-5, 5-10, 5-12 to 5-14). Increases not only in quantity, but also in horizontal and vertical continuity, of fuels have substantially increased the probability of large-scale, catastrophic fires (Kilgore and Sando 1975, van Wagtenonk 1985).

Unnaturally dense stands mean more competition for available water, and therefore greater moisture stress. During periods of drought, notably the current one (fig. 4H), extensive mortality is the result—some directly from drought stress, much from stress-induced bark beetle outbreaks. These stands may be more prone to damage from defoliating insects and various root and stem diseases as well. The dead and dying trees also add greatly to the already high fuel loads, thereby increasing intensity and rate of spread in the event of a wildfire. More snags and large woody fuels are likely to increase fire spotting and suppression difficulty, and greater heating damage to soils may result from consumption of more large materials. Moreover, opening of the canopy as a result of tree mortality permits more solar radiation and wind to reach the ground, resulting in warmer and drier fuels (Countryman 1955), which ignite more easily and support more intense, faster-spreading fires.

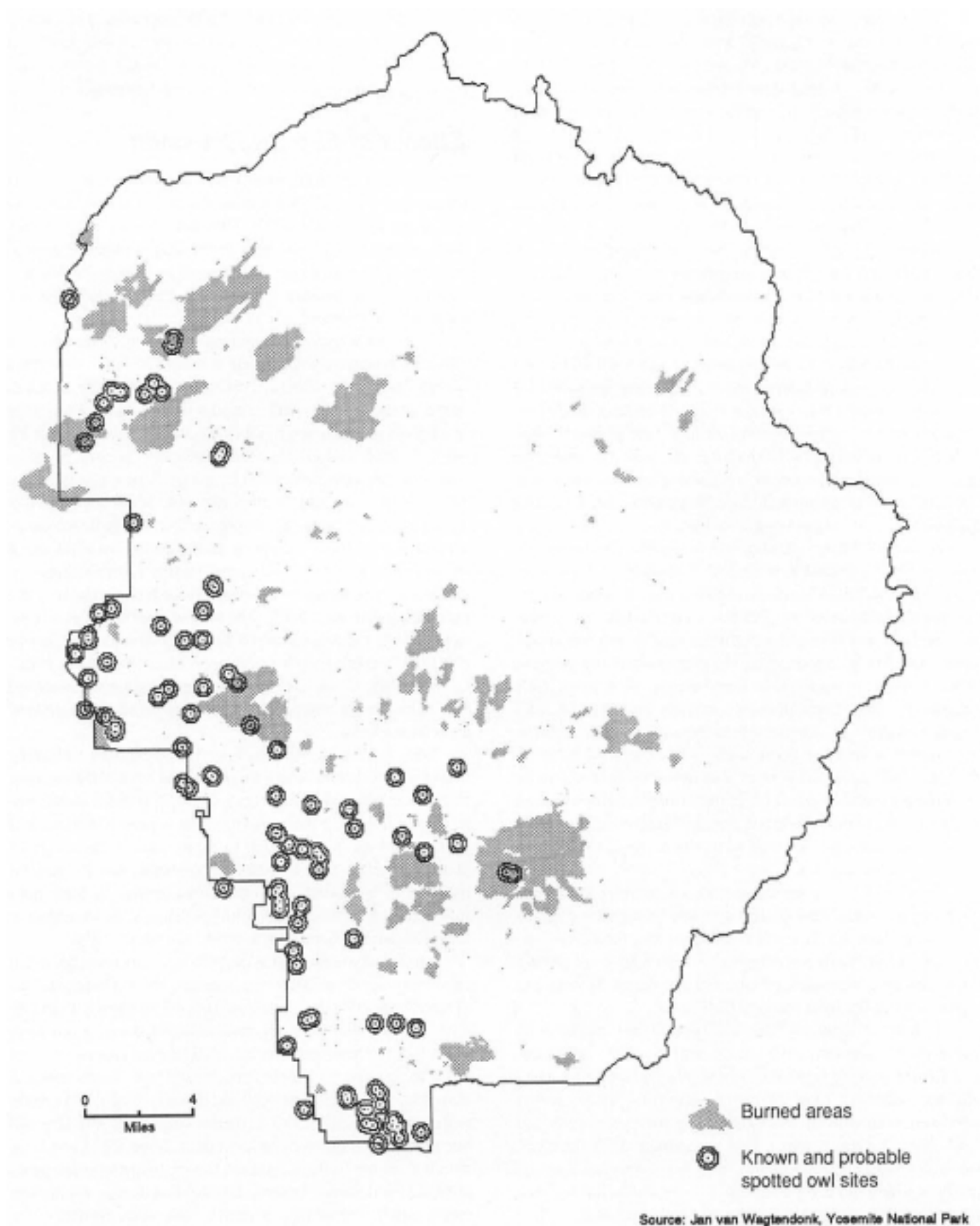


Figure 12C--Known and probable spotted owl sites and lightning fires in Yosemite National Park from 1930 through 1989 (based on data from Gould pers. comm., Steger pers. comm., and J. W. van Wagtendonk pers. observ.).

Implications for Spotted Owl Management

Several changes at least partly attributable to fire suppression (for example, increased stand density, greater development of middle and lower canopy layers, more snags, more coarse woody debris) have been associated with biologists' perceptions of suitable owl habitat. Other such changes may be detrimental to habitat quality. Excessively dense understories may impede foraging and, to the extent that diversity of tree species-to include pines and oaks-is important, continued exclusion of fire may be degrading habitat quality. Much uncertainty still clouds our understanding of which stand attributes are critical for owls and which are only incidental. Nevertheless, it is possible that fire exclusion in Sierran mixed-conifer forests has led to a net improvement in spotted owl habitat there.

If owl habitat has improved as a result of fire suppression, such improvement may well be illusory and short-lived. Fire is inevitable in these forests, and the probability of catastrophic fire-certainly one of the greatest threats to owl habitat-increases as surface fuels and ladder fuels continue to accumulate (Kilgore and Sando 1975, van Wagendonk 1985). Overly dense stands are subject to extensive mortality from drought and insects, including loss of the most desirable large, old trees.

Another possibility is that owls were highly successful in presettlement stand structures resulting from the unimpeded functioning of natural processes, including fire. For Sierran mixed-conifer forests, such a landscape probably consisted of a complex array of mostly small, even-aged aggregations and/or stands representing a wide range of age- and size-classes. Compared with current stand structures, stands would have been less dense, and groups of different-sized trees would have been separated more horizontally into even-aged aggregations with less vertical diversity within groups.

In either case, a management policy characterized as "hands-off plus fire exclusion" (allow forest succession to proceed uninterrupted by periodic natural disturbances) would likely lead to degraded and depauperate, rather than healthy and biologically diverse, ecosystems. A more prudent and conservative policy for the spotted owl, as well as for other species and ecosystem components, would be to use our understanding of natural ecosystem processes (including fire) to guide management (see management options later in this chapter and in Chapter 13).

Fuels

Nesting and roosting areas in Sierran mixed-conifer forests exhibit structural characteristics (Chapter 5) that affect fire behavior. These stands have large trees, closed canopies, and multiple layers. Vertical and horizontal structures are continuous, encouraging the movement of fire into tree crowns. Such movement is discouraged if lower canopy layers are removed, interrupting the upward spread of fire.

The limited quantitative data on surface fuels at spotted owl sites (see tables in Chapter 5) suggest that loadings of large-

diameter (greater than 11 inches) woody fuels are variable, but generally moderately heavy when compared to the range of loadings of natural fuels described by Blonski and Schramel (1981) for mixed-conifer forests in the Sierra Nevada. The guidelines in Chapter 1 for retention of at least 10-15 tons/acre of large downed wood represent the low end of the range of values observed in owl habitat-a loading probably acceptable from a fuels standpoint in most situations. Residues less than 11 inches in diameter probably are less essential to owls. Removal of smaller fuels, especially those less than 3 inches in diameter, results in reduced fire intensities, lower rates of spread, and lower resistance to control.

Fire and Fuels Management Options

Chapter 1 includes general guidelines for fuels management as part of its recommendations for interim management of "Other Forested Public Lands" in the Sierra Nevada. An alternative approach for interim management of "*Selected Timber Strata*" presented in Chapter 13 also includes guidelines for fuels management. In addition, Chapter 13 offers suggestions for fuels management as part of a set of potential long-term strategies to manage for owl habitat in Sierran mixed-conifer forests. Management activities described in Chapters 1 and 13 involve various kinds of cuttings. Because of the additional fuels created by these cuttings, and the warmer and drier microclimate at the forest floor resulting from stand openings, adequate treatment of slash fuels is essential. Otherwise, wildfire hazard is likely to be greater than before the activity (Countryman 1955, Weatherspoon and Skinner 1992). Several options are normally available to treat fuels, and revenues from harvested timber often will fund part or all of the planned fuels management.

In this section, we discuss a general approach for using prescribed burning to manage fuels (in addition to any other benefits that might accrue) in areas of nesting and roosting habitat where commercial harvesting of timber or other wood products will not be done. Such areas might include "*Protected Activity Centers*" (Chapter 1) and any other areas of owl habitat from which logging has been excluded administratively or legally. They might also include "*Selected Timber Strata*" in locations where harvesting is not economical for various reasons, given the constraints outlined in Chapter 1. Effects of prescribed burns should be carefully monitored as part of adaptive management experiments designed to improve our understanding of owl habitat and our ability to manage for it (Chapters 2 and 13).

Considering the significant and increasing risk of stand-destroying wildfire, as discussed earlier, we recommend that prescribed burning in these areas be given a high priority. Without substantial increases in funding for prescribed burning, the likelihood of losing large acreages of owl habitat to severe wildfires will increase over time. Additional prescribed burning would produce more smoke at a time when regulation of air quality is becoming increasingly restrictive. Consequently, the benefits of underburning-for owl habitat, for other ecosystem values, and for reducing smoke from wildfires-and associated

tradeoffs in air quality will need to be clearly defined and articulated. This should be coupled with increased utilization of woody material and greater use of nonburning methods of fuels management in timber harvest areas, to the extent that they make sense ecologically and managerially. The prescribed burning recommended here should be coordinated, on a broad scale, with fuels management activities described in Chapters 1 and 13 to ensure the most effective and efficient use of dollars and other resources for protecting owl habitat. In many areas, succession and fuel accumulation have progressed to the point that prescribed burning is impractical as a first treatment. Outside "*Protected Activity Centers*," such areas may require some combination of understory thinning and mechanical treatment of fuels, or removal prior to burning, to ensure that fire intensities remain within an acceptable range. We suggest the following priorities for prescribed burning within nonharvested areas of owl habitat in the Sierran mixed-conifer type.

First Priority

All hazard-reduction objectives of prescribed burning involve reducing amounts and continuity of fuels. Our recommended first priority is to isolate (that is, disrupt fuel continuity around) known nest and roost sites within "*Protected Activity Centers*," using a band of prescribed burns. We recognize that this strategy poses some small risk to existing birds, but these risks can be at least partially mitigated. To the extent possible, burns should be concentrated, at least initially, on south-facing slopes (aspects from southeast through west) and ridges surrounding or adjoining nest/roost sites. Compared with more northerly slopes, these aspects have drier, more flammable fuels likely to support severe wildfires under a wider range of burning conditions (given effects of fire suppression). On the other hand, southerly slopes offer several advantages for prescribed burning: (1) They dry out earlier in the year, sometimes allowing spring burns to be done with minimal construction of firelines (thus lower cost) at times when fire will not spread onto adjacent northerly slopes. (2) Stands on south-facing slopes tend to be more open, with less dense understory to provide troublesome fuel ladders. (3) They tend to have a higher proportion of ponderosa pine, which not only resists fire damage rather well but also provides litter that can carry fire at the cool, moist end of a prescription-frequently desirable conditions for a first burn.

After many decades of fuel accumulation, initial prescribed burns can result in excessive consumption of duff and coarse woody debris. This is undesirable for at least two reasons: First, duff and coarse woody debris are important substrates for hypogeous fungi-prime food for flying squirrels (Chapters 4 and 10); and second, long-duration heating from extended smoldering of duff can damage tree roots and root crowns, sometimes causing delayed mortality even in large, old trees (Thomas and Agee 1986, Swezy and Agee 1991, Sackett pers. comm.). Conducting initial prescribed burns in the spring, when the moisture content of duff and large fuels is high, will help to minimize the problem of excessive duff consumption. The more flammable surface fuels-litter and small woody debris-can still be largely consumed. An additional advantage of low consumption of duff

and large woody fuels is a reduction of atmospheric emissions. As adaptive management experiments continue over time, efforts should be made to align prescribed burns more closely with natural fire regimes in terms of the frequency and season of burns. In the meantime, however, effects of initial spring prescribed burns should be carefully monitored to assure that species diversity is retained and that birds and other wildlife are not disturbed during the breeding season.

In stands with many small understory trees and low crowns, burning should be initiated carefully, using small test burns at first. Flame lengths and their effect on torching of small trees should be closely monitored, and firing patterns should be adjusted as necessary to keep flame lengths within prescribed limits (Martin and Dell 1978, Kilgore and Curtis 1987, Weatherspoon et al. 1989). An initial prescribed burn will usually create some interruption of vertical fuel ladders (after scorched needles drop to the ground). Many small trees will be killed, however, and often more dead fuels will be created than consumed. Such understory burns, therefore, carry an implied commitment that the stand will be reburned at least once, generally within 10 years or so, to clean up fuels created by the first prescribed burn and to reduce vertical fuel ladders further.

Second Priority

After nest and roost sites have received some protection, a more general program of prescribed burning should be initiated. The objective is to break up fuel continuity on a larger scale and to begin to restore fire as a natural process in the ecosystem. Southerly slopes and ridgetops would be favored for burning, as suggested above. Followup burns would be implemented as needed to effect and maintain a meaningful interruption of fuel continuity and reduction in wildfire hazard. Burns should be well-distributed, creating a mosaic of broad "fuelbreaks" covering one-third or more of the total area. Such a program would be expected to limit substantially the size and severity of subsequent wildfires. Special emphasis should be given to prescribed burning that reinforces natural and constructed barriers to fire, such as rocky outcrops, bare ridges, roads, and constructed fuelbreaks. These provide relatively defensible areas from which firefighters can safely implement fire suppression strategies.

As indicated earlier, the approach discussed in this chapter assumes no commercial harvesting (including biomass harvesting of small trees). Outside "*Protected Activity Centers*" or similarly restrictive areas, however, initial prescribed burns in some stands with dense understories and dangerous fuel ladders may be facilitated by felling many of the small trees before burning. To limit intensity and consumption, and thus damage to the residual stand, the prescribed burn could then be done before the newly felled trees have fully dried.

Third Priority

For long-term protection, prescribed burning should be applied throughout owl habitat in the mixed-conifer zone with a frequency distribution similar to presettlement fire intervals. Northerly aspects and other areas not previously included in the prescribed burning program should be incorporated. Limitations

on such a program and factors to consider include: (1) availability of resources; (2) need for improved information from research and monitoring activities concerning habitat attributes, fire history, and fire effects; (3) need for prescribed fire to maintain and improve owl habitat in the absence of other silvicultural tools; (4) need for fire to provide other ecosystem values; and (5) smoke management and air quality implications of a widespread prescribed burning program (including information about estimated background levels of smoke during presettlement fire regimes, and tradeoffs between increased smoke from prescribed fires versus reduced smoke from wildfires). If the second priority program is carried out successfully-coupled with appropriate fuels management in adjoining harvested areas (Chapters 1 and 13)--occurrence of large, catastrophic wildfires within owl habitat will be of less concern. The focus of prescribed fire for this third stage will then shift generally from hazard reduction to reestablishment of an important ecosystem process. Long-term sustainability of owl habitat on a landscape scale should result.

Red Fir

Fire Regimes

The relatively few studies of natural fire regimes in the red fir type have indicated mean fire intervals ranging between about 40 and 100 years (Kilgore 1981, Pitcher 1987, Taylor and Halpern 1991). Higher-elevation areas tend to have less frequent fires because biomass (fuel) accumulates more slowly and weather conditions that will support a fire occur less often. Despite longer fire intervals than in the mixed-conifer type, fire has been the dominant disturbance factor associated with episodes of regeneration in much of the red fir type. A range of severities and frequencies of fire has led to a complex pattern of various patch sizes and tree ages (Pitcher 1987, Taylor and Halpern 1991). Compared with lower-elevation forest types, fire suppression has had less effect on the red fir type. Suppression activities began later in red fir forests, and fewer fires would have burned there even without suppression. In addition, because red fir forests are largely monospecific and red fir is relatively shade tolerant, the successional trend toward more shade-tolerant species in the absence of fire (a concern in the mixed-conifer type) is not a factor in the red fir type.

Despite many lightning-caused ignitions in the red fir type (Maupin pers. comm.), such fires seldom have gotten large on lands where a suppression strategy is used, because initial attack is almost always successful. The behavior of natural fire has been extensively documented in Yosemite and Sequoia/Kings Canyon NPs, where much of the red fir type is included in the prescribed natural fire zone. To date, no evidence suggests that the prescribed natural fire programs in the NPs have had an

adverse impact on the owls found there. Lightning fires in the red fir type usually burn with relatively low intensity and spread slowly over long periods, with occasional episodes of rapid spread during periods of severe fire weather. Crown fire is unusual in this type except under rare high-wind events, partly because sparse understory vegetation (Rundel et al. 1977) provides limited fuel ladders. Some examples of crown fire, however, were observed during the 1987 fire season. Torching also has been observed when human-caused fires burned into the red fir forest under extreme conditions.

Sixteen percent of the fires recorded in Yosemite NP between 1930 and 1983 occurred in the red fir zone, even though it comprises only 8 percent of the park. The majority of those fires were single trees, although larger fires occurred when red fir was mixed with chaparral (van Wageningen 1986).

Fuels

Color photo 5-1 provides an excellent illustration of typical fuel conditions in red fir. Fuel bed characteristics are quite different from those in the other habitat types. The short needles form a dense litter layer, which is further compacted by a heavy snow pack. This litter burns slowly, with relatively low intensities. Fuel ladders are nearly always interrupted. Dead-and-downed fuel loadings may be heavy in older stands, but fuel moistures remain high during most years in these high-elevation stands.

Fire Management Options

Fire may be allowed to play its natural role in much of the red fir type. Large sections of red fir forest found in wilderness areas should be evaluated for inclusion in wilderness fire-management programs that emphasize the role of fire as a natural process.

Southern California Mixed-Conifer

Fire Regimes

The natural role of fire in the southern California mixed-conifer community is similar to that described for the Sierran mixed-conifer community. Studies of fire history in the Los Padres NF (Talley and Griffin 1980) and the San Bernardino Mountains (McBride and Laven 1976, McBride and Jacobs 1980) suggest slightly longer mean fire intervals in these forests than those found in the Sierra Nevada. This may be explained by the lower incidence of lightning storms there, as well as smaller contiguous areas of mixed-conifer vegetation. In the southern California mixed-conifer type, as in the Sierra Nevada, the early

fire regime was typified by frequent low- to moderate-severity fires, which burned over long periods under a variety of fuel and weather conditions (Minnich 1988).

Fire suppression has been effective in reducing the number of large fires in the mixed-conifer type in the mountains of southern California. An analysis of fire records by McBride and Laven (1976) indicated that fire suppression has been effective in sharply reducing the number of acres burned on the San Bernardino NF, for example, from an annual acreage of 5,890 acres during the 1940s to 3,774 acres during the 1960s.

Talley and Griffin (1980) found evidence that twentieth century fire regimes result in infrequent fires of an intensity causing widespread mortality in pine stands that survived the frequent low- to moderate-severity fires of the past. Coniferous forests, which once burned more frequently than the chaparral stands below them, now burn at a frequency similar to that in the chaparral.

Examination of fire records indicates that most large wild-fires in mixed-conifer forests in southern California fall under Scenarios 1 and 3, described for the Sierran mixed-conifer type.

Fire Management Options

Current practices of protecting all pairs of owls in this type should be continued. The fire management options described for Sierran mixed-conifer forests apply in southern California as well. It is essential, however, that fuels also be managed in the chaparral communities surrounding the conifers, to avoid catastrophic wildfires that spread from below into the mixed-conifer zone.

Live Oak/Bigcone Douglas-Fir Forests

The live oak/bigcone Douglas-fir community provides habitat for an estimated 41 percent of owl sites in southern California (tables 1B and 3I). Within the lower portions of its elevational range, this community occurs near streams in moist, shaded canyons and draws, where aspects are mostly north and east. As elevation increases, it occurs on other aspects and is less restricted to canyons (McDonald and Littrell 1976). Typically, bigcone Douglas-fir comprises a scattered overstory of single trees or small groups of trees, and tree-sized canyon live oaks form a relatively continuous midstory canopy. Shrubs and herbaceous plants are largely absent in the understory except beneath openings and along the margins of stands (McDonald 1990). Stands of live oak/bigcone Douglas-fir usually intergrade with chaparral along their margins.

Fire Regimes and Fire Effects

McDonald and Littrell (1976, p. 319) described "the overall pattern of the bigcone Douglas-fir-canyon live oak community [as] that of a stable, self-perpetuating, somewhat exclusive community, with tendencies toward the climax or even postclimax successional stage." The community evidently is not well-adapted to frequent fires. Bigcone Douglas-fir is unusual among conifers in its ability to sprout from a fire-scorched crown (color photo 5-39), but it is weakened from repeated fires that deplete energy reserves (McDonald 1990). It does not survive "torching" of the crown (consumption of foliage by flames). Seeds contained in cones in torched crowns almost certainly would not survive to provide regeneration. Indeed, natural regeneration of the species is very slow following severe fires (Minnich 1980). Young bigcone Douglas-firs are moderately shade-tolerant, and establishment of natural regeneration is often most successful in the partial shade provided by the canyon live oak canopy (McDonald 1990). Young trees grow slowly in the understory, however, and are easily destroyed by surface fires.

Oaks in general are not noted for their resistance to fire damage. Even among oaks, however, canyon live oak is unusually sensitive to damage and top-kill by fire (Minnich 1980, Plumb 1980). Its thin, dry, flaky bark ignites easily, often carrying fire several feet up a bole and commonly burning completely through the bark to expose the underlying wood. Frequently, heat kills enough cambium to girdle the bole, even with low-intensity surface fires (Plumb 1980). The relatively closed, compact canopy architecture also tends to trap heat from a fire beneath the canopy, thereby increasing crown scorch. On the other hand, canyon live oak sprouts vigorously from the root crown following top-kill by fire, and frequently after sublethal damage as well.

The unusual susceptibility of canyon live oak to top-kill by fire suggests that stands with many large, old trees (seemingly high-quality owl habitat-Chapter 5) probably have not experienced fires of any significance for many decades (Minnich 1988). The species grows more quickly to tree size in more mesic habitats, where fire intervals also are generally longer. Canyon live oaks that escape burning long enough to attain tree stature, in turn, tend to bestow a fire-retardant quality on the stands in which they grow (Minnich 1980). Possible reasons include: (1) chaparral shrubs or other understory plants that might provide a flammable fuel ladder into tree crowns are virtually absent; and (2) litter tends to be meager beneath canyon live oak and it is not particularly flammable, perhaps in part because of dry ravel on steep slopes that promotes mixing of litter and soil. Minnich (1977, p. 447) described fires spreading from chaparral into live oak/bigcone Douglas-fir stands that "usually incinerated the outermost fringe of stands. With further progress into the grove, the pattern of total combustion graded into a hot surface fire which only scorches the oaks as the distance between the tree canopy and ground fuels increases." Where wind and other burning conditions sustain a crown fire through the stand, however, restoration of prefire stand conditions will likely take a long time. Without intervention, canyon live oak sprouts will come up in a sea of seedling chaparral

shrubs. For many decades, the new community will be more likely to reburn than the old one-until the oaks again attain tree stature and shade out the shrubs. Meanwhile, bigcone Douglas-fir probably will be very slow to return, particularly if no surviving seed trees are nearby.

Fire and Fuels Management Options

We do not recommend prescribed burning within live oak/bigcone Douglas-fir stands (see Plumb 1980). From the standpoint of wildfire hazard, these stands are relatively nonflammable, as described earlier. They probably will not support a stand-destroying crown fire except under extreme conditions in which prescribed burning or other surface fuel reduction will have made little difference in fire behavior. Under less extreme conditions, the stand probably will support a moderately intense surface fire, which would top-kill many or most of the live oaks and allow many of the bigcone Douglas-firs to crown sprout. Restoration of suitable owl habitat would take place sooner than after a crown fire. If prescribed burning were done, it would be difficult and expensive in many stands because of the steep, broken terrain. Moreover, given the discontinuous, low-flammability fuels occurring in many stands, moderately severe burning conditions probably would be required to carry fire and reduce fuels significantly, and those conditions might produce levels of damage to canyon live oaks approaching those that prescribed burning was intended to prevent. To the extent that the canopy is opened by top-kill of oaks during prescribed burning, chaparral shrubs probably would invade the stand, making it more likely to burn severely in the future.

If the decision is to use prescribed burning, it should be concentrated on gentler slopes where access is easier, fuels are more continuous, and probable damage from wildfires is greater. Minnich (1980) observed 37 percent survival of bigcone Douglas-fir following wildfires on slopes less than 20 degrees, but more than 90 percent survival on slopes greater than 40 degrees.

A better fuels management strategy to protect live oak/bigcone Douglas-fir stands may be to concentrate prescribed burning in chaparral near these stands. Highest priority should be given to the more flammable chaparral types and to more decadent chaparral with higher dead-to-live fuel ratios, which would support more intense wildfires and thus be more likely to carry a crown fire into adjacent trees. Similarly, higher priority should be given to chaparral near live oak/bigcone Douglas-fir stands with more continuous surface fuels and those on gentle to moderate slopes (as opposed to very steep, broken slopes and canyons). Movement of fire into live oak/bigcone Douglas-fir should be minimal if prescribed burns are planned for relatively moderate burning conditions (which should be suitable for burning decadent chaparral or relatively flammable chaparral species) and in such a way that slope and wind direction favor movement of the fire away from the live oak/bigcone Douglas-fir stand. Prescribed burning of decadent chaparral should improve owl foraging habitat because of increased production of woodrats (more succulent and nutritious foliage in the new growth) and improved access to woodrats (see Chapter 10).

In the event of a severe wildfire in live oak/bigcone Douglas-fir, active measures should be taken to restore owl habitat. Because prospects are poor for natural regeneration of bigcone Douglas-fir, nursery-grown seedlings should be planted as soon as possible. Competing shrubs and other vegetation should be controlled adequately to ensure survival and rapid early growth of the bigcone Douglas-fir seedlings. Some thinning of sprouting clumps of canyon live oaks might speed their return to tree size.

Southern California Riparian/ Hardwood

Accumulations of dead-and-downed woody fuels are generally low in this type. Fire behavior depends on understory composition, which can be variable (color photos 5-29 to 5-32, 5-45 to 5-47). Areas with a grass understory burn rapidly with low to moderate intensities. Effects are generally benign. Stands with a shrub understory show great variability in fire behavior and effects, depending on species composition and abundance of shrubs. These stands should be examined on a case-by-case basis, because they are of great importance, relatively limited in acreage, and vary in their vulnerability to wildfire. Management should focus on maintaining a closed canopy of trees. In some stands, prescribed burning or other fuels treatment may be needed to prevent overstory mortality from wildfire. Fire also may be necessary in some situations to regenerate overstory trees, such as oaks.

Considerations for Fire Suppression in Spotted Owl Habitat

The wildland fire agencies have demonstrated the efficacy of initial attack in excluding wildland fire from some types of spotted owl habitat (Sierran mixed-conifer, red fir, and southern California mixed-conifer). Such suppression efforts are essential to prevent large, severe wildfires, while concurrently making efforts to condition stands to reduce wildfire hazard. Continued success depends on maintaining sufficient initial attack resources to protect the habitat. Wiitala (1991) proposed a way to quantify the risk of experiencing unacceptable fire events in areas that are highly valued, but for which we have no method of assigning a monetary value for input into the loss portion of cost-plus-loss

equations. A similar analysis should be developed for California owl habitat, to justify the initial attack organization needed for its protection.

A consideration in suppression of wildfire in high-value areas is the trade-off between efficient suppression that minimizes the fire size and the damage that can result from aggressive suppression action. The concept of appropriate suppression response has been articulated by Mohr (1989) and Mohr and Moody (1991), emphasizing techniques that effectively and efficiently suppress fires while minimizing direct impacts.

Selecting suppression strategies at initial attack, extended attack, and project fire level also requires weighing the advantages of backing off to the exterior of high-value areas to minimize suppression impacts, against the amount of damage that the fire is expected to cause within the selected perimeter. The fire manager has considerable latitude in selecting a strategy, ranging from aggressive control to confinement. Selection of suppression alternatives should be based on projected or observed fire behavior to predict fire effects. This analysis will be fire-specific because of variation in such factors as fuel loading, fuel moisture, weather, and topography. Interaction among wildlife biologists or resource advisors, fire behavior analysts, and operations personnel is essential to develop a balanced display of the suppression costs and resource damage of alternatives. Successful implementation requires preplanning by fire managers in consultation with biologists.

Fire suppression must be done in a manner that reflects a high regard for public and firefighter safety. The following additional factors should be considered when managing wildfires that start in or threaten spotted owl habitat:

1. The degree of involvement of canopy layers, based on the intensity of surface fire and the amount of torching predicted in each canopy layer.
2. The expected amount of consumption in litter and duff layers.
3. The relative patchiness of the burn, and the percent of various fire intensities projected within the fire perimeter.
4. The expected amount of downed-log volume to be consumed, especially logs greater than 9 inches in diameter. This evaluation should include both rotten and sound logs.
5. Location of the fire relative to known nest sites.
6. Timing of the event relative to the owl's breeding season.
7. The quantity and quality of habitat in the area of the fire. If the fire is burning in an area where suitable owl habitat is rare, greater effort would be taken to minimize habitat destruction by the fire.
8. Expected impact on the owl's prey base.

Conclusions

Fire has been a dominant force in shaping the forested ecosystems that provide habitat for the California spotted owl. The various habitat types used by the owl differ in terms of (1) the influence of historical fire regimes on their structure, composition, and function; (2) the extent to which the habitat types have been altered by human activities since European settlement; and (3) the risk of substantial habitat loss by severe wildfires. In this chapter we have summarized fire management considerations relating to protection and possible enhancement of owl habitat, with emphasis on the Sierran mixed-conifer and the live oak/bigcone Douglas-fir forest types.

The Sierran mixed-conifer type is the State's most important and extensive habitat type for the California spotted owl. Human activities since the mid-1800s—especially sheep grazing, fire suppression, and "selective" cutting—have profoundly affected the structure and composition of these forests. Changes include a marked increase in the density of shade-tolerant understory trees. The vertical fuel ladders thereby created, along with substantial increases in surface fuels, have greatly increased the potential for stand-replacing crown fires. Severe wildfire in Sierran mixed-conifer forests may represent the greatest threat to current owl habitat.

The wildland fire agencies must maintain an effective suppression organization to minimize the damage from such fires. Problems resulting from many decades of over-zealous suppression cannot be resolved overnight by allowing wildfires to run their course in highly hazardous fuel complexes. Concurrently, however, managers must pursue aggressive, environmentally sound fuels management programs to reduce wildfire hazard in and around owl habitat. As described in this chapter, prescribed fire has an important role to play in reducing hazard and enhancing a variety of ecosystem values associated with the natural functioning of fire. In addition, fuels management methods (including but not limited to prescribed fire) should be considered integral components of silvicultural approaches to managing owl habitat, such as those discussed in Chapters 1 and 13.

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Chapter 13

Projected Trends in Owl Habitat

Kevin S. McKelvey and C. Phillip Weatherspoon

Here we attempt to synthesize many of the analyses presented in other chapters in this document, and to look ahead to the future. As such, this chapter is necessarily more speculative and conclusions expressed here should not be viewed as hard and prescriptive. We hope, however, to highlight areas of concern for future owl habitat, and for the health of the forest ecosystem more generally. Finally, we propose alternate forest management methods that we believe have merit. We do not consider the management methods described here to be an exclusive set to be prescribed forestwide. Rather we view them as potential experiments which, if effective, will alleviate many of the shortcomings that we perceive in current management systems as they relate to owl habitat. This report covers a wide range of forest types and topographic regions. We will focus almost exclusively on the Sierran mixed-conifer forest type, as it contains an estimated 82 percent of the spotted owl sites in the Sierra Nevada and 62 percent of all known California spotted owl sites.

The Forest, Past and Present

Vegetation Dynamics

Forests of the Sierra Nevada have been impacted by nonaboriginal man over the last 150 years. The first major perturbation, on lands that now are managed by the Forest Service (FS), was the grazing of millions of sheep (Chapter 11). This grazing pressure and the fire patterns associated with its promulgation impacted regeneration and the grass/forb community. This pattern probably amplified a structure already maintained by frequent fires—one of open stands dominated by large, old trees (Chapter 12). It also resulted in excellent seed beds for tree regeneration by creating bare-soil conditions over much of the forest (figs. 13A and 13B as examples; Chapter 11).

With removal of sheep and fire, stands experienced ingrowth of conifers, dominated by shade-tolerant species such as white fir. Stands became dense, and a combination of logging and natural attrition of the old forest led to a decline in the number of large, old trees. Past logging activities that concentrated on removal of the large, valuable trees broke up the patchy mosaic of the natural forest, and this too encouraged development of dense regeneration patterns with very little horizontal heterogeneity (figs. 11P-11S; Chapter 12). These developments, particularly in Sierran mixed-conifer and ponderosa pine/hardwood forests, reduced large-diameter trees in many areas to a

small, remnant population. This condition can be seen by comparing owl nest locations, which generally are in larger, denser stands in today's forest (color photos 5-9 to 5-16 as examples), to forest conditions about 1900 (figs. 13A to 13D as examples).

These changes have not occurred to the same degree in the red fir as they have in mixed-conifer and ponderosa pine types at lower-elevations. The red fir type differs from the mixed-conifer in several particulars, including in its natural disturbance regime. Fires are less frequent, occurring at intervals of 40+ years (Taylor and Halpern 1991) rather than the 5- to 30-year return periods observed in mixed-conifer stands (Chapter 12). The forest consists of blocks of various sizes, often with a high degree of horizontal heterogeneity (color photos 5-1 to 5-6). In many areas fire was the dominant disturbance factor responsible for this mosaic (Pitcher 1987). In addition, windthrow created small gaps, and red fir regeneration often established more or less continuously between disturbance events (Taylor and Halpern 1991). This led to a complex horizontal pattern with the juxtaposition of blocks of various ages and sizes. Removal of fire from the red fir type has had less impact than in the Sierran mixed-conifer type because of the longer mean fire interval. Many red fir stands would not have burned in the twentieth century even if the natural fire patterns were intact. Red fir also occurs in mostly pure stands at higher elevations. On these sites, red fir appears to be a self-perpetuating, climax species (Barbour and Woodward 1985, Taylor and Halpern 1991), and the successional trend toward more shade-tolerant species that characterizes the mixed-conifer zone is not a factor.

Red fir was also not extensively logged until recent years. Most logging of red fir in the Swain Mountain area, for instance, occurred after 1960 (Chapter 7). Partial cutting has not broken up the large-diameter groups and, in many places, the forest has never been logged (color photos 5-1 to 5-6 as examples). The pattern in red fir is more that observed in the Pacific Northwest-recent, often even-aged harvest intermingled with blocks in reasonably pristine condition. In logged areas, regeneration records maintained by the FS R5 show that survival of planted seedlings is low (Fiske pers. comm.; fig. 13E).

Fire Patterns

Fire patterns in the Sierran mixed-conifer zone have changed radically in the twentieth century. The annual acreage burned may have declined by two orders of magnitude when compared with historic levels (Chapter 12). This, in turn, has led to historically unprecedented buildups in fuels and to stand structures that are prone to crown fires (Chapter 12). Because of these conditions, fires that escape initial suppression efforts—usually those occurring during extreme weather conditions—tend to become large, stand-replacing events.



Figure 13A--Sugar and ponderosa pine in Foresthill block showing size of timber and open character of forest. Note extensive, branchless tree trunks and the absence of underbrush on the forest floor.

Date: -----7 July 1911

Source: -----Tahoe National Forest Historical Photo

Photographer: -----USDA Forest Service



Figure 13B--A woman and her dog following an old road through a stand of old-growth Jeffrey pines.

Date: -----About 1920

Source: -----Lassen National Forest Historical Photo

Photographer: -----USDA Forest Service



Figure 13C--Pure stand of cedar along Mill Creek above Morgan Springs.

Date: -----About 1920

Source: -----Eldorado National Forest Historical Photo

Photographer: -----USDA Forest Service



Figure 13D--Near Strawberry, a virgin forest including sugar pine, ponderosa pine, fir, and incense-cedar. Observe the downed, rotting tree and open character of the forest floor.

Date: -----About 1920

Source: -----Stanislaus National Forest Historical
Photo

Photographer: -----USDA Forest Service

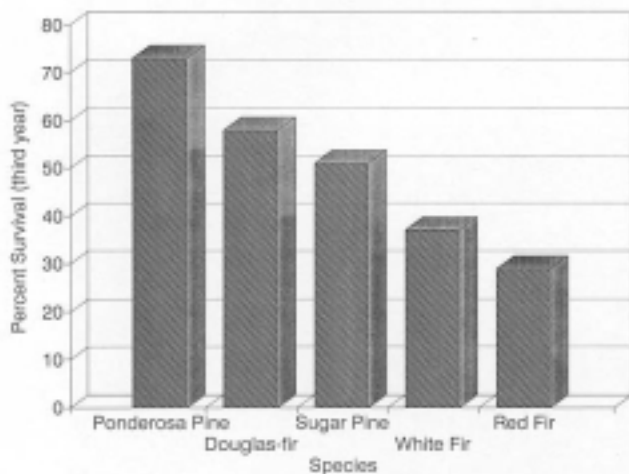


Figure 13E—Regeneration survival in plantations, by species, based on 3-year postcut inventories. Survival rates were averaged over the years 1986-1991 (Fiske pers. comm.).

Owl Habitat in Current Forests

Spotted owls in the Sierra Nevada have used all of the dense (>40 percent canopy closure) mixed-conifer stands at or greater than expected levels for nesting (Chapter 5). The only stands used significantly greater than expected, however, were dense stands with large-diameter trees [>24 inches in diameter at breast height (d.b.h.)] in the overstory. Within these stands, snag densities were higher than in the general forest matrix, and the average nest tree exceeded 40 inches in d.b.h. Most of the nest trees appeared to be old-growth remnants of stands present at the turn of the century (Chapter 5). These stands tend to be very heavily stocked with trees in smaller diameter classes (color photos 5-9 to 5-16, for example).

We have few data concerning nest stand selection in the red fir type. The nests that we observed on our field trips were in uncut blocks of timber (color photos 5-1 to 5-6, for example).

Future Trends

Human Population Trends

The human population in both the Sierra Nevada and southern California is growing rapidly (fig. 13F). Of particular concern is population growth in the foothill regions of the mid-Sierra Nevada. In these areas (Nevada, Placer, El Dorado, Amador, Calaveras, and Tuolumne Counties), human populations have increased by 50 percent over the last 10 years and are expected to continue to grow at that rate through the year 2000. From 1980

to 1990, they were among the top 10 California counties in growth. By the year 2000, the combined population of these counties is estimated to exceed 670 thousand (Rountree 1992). A large proportion of this population will be living in widely dispersed housing "in the pines." Impacts from this type of development on spotted owl habitat are unknown. We do know, however, that spotted owls currently occur in these foothill areas and that this type of housing pattern makes management and monitoring very difficult. Any resulting negative impacts on the owls will be difficult to detect and even more difficult to control.

While much of the population growth in southern California is in the basins, towns in the San Bernardino Mountains, such as Big Bear Lake, are expected to grow 50 percent by 2010 (Ruth

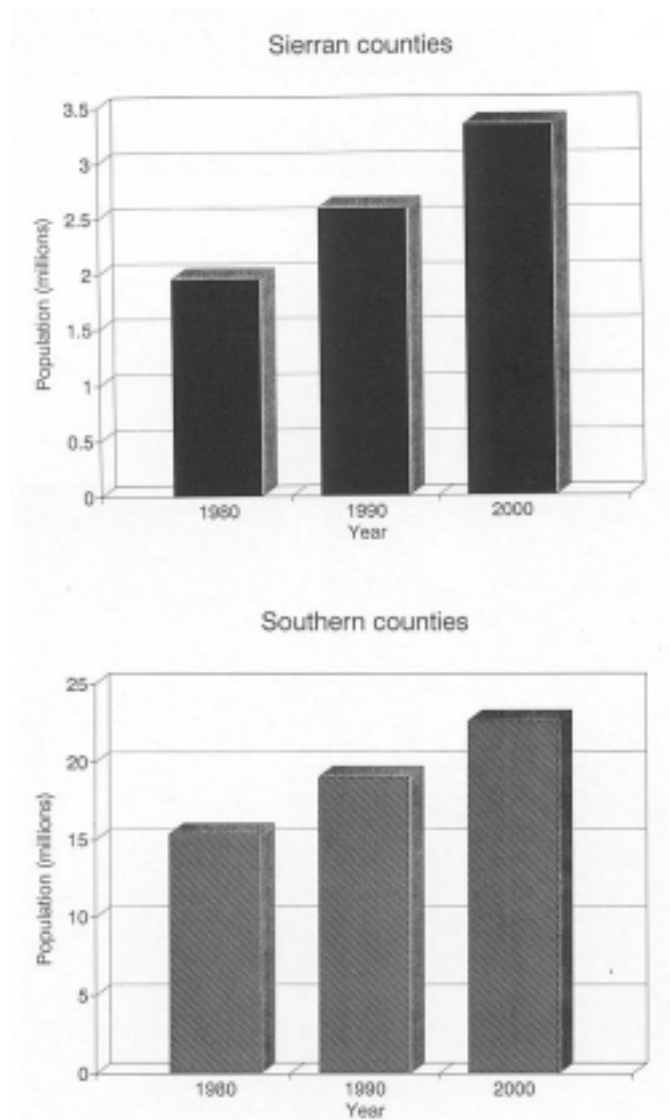


Figure 13F—Human population trends in the Sierra Nevada and southern California. Only counties containing spotted owls were included in this analysis (data from Rountree 1992).

pers. comm.). Impacts of increased population on the spotted owl in southern California will most likely be more direct than they are in the mid-Sierra Nevada. Because many owls in southern California depend on narrow riparian/hardwood forests, pressure on them will increase as waters are diverted to a variety of human needs.

Fire Trends

As the human population increases, human-caused wildfires can also be expected to increase. The presence of so many houses within the forest will shift the emphasis of fire suppression even further from one of saving forests to one of saving property. Fuels will also continue to accumulate. Especially as a direct result of our current drought, recent bark beetle infestations will contribute a major pulse of new fuels over the next few decades. The likely result is a gradual increase in the number and acreage of large, stand-replacing wildfires.

Cutting Trends: Land Management Plans

According to Land Management Plans (LMPs) collectively for National Forests (NFs) of the Sierra Nevada, 65 percent of the forested acres are classified as suitable and available for timber production (USDA, FS 1986-1991b). If we exclude from the forested base the acres that are physically unsuitable because they cannot produce timber in commercial quantities, cannot be successfully regenerated, or have unstable soils, 74 percent of the lands that can potentially produce timber will be harvested in some manner (table 13A). On many acres, harvest will be light.

Table 13A--Categorization of forested acreage from the Land Management Plans.

National Forest	Thousands of acres			
	Forested	Physically unsuitable ¹	Suitable and available ²	Suitable and unavailable ³
Lassen	825.1	0	596.3	228.8
Plumas	1,102.4	145.7	898.9	57.8
Tahoe	681.6	31.7	528.5	121.4
Eldorado	458.0	63.2	307.6	87.2
Stanislaus	784.6	308.3	328.5	147.8
Sierra	562.9	26.8	328.9	207.2
Sequoia	679.0	40.0	345.0	294.0
All Forests	5,093.6	615.7	3,333.7	1,144.2

¹ Includes acreage not capable of producing commercial timber, in which irreversible damage would be caused if timber were harvested, and that cannot be regenerated in 5 years after harvest.

² Includes lands capable of producing commercial timber that have not been withdrawn from timber management, lands that can be regenerated within 5 years after logging, and lands that can be managed for timber production without irreversible damage. Suitability here refers to areas that could physically sustain timber yields over time, not necessarily spotted owl suitability.

³ Includes lands that are physically suitable but that have been withdrawn from timber management for dedication to other uses (for example, Wilderness Areas, Spotted Owl Habitat Areas, and so on).

Seventy-two percent of the timber volume removed from these lands will be taken through even-aged systems, the most common even-aged system being the clearcut (table 13B). Of the 528,474 acres of suitable timber land on the Tahoe NF, for instance, 68 percent will be managed for even-aged silviculture (24 percent long rotation, 44 percent short rotation) (USDA, FS 1990). On the Plumas NF, 52,000 acres are scheduled for even-aged cutting per decade and 8,000 acres for selection cutting methods (USDA, FS 1988b; table 13C).

Even-Aged Logging and Owl Habitat

Clearcuts, seed-tree, and shelterwood cutting methods all have the same goal: produce even-aged stands. In this regard, seed-tree and shelterwood systems can generally be thought of as two-stage (sometimes three-stage) clearcuts. In nearly all of these cutting systems, all of the original stand will be removed before the new stand is scheduled to be cut.

Table 13B--Harvest volumes from the forest Land Management Plans.

National Forest	Millions of board feet			
	Clearcut	Seed tree/shelterwood ¹	Other ²	ASQ ³
Lassen ⁴	40.6	23.5	31.9	96.0
Plumas	144.2	31.3	90.0	265.5
Tahoe	64.7	48.2	29.4	142.3
Eldorado	58.4	55.4	23.4	137.2
Stanislaus ⁴	3.9	67.6	16.5	88.0
Sierra ⁴	25.5	32.5	30.0	88.0
Sequoia ⁴	64.8	3.1	29.1	97.0
All Forests	402.1	261.6	250.3	914.0

¹ Includes removal sales as well.

² Includes all other sale types that enter into the calculation of ASQ.

³ Annual sale quantity.

⁴ These data are given in cubic feet in the LMPs.

Table 13C--Number of acres scheduled for logging, annually, during the first decade of draft and final Land Management Plans for Sierran National Forests, by prescription.

National Forest	Acres per year			
	Clearcut	Seed tree/shelterwood ¹	Selection ²	Intermediate ³
Lassen	1,600	1,000	1,400	10,200
Plumas	4,000	1,200	800	16,286
Tahoe	2,046	1,657	162	3,500
Eldorado	2,084	1,836	948	2,700
Stanislaus	510	2,386	8,728	1,500
Sierra	1,550	1,170	2,970	4,000
Sequoia	1,734	128	742	6,727
All Forests	13,524	9,377	15,750	44,913

¹ Includes acres of overstory removal.

² Both group- and individual-tree selection.

³ Includes stand improvement, thinning, salvage, etc.

⁴ This figure represents the acres to be examined rather than the acres to be treated.

In terms of owl biology, the primary impact of traditional, even-aged logging practices lies in the creation of simple stand structures and, perhaps more importantly, the removal of all large, old trees from vast areas of the forest. Even if silvicultural prescriptions are modified so that snags and live culls are left at the first cutting, no provision is made for a predictable recruitment of replacement trees for these relics when they fall. This, in turn, will lead to a loss of large-diameter, downed woody materials. Log slash can create much small-diameter woody debris, but it cannot replace the large logs. In an even-aged system, these old-growth features can be recreated only by an extreme extension of the rotation interval. Even if the rotation were extended to 150 years, for instance, no trees would match the average age of the forest at the turn of the century (Chapter 11). Decadent features in stands are functions of age, not just d.b.h. (fig. 13G), and any animals that depend on decadent features (cavities, broken-tops, snags), or the large woody debris that they create, will simply drop out of these forests (see Chapters 4, 5, and 10 for examples specific to the spotted owl and its prey species). The rate of conversion to even-aged systems in the western Sierra Nevada is estimated by the LMPs to be 229,000 acres per decade.

Even on lands set for selection logging (about 80,000 acres per decade), we have no guarantee that harvest prescriptions will leave many of the large, old trees. Ideally, stands managed for individual-tree selection are harvested in a manner that brings the diameter distribution in the stand into conformity with an idealized distribution characterized by a declining exponential function (in forestry referred to as an inverse "J"). The number of large trees within the stand is dictated by the slope of this function (fig. 13H) and the specified intercept representing the number of trees in the smallest diameter class (or, alternatively, the designated diameter of the largest tree). In selection systems, timber is removed from all diameter classes, as required to maintain this diameter distribution. Little evidence exists, however, that historic patterns of partial cutting have followed classic single-tree selection theory. "Selective" harvest in the Sierra Nevada has, in the past, primarily targeted the large trees. This system, sometimes called "pick and pluck,"

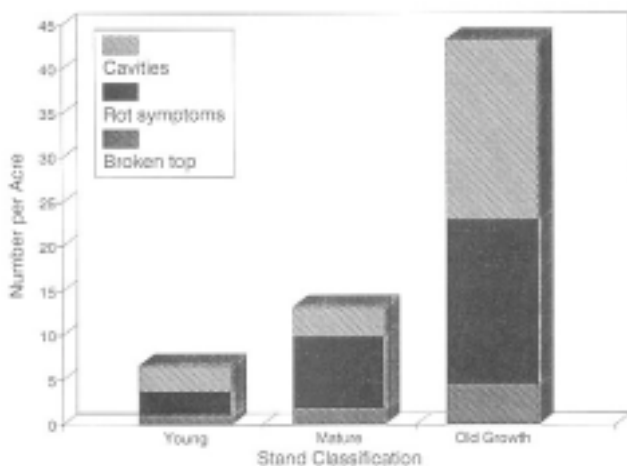


Figure 13G—Increasing decadence as a function of stand age, based on data from Bingham and Sawyer (1992).

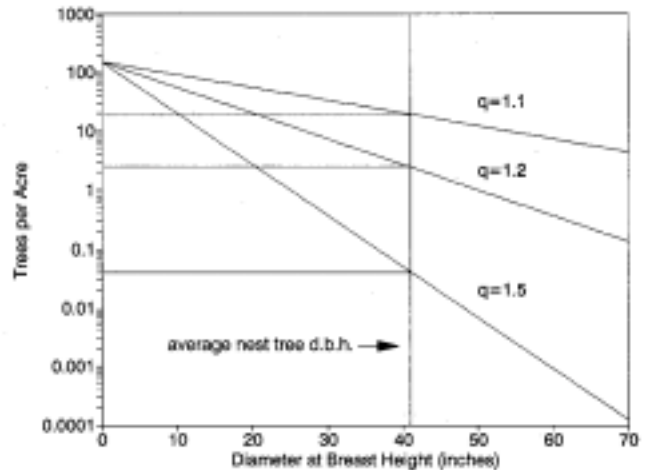


Figure 13H—Theoretical, uneven-aged distributions. Uneven-aged management allows for retention of very large trees. "Q" values of 1.2--similar to those measured in owl nest stands--will leave two to three trees per acre 40 inches in diameter at breast height on a site.

will not produce the simple structures that characterize even-aged methods, but its effect on the presence of large, old trees is similar. If the large trees are removed and no stocking control is performed on the smaller stems, replacement trees in these diameter classes will be produced very slowly, if at all, and they will consist primarily of the more shade-tolerant species. Even with classical single-tree selection, a gradual loss of shade-intolerant species would be likely.

A large proportion of the future forest, as projected by the LMPs, will very probably be split between areas of even-aged plantations and areas of dense, and increasingly small-diameter stands.

A Different Paradigm

Two important questions that the FS needs to answer are: (1) What kind of forest structures does it want to create and perpetuate? (2) Are the life history requirements of spotted owls and other species associated with late-seral forest conditions met by those forest structures? Fundamental to these questions is the paradigm that guides NF timber management. Insights to this paradigm can be gained by studying the LMPs produced by the Sierran NFs. The LMPs are as much statements of goals, priorities, and paradigms as they are implementation strategies. The scheduling appendix for timber removal on Stanislaus NF, for example, states these goals clearly:

A regulated forest should be regarded as an objective that may never be fully attained... However, the concept of regulation as an objective, is the tool used to control present harvest levels and plan future harvests to assure sustained yield within reasonable limits.

A forest consisting of wild and unmanaged stands with highly variable stocking levels and age-class distribution is made to approach regulation through harvest and scheduling regeneration over a period of time called the conversion period. During the conversion period an attempt is made to meet three criteria:

1. *Obtain the maximum yield of timber possible.*
2. *Provide for essentially a non fluctuating yield over the conversion period.*

3. *Provide a balance of age-classes and stocking levels capable of producing the forest's full potential timber growth at the end of the conversion period (USDA, FS 1991b, appendix D, D-3).*

This description closely follows the ideal of the "fully regulated forest" as it is presented in forest management text books (for example, Davis and Johnson 1987, chapter 14). By this definition, the regulated forest differs in fundamental ways from a wild forest, and the current status of the forest is seen as being in a conversion period in which wild stands are brought into regulated conditions through harvest and regeneration. Really only one general template is used to define a fully regulated forest-the diameter distribution, forest wide, should fit an "inverse J" distribution form, with optimized spacing (Husch et al. 1982). This pattern can be achieved through a series of large blocks (even-aged clearcutting), blocks smaller than 2 acres (group selection), or on an individual tree basis (individual-tree selection). All three models are generic, derived from European forestry in the late 1800s (Davis and Johnson 1987) and used for timber production in Europe, New Zealand--and in the Sierra Nevada. The purpose of the classic, fully regulated forest, in any of its permutations, is to allow for an even flow of wood products, not necessarily to mimic natural stand conditions and processes:

The essential requirements of a fully regulated forest are that age and size classes be represented in such proportion and be consistently growing at such rates that an approximately equal annual or periodic yield of products of desired sizes and quality may be obtained in perpetuity. A progression of size and age classes must exist such that an approximately equal volume and size of harvestable trees are regularly available for cutting (Davis and Johnson 1987, p. 540).

Most other LMPs share a single emphasis concerning their paradigm for timber management. No certainty exists that ecosystem processes, whether they are the population dynamics of a single species or the successional trends of a multi-species complex, will be maintained in a fully regulated forest. The concept of forest regulation has traditionally not been defined in these terms, and the long-term ecological consequences of the paradigm are unknown.

Recent discussion has concerned a significant shift in the basic forestry paradigm, from one that stresses the production of commodities (or amenities) to one in which the maintenance of ecosystem processes is the primary goal (National Research Council 1990). This new paradigm "...involves a shift in management focus from sustaining yields of competing resource outputs to sustaining ecosystems" (Kessler et al. 1992, p. 221). Toward this objective, the goal of management activities is to maintain, protect, and, where necessary, to create natural forest structures. Logging is practiced only to the extent and in a manner that it does not impair ecological processes or environmental assets. This system does not guarantee an even flow of wood products from the forests. The efficacy of silvicultural practices is evaluated by biological rather than market-based criteria.

Under this paradigm, logging would be explicitly designed to achieve or maintain ecological goals. These goals might, for

instance, include remedial actions such as the generation, within a topographically defined unit such as a drainage basin, of a pattern of stand structures that mimic historical stand conditions. Because those structures were very different from the stands that presently exist, much manipulation of vegetation will need to occur before the goal is achieved--and active management will subsequently be needed to maintain it. A great deal of sophisticated silviculture will be required. What represents a major paradigm shift is that the silviculture will not be constrained by the equal volume/equal entry area requirements that are definitional to the concept of the fully regulated forest. This is not to say that forest regulation and a sustainable yield of forest products are necessarily incompatible with ecosystem functioning. Rather, it is a question of priorities: The new paradigm "...would involve a view of forest lands--including soils, plants, animals, minerals, climate, water, topography, and all of the ecological processes that link them together--as living systems that have importance beyond traditional commodity and amenity uses" (authors' emphasis) (Kessler et al. 1992, p. 222).

Under this paradigm, the answer to the first question (the type of forests we want) is that we wish to create forests in which natural processes are fully functional and stable. The answer to the second question (how spotted owls fit into this structure) is the subject of the remainder of this chapter.

Current Stand Structures at Spotted Owl Nests

Nest stands have definable properties--high canopy closure, a considerable snag component, and the presence of large, old trees that are used by the owls for nest sites. To generate and maintain these stand structures we need to be more specific. Data on the silvicultural characteristics of owl nest stands is, however, surprisingly sparse.

To evaluate the diameter distributions of owl nest stands, we obtained diameter distributions for areas immediately adjacent to 24 nest trees in the mixed-conifer zone of Lassen NF and 11 nest trees in the Sierra NF. These data were based on plots

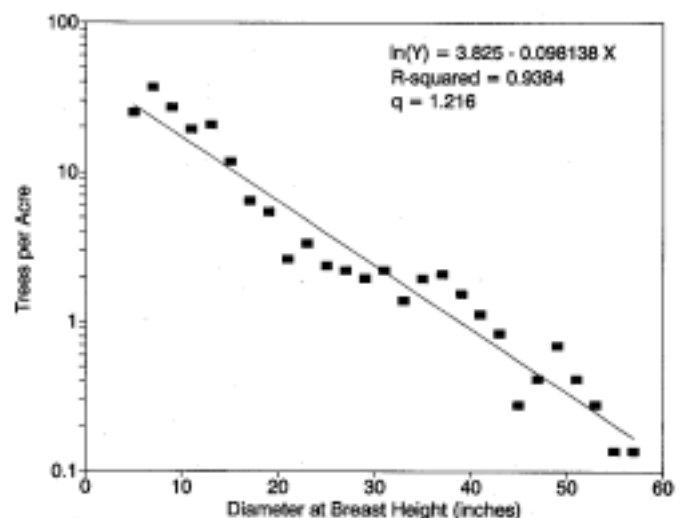


Figure 131--Log-linear display of the mean number of trees/diameter class, based on 24 nest sites in the Lassen National Forest.

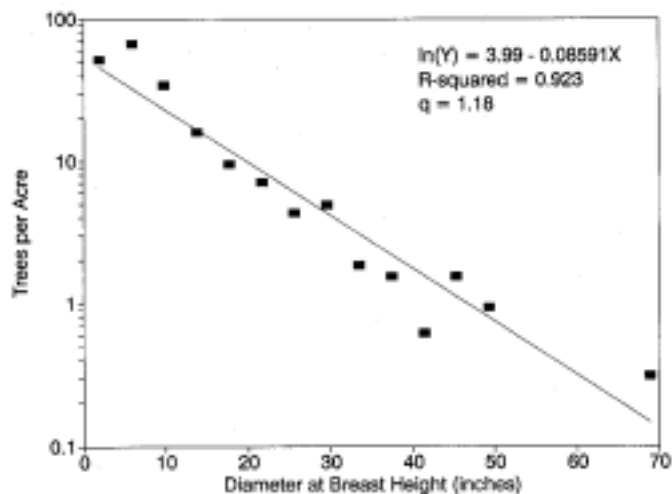


Figure 13J-Log-linear display of the mean number of trees/diameter class, based on 11 nest sites in the Sierra National Forest.

centered on the nest tree and forming a cross with the nest tree at the center. All trees 15.7 inches in d.b.h. were sampled within an area of 0.296 acre. Smaller trees were sampled within four subplots 32.8 feet square. To avoid any possible bias by the inclusion of a large, central tree, the nest tree itself was excluded from density calculations. When the natural log (ln) of the mean tree density (stems/acre) for the combined plots in these two areas was regressed on d.b.h., the resulting pattern was linear (figs. 13I and 13J), suggesting a classic "inverse J" form-the idealized distribution for uneven-aged management-with a "q" value between 1.18 and 1.21 [here q is based on 2-inch d.b.h. groups (Daniel et al. 1979)]. This pattern, by itself, is not sufficient to suggest that uneven-aged management is warranted. Stands with differing structures will tend to conform to the inverse J when they are combined. Viewed individually, nest stands in Lassen NF formed three logical groups (figs. 13K and 13L). Eight of the stands lacked the larger diameter classes and conformed closely to the log-linear model. Thirteen of the stands

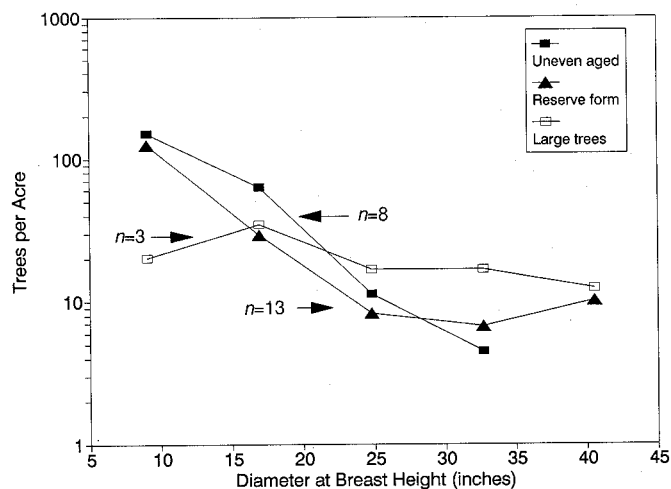


Figure 13K-Nest sites on the Lassen National Forest divided into logical groupings based on stand structure. Data presented are the mean values for each group. The groups consisted of 8, 13, and 3 sites, respectively.

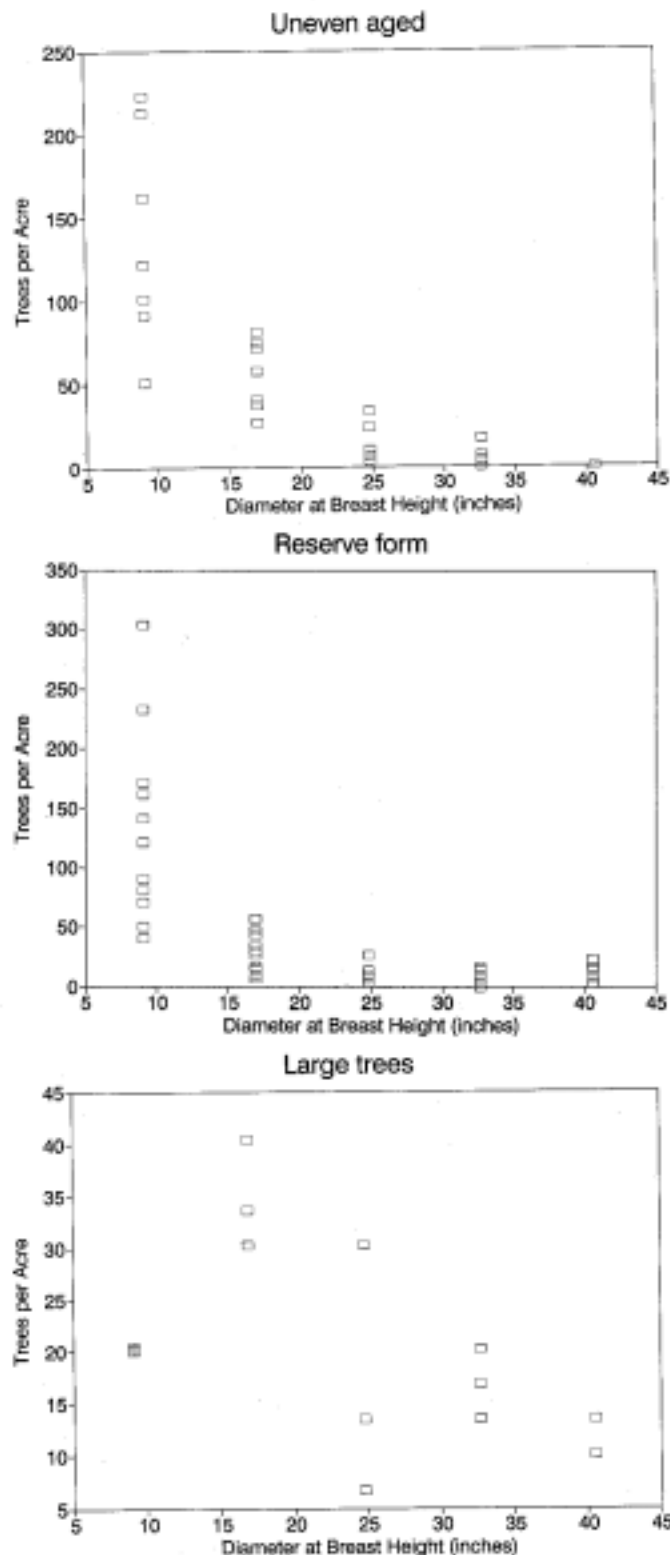


Figure 13L-Diameter distributions for the three types of nest stands measured in the Lassen National Forest. Both the "reserve form" and the "large trees" groups had more large-diameter stems than an idealized, uneven-aged stand structure would specify.

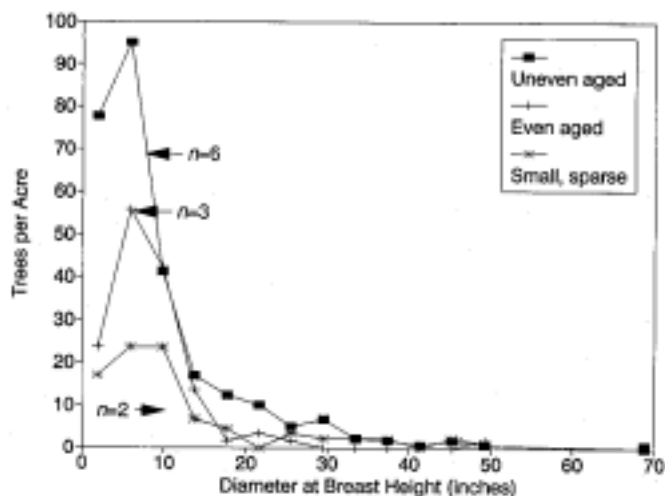


Figure 13M—Nest stand structures in the Sierra National Forest. None of these stands had a large proportion of large-diameter stems, and several were dominated by small-diameter trees,

generally conformed to the uneven-aged structure in the smaller diameter classes, but not in the large diameter classes. Three stands had most of their trees in the larger diameter classes. Nest stands on the Sierra NF also grouped logically into three classes (fig. 13M). Six of them generally fit an uneven-aged distribution form, but the others did not. Stands at two of the sites were made up primarily of stems <12 inches in d.b.h..

Most of these stand structures could be produced through a variety of management methods. Partial removal of the over story in the past and subsequent ingrowth probably led to the formation of many of these stands. We have no reason to believe that uneven-aged management, if properly applied, could not be used to maintain these structures—but the system should be sensitive to maintaining the large trees, and perhaps modified to generate "reserve form" stands. Reserve form stands are characterized by an inverse "J" distribution in the smaller diameter classes and a normal distribution in the larger diameter classes. In all stands lacking frequent large stems, at least one large tree was present the nest tree, which was not included in the calculations.

The simple premise that forest structures similar to owl habitat can probably be created and maintained through silviculture does not answer a fundamental question. In the long run, are these the types of stands we wish to maintain? We have many reasons to doubt whether these stand types represent either a necessary or ideal template as an owl nest site. Perhaps the most important reason is that dense stands characterized by single tree-sized openings would have been unusual in mixed-conifer forests before the turn of this century. Dense stands would have existed, particularly in riparian areas and at higher elevations (figs. 13C and 13D), but they would not have been widely distributed across the landscape. A second reason is that these stands are unstable—the stand structure is likely to be altered quickly and unpredictably due to the probability of stand-replacing fires or insect and disease outbreaks. We do not know whether owls inhabited the more open stands that dominated much of the landscape in the past (figs. 13A and 13B). Because such stands are rare today, we are unable to infer anything from current owl

locations. We do, however, need to begin to explore potential, alternate stand structures. These structures should be chosen to better mimic natural stands, to maintain tree species diversity, and to be more resilient to wildfires.

Some Potential Management Systems for Mixed-Conifer Ecosystems

General Considerations

A fundamental assumption underlies management of owl habitat, as well as much of forest management in general: Ecosystems are inherently dynamic; they do not stand still. Changes take place both rapidly (through a variety of natural and man-made disturbances) and slowly (through climatic change and natural successional processes), and occur at many spatial and temporal scales. Changes have occurred in the past, and they will occur in the future even if we "do nothing." Given this assumption, management recommendations should consider provision of adequate amounts and distribution of suitable owl habitat both in the short-term and in the long-term. For the short-term, Chapter 1 details management recommendations to be applied during an interim period of at least 5 years. These recommendations are intended to provide some degree of protection to existing owl habitat and to maintain future options for whatever long-term management strategy may be adopted at the end of the interim period. Below, we offer an example of one way in which the short-term (interim period) recommendations in Chapter 1 could be implemented in stand types shown to be selected for nesting by the spotted owl. These short-term practices and resulting stand conditions are not designed to be sustainable over long periods, however. The remainder of this section, therefore, offers potential silvicultural strategies that might be useful for producing and maintaining owl habitat over the long-term.

An Example of a Short-Term Approach

Recommendations in Chapter 1 set limits for cutting large trees and managing other stand components. By definition, management practices cannot exceed these limits—for example, cut more large trees than specified and still conform to the recommendations. In some situations, however, management objectives may be better achieved by not taking the recommendations to their limits. Following is one example of such an approach to interim management of "Selected Timber Strata" (P4G, M4G, M4N, M5G, M5N, M6—codes for timber strata defined in table 1C). (Compare item #1 under "Other Forested Public Lands" in Chapter 1.) Objectives that this example could help to meet include: (1) provide for a shorter recovery period for nesting/

roosting habitat; (2) keep some stocking in middle and lower canopy layers, both to retain existing multiple-canopy character of the stand and to ensure quicker replacement of large trees; (3) provide for some thinning in middle and lower canopy layers to promote growth of trees in these layers into desirable larger size classes; and (4) provide some quantification of fuels management treatments, including reduction of vertical fuel ladders (Chapter 12). Managers should recognize that this example (like any other that places additional constraints) is more restrictive than the basic interim-period recommendations in Chapter 1. Thus, in exchange for the potential benefits indicated above, timber volumes (and associated revenues) will generally be lower, and costs of treating submerchantable stems and other fuels will generally be higher. (Basal area limits and other quantitative data in this example are only approximations. They are not based rigorously on Chapter 5 or any other real data pertaining to owl habitat. If an approach similar to this is to be used, it should be based on the best and most nearly site-specific data available.)

A. Enter a stand for harvesting only once before a long-term strategy for managing the California spotted owl has been implemented on public lands.

B. For stands with a Dunning and Reineke (1933) site index (SI) of ≥ 60 , enter the stand for harvesting only if total basal area of live trees ≥ 5 inches d.b.h. is greater than 200 square feet per acre. Harvesting will not reduce total basal area to less than 200 square feet per acre or canopy closure to < 40 percent. For stands with SI < 60 , the corresponding basal area limit is 160 square feet per acre. To the extent possible, a mix of tree species should be retained.

C. Remove no live tree ≥ 30 inches in d.b.h.

D. For stands with SI ≥ 60 , limit cutting in the 21- to 30-inch d.b.h. class so that the combined basal area of live trees in d.b.h. classes 21-30 inches and 30+ inches is no less than 120 square feet per acre. A wildlife biologist should be involved in training tree markers to identify potential nest and roost trees in the 21- to 30-inch d.b.h. class so that those trees (including live culls) will be retained as part of the residual basal area. In stands currently having less than 120 square feet per acre basal area in those two size classes, no cutting of trees 21-30 inches d.b.h. will take place. For stands with SI < 60 , the corresponding basal area limit is 100 square feet per acre.

E. For stands with SI ≥ 60 , limit cutting in the 11- to 20-inch d.b.h. class so as to retain a basal area of at least 60 square feet per acre in that diameter class. In stands currently with basal area < 60 square feet per acre in that d.b.h. class, no cutting of trees 11-20 inches d.b.h. will take place. If the stand is entered for harvesting, and if current basal area in the 11- to 20-inch d.b.h. class is > 80 square feet per acre, this diameter class will be thinned to a basal area of 60 to 80 square feet per acre. For stands with SI < 60 , the corresponding range of basal areas would be 40 to 60 square feet per acre.

F. Limit cutting in the 5- to 10-inch d.b.h. class so as to retain a basal area of at least 20 square feet per acre in that diameter class. In stands currently having < 20 square feet per acre basal area in that d.b.h. class, no cutting of trees 5-10 inches in d.b.h. will take place. If the stand is entered for harvesting, and

if current basal area in the 5- to 10-inch d.b.h. class is > 30 square feet per acre, this diameter class will be thinned to a basal area of 20 to 30 square feet per acre. Trees cut in the 5- to 10-inch d.b.h. class will be removed from the stand. Utilization of these trees is encouraged.

G. If the stand is entered for harvesting, and if canopy cover in trees 0-4 inches in d.b.h. is, greater than 20 percent, trees will be felled, crushed, masticated, or otherwise rearranged to reduce canopy cover in that size class to no more than 20 percent. The surface fuel bed resulting from these trees, as well as slash from logging of larger trees, should be treated mechanically or with prescribed fire to reduce wildfire hazard to an acceptable level. The emphasis should be on reducing vertical and horizontal continuity of fuels and associated risk of crown fires, especially in the vicinity of large trees. Fuel treatments and logging activities should be designed to minimize disturbance of duff and coarse woody debris. In most cases this will preclude machine piling of slash. Where prescribed burning is used, it should be done when lower duff and large woody debris have high moisture contents to minimize consumption of these materials.

H. Follow guidelines in Chapter 1 for retention of snags and downed wood.

Some Potential Long-Term Strategies

A full discussion of management activities that may be appropriate to manage for owl habitat over the long-term is beyond the scope of this chapter. Instead, our purpose is to provide a sampling of ideas and considerations to stimulate thinking. Innovative managers and resource specialists may be able to use some of these ideas as a starting point in developing suitable management regimes to fit their local conditions and needs. On public lands, initial (interim period) implementation of the long-term strategies described here would be compatible with recommendations (Chapter 1) for "*Other Timber Strata*" used for nesting by owls but not significantly selected in relation to availability. We encourage managers of private lands to explore these approaches as well. Treatments should be viewed as ongoing management experiments (adaptive management, Chapter 2). Effects of treatments on stand structure and key ecosystem components should be carefully monitored, and owl habitat models should be tested. These experiments would incorporate information from monitoring and research activities into feedback loops that would serve to improve both our management practices and our knowledge of what constitutes suitable owl habitat.

Although the scenarios discussed below describe generalized target stand structures and associated management practices primarily at the stand level, great flexibility exists for distributing variations and combinations of these structures across the landscape and through time. In these scenarios, silviculture would be viewed as the art and science of shaping stands and landscapes to meet management objectives-spotted owl habitat in this case. Timber volume would be an output of, rather than a driving force for, the silviculture undertaken to meet management objectives. Protection of current or future habitat would

continue to be a primary concern. Accordingly, appropriate fuels management would be integrated with silvicultural activities.

We focus here on good-quality nesting and roosting habitat for the spotted owl as the "target" conditions for management activities. Foraging habitat appears to be more variable and less restrictive (Chapter 5), and its requirements should be met more easily and with a wider range of management practices. In contrast, successful management to produce, maintain, improve, and protect nesting and roosting habitat may require significant changes from conventional management practices. Some institutional barriers may need to be overcome. It will be more complex and expensive but should provide new and stimulating professional challenges for a variety of specialists to exercise creative thinking and pursue interdisciplinary objectives and activities.

We make several simplifying assumptions about attributes of suitable nesting/roosting habitat (Chapter 5) to help define target stand structures and associated management practices: (1) high canopy closure; (2) stand basal area and canopy closure distributed among two or more size classes of trees; (3) diversity of tree species within the stand; (4) "adequate" numbers of large live trees; (5) "adequate" numbers of large snags; and (6) "adequate" quantities of duff and large woody debris.

Accepting these six assumptions places limits on the range of stand structures that can be targeted by management. Both classical, even-aged silviculture and the classical, single-tree-selection form of uneven-aged silviculture have difficulties in meeting one or more of these assumptions, for reasons discussed below. We believe that two other kinds of stand structures—mosaics of small, even-aged groups or aggregations, and two- or three-storied stands—hold greater promise for producing and maintaining suitable owl habitat over the long-term. We recommend that these two structures, together with their associated silvicultural and fuels management practices, receive emphasis in long-term, adaptive management experiments concerned with owl habitat. Both can be considered intermediate between even- and uneven-aged (single-tree selection) management. But they can be thought of as representing two ends of a continuum, with many intermediate structures differing in density and spatial arrangement of age/size-classes to help meet various specific objectives and to increase diversity across the landscape. Even- and uneven-aged (single-tree selection) methods should be included in these experiments, but at a reduced level.

Even-Aged Silviculture

The requirement for two or more size-classes of trees (assumption #2 above) probably could be met with even-aged silviculture, but it would involve significant modifications from conventional practice. The natural segregation of crown classes could be emphasized by "thinning from the middle"—that is, thinning in codominant and intermediate trees, thereby promoting the separation of dominant from suppressed crown classes and increasing growth in the dominants. Suppressed trees probably would not survive long enough to be of much value for owl habitat unless stand density were reduced below usual target stocking levels, or the lower canopy level consisted largely of

shade-tolerant species. The latter scenario probably would be more practical and sustainable in mixed-species stands.

Assuming that such an approach eventually would meet needs for a two- or more-storied stand, the rotation age necessary to meet tree size and decadence requirements (assumptions #4 and #5) probably would be much longer than called for in currently practiced even-aged management. As compared with alternative silvicultural methods, the time from plantation establishment to achievement of conditions suitable for owl nesting and roosting is likely to be much longer. This long time period would necessitate development and/or retention of suitable replacement habitat in the interim.

Whatever may be the disadvantages of even-aged silviculture with respect to owl habitat, even-aged plantations in the Sierra Nevada will continue at some level for the foreseeable future, if for no other reason than because severe wildfires will continue to occur. Even-aged plantations, therefore, should be included in owl-related management experiments.

Uneven-Aged Silviculture Using Single-Tree Selection

To meet the need for tree species diversity (assumption #3 above), stand openings must be large enough to permit regeneration of shade-intolerant species such as ponderosa pine. This requirement generally is not met with the single-tree selection form of uneven-aged silviculture, at least where openings are mostly the size of individual large trees rather than groups of trees. Furthermore, retention of the smallest size-classes of trees well distributed through a stand—a necessity for sustaining this stand structure through time—creates dangerous fuel ladders and makes prescribed burning or other fuels management treatments essentially impracticable. As described earlier, many owl nesting stands had roughly an inverse J-shaped diameter distribution characteristic of uneven-aged stands. Composition of the smaller size classes, however, was strongly weighted toward shade-tolerant species, especially white fir. This resulted from many decades of fire suppression, augmented by partial cutting and preferential harvest of pines. In the absence of stand openings by cutting or by natural agents of disturbance such as fire and insects, these stands will become increasingly dominated by shade-tolerant conifers. Single-tree selection should be included at a reduced level in management experiments to evaluate changes in structural attributes, owl use, managerial difficulty, and costs of implementation. Combining single-tree selection with group selection (discussed below) may work to maintain some vertical structure while permitting regeneration of shade-intolerant species.

Mosaic of Small, Even-Aged Groups

One kind of structure that may have promise for production and long-term maintenance of owl habitat is a multi-aged mosaic of small, even-aged groups or aggregations. Groups would generally range in size from about 2 acres down to a quarter-acre, or possibly less. Probably this type of structure best approximates presettlement stand structures (Chapter 12), thus warranting serious consideration. Openings would be sufficiently large to permit regeneration of shade-intolerant as well as shade-tolerant

species. Multiple size classes in general would be separated horizontally rather than vertically, but in sufficient proximity to satisfy this attribute of suitable owl habitat. The horizontal separation of size classes also would confer some degree of resistance to crown fires (Chapter 12).

Group selection cuttings, or modifications thereof, would be used to create and maintain this structure over time. Keeping track of a large number of small openings and groups for management purposes, long considered a major obstacle to the use of group selection, should be significantly easier with the advent of geographic information systems and satellite-based global positioning systems. Treatments certainly would be more complex and more expensive than with even-aged management, however, especially on steeper slopes.

Viewed from the standpoint of area regulation-approximately equal areas maintained in each of several age-classes-a given "stand" of, say, 20-100 acres under steady-state conditions might contain three to six or more different age-classes. Each age-class would comprise many small, variable-sized aggregations and occupy a total area roughly equal to the area of the entire stand divided by the number of age-classes. "Rotation age"-the age at which the oldest aggregations would be regenerated-could be as long as needed to meet and maintain targets for large and/or decadent trees and snags. Periodic entries preceding regeneration cutting for a given age-class could be used to adjust stand structure to meet desired habitat attributes. These intermediate treatments might include thinning to speed development of large trees or to alter species composition, creating snags by girdling or other means, or wounding selected trees to induce decay. In practice, these intermediate treatments would take place within the various age-classes (aggregations) in the stand when the oldest age-class is being regenerated. As an example, if six age-classes and a 240-year "rotation" were selected, entries could be made every 40 years to regenerate one-sixth of the stand and conduct appropriate intermediate cuttings in the remainder of the stand. Or 20-year entries could be made, but regeneration cuttings would be made only every other entry. Successive age-classes would be separated by about 40 years.

In groups to be regenerated, all trees could be removed or, especially in larger groups, scattered live trees and/or snags could be retained. To facilitate fuels treatment and reduce damage to the surrounding stand, cut trees should be felled as much as possible into the newly created opening. Site preparation/fuels treatment methods used on clearcuts should be usable in these small openings, although they are likely to be much more expensive. One promising possibility may be jackpot burning of slash concentrations in the opening at a time of year when fire would not spread into the adjacent stand, thereby minimizing the need for firelines. Shortly thereafter, the rest of the stand could be underburned during somewhat drier conditions. Alternatively, the rest of the stand could be underburned at the same time as the openings. Local trials would help define a workable regime. In any case, we recommend that fuels be treated after each entry into the stand to reduce chances of severe wildfire. Various fuels-treatment methods may be appropriate for a given area. Prescribed underburning, however, has the advantage that it

would begin to restore the natural role of fire and associated processes in the ecosystem (Chapter 12). In the scenario described earlier, with successive age-classes separated by 40 years, the youngest (40-year-old) trees probably would be large enough to tolerate an underburn without excessive mortality, assuming early vegetation management to permit relatively rapid early growth.

Openings could be regenerated either naturally or artificially, and with or without vegetation management. Even with planting and vegetation management, growth of tree seedlings would be slower in an opening typical of group selection than in a larger opening because of competition for site resources from large trees surrounding the opening. Without planting and some control of nonconifer vegetation, however, development of conifers could be delayed for several decades. Fuels treatment would be complicated as well.

Development of a mosaic of small groups could be initiated in a wide range of stand conditions-for example, an older plantation, a variable-aged young-mature stand, or an old stand becoming excessively unbalanced in terms of size-class distribution or species composition.

Two- or Three-Storied Stands

Another kind of structure that might be suitable for production and maintenance of owl habitat is a two- or three-storied stand. It differs from the even-aged aggregation structure in that each age/size-class would be more or less uniformly distributed throughout the stand (although many variations in spatial arrangement would be possible). In a two-storied stand, the upper canopy would be sufficiently open to permit regeneration of shade-intolerant species in the understory. If a third canopy layer were to be managed, both of the upper two canopy layers would need to be thinned enough to allow regeneration and growth of multiple species. Typically, this kind of structure would be initiated with a shelterwood cutting. After regeneration is established, the overstory would be retained indefinitely-a practice referred to as irregular shelterwood-instead of being removed as occurs with even-aged management. Understocked stands, traditionally a high priority for clearcutting, could instead be underplanted, leaving most of the overstory in place. An overstory infected with dwarf mistletoe could be underplanted with species other than the one(s) infected.

If desired, this kind of structure could be initiated relatively early in the life of a plantation by having a heavy commercial thinning double as a shelterwood-type regeneration cutting. The cut would be followed by site preparation/fuels treatment and underplanting with the desired mix of species. Throughout the "rotation" of such a stand, thinnings could be applied as needed to maintain desired size classes and species. These should be followed by prescribed burning or other fuels treatments. Snags could be created as needed. Once created, the stand would never be devoid of large trees: each regeneration cutting would be accompanied by retention of some trees in one or two overstory layers. Thus a relatively short period of time would elapse between a regeneration cutting and restoration of a desired stand structure.

Fuels treatments, including use of prescribed burning, should not be particularly difficult for a two-storied stand. Initial site preparation/fuels treatment before establishment of the understory would be the same as for a shelterwood cut. Subsequent treatments would be comparable to those for an even-aged plantation. Separation of canopy layers normally would be sufficient to keep wildfires out of overstory crowns. A three-storied stand could be somewhat more problematical, in terms of maintaining adequate stocking of shade-intolerant species, protecting the small understory during fuels treatments, and keeping wildfires out of the overstory. In all these respects, a three-storied stand would begin to approach conditions in a single-tree selection stand.

Conclusions

We believe that the dynamic trends in forest structure and fuels profiles that are occurring on NFs in the Sierra Nevada are cause for concern. The most troubling aspects are the loss of old, large-diameter trees and associated woody debris, a shift toward more shade-tolerant species, the buildup of fuels associated with mortality in the small diameter classes, and the continued presence of abundant ladder fuels that enable crown fires to occur. We do not believe the management directions elucidated in the current LMPs alleviate these trends; in fact, single-tree selection systems are likely to accelerate them. Even-aged systems can reduce fuel loadings and encourage the growth of shade-intolerant species, but they do so at the expense of the remnant large trees. We believe that other options exist that could deal directly with these concerns. Management plans should focus on addressing undesirable trends, designing potential solutions, and proceeding experimentally to implement those plans on the landscape.

Owl habitat can be described in terms that are compatible with silvicultural methods. In this chapter we have presented preliminary examples of how this process might proceed. The FS can easily gather basic stand-level statistics from known owl nest stands throughout the range of the California spotted owl. To date, most of the data collected are either very coarse (for example, at the timber strata level) or based on ocular estimation and, therefore, are not as reliable as we would like.

Looking to longer-term solutions, we need to begin changing the forest structure back to a form more akin to historical patterns: to generate fire-resistant structures with small-scale horizontal heterogeneity and a significant large-tree component. The silvicultural systems suggested here provide for the maintenance of large trees and complex stand structures, while signifi-

cantly decreasing the risk of catastrophic wildfire. Through management experiments, we need to ascertain which, if any, of these stand structures may also be suitable for spotted owls.

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Appendices

Appendices

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Appendix A-Technical Assessment Team and Chronology of Activities

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Chronology of Activities

4-6 June 1991--Sacramento

The Core Group met to set up a tentative calendar; schedule field trips; identify and schedule needed workshops; assess the information needed from each National Forest, such as maps and other spotted owl data; discuss other needs, such as a reference library and computer hardware and software.

11 June--Sacramento

Arranged for office furnishings and equipment..

- 12 June-Berkeley
Meeting to discuss editorial needs and related matters.
- 18 June-Sacramento
Review of timber sales in planning stage or under contract.
- 24-29 June-First field trip
On-the-ground inspection of California spotted owl habitat and research study areas in the Sierra Nevada, including nesting, roosting and foraging sites. The first two days were spent on the Eldorado National Forest (NF) and Fruit Growers Supply Company's lands; the third day was on the Tahoe NF, taking us to one of our highest elevation nests at 7,000 feet; the fourth day was spent in visiting Sierra Pacific Industries' lands on the Tahoe NF; the fifth day was on the Plumas NF; and the sixth day was spent on the Lassen NF.
- 8-13 July-Second field trip
This week was a continuation of visits to California spotted owl habitat and research study areas. The first day was spent on the Stanislaus NF and Fiberboard Industries' lands; the second day was on the Sierra NF; Sequoia National Park was visited on the third day; the fourth day was spent on Sequoia NF; the fifth and sixth days were spent on the Los Padres NF visiting the southern part and northern part, respectively.
- 22-26 July-Sacramento
The Team invited Forest Biologists and Conservation Biologists to attend up-coming meetings.
- 26 July
Meeting with fire specialists. Informal discussion of fire history and current fuel conditions in the Sierra Nevada and southern chaparral areas.
- 26 July
Meeting to discuss information needs on timber resources.
- 29-30 July-Sacramento
29 July
Met with Sierran Forest Biologists (from the Lassen, Plumas, Tahoe, Eldorado, and Lake Tahoe Basin Management Unit) to apprise them of the September 27-28 Biology Workshop to be held in Sacramento. Additional invitations went to the Sierra, Sequoia, Angeles, San Bernardino, Cleveland, and Los Padres NFs.
- 5-9 August-Sacramento
Technical Assessment Team still contacting people with regard to the upcoming Biology Workshop.
- 5 August
Session with biologists from Tahoe NF.
- 6 August
Meeting with Northern Spotted Owl Recovery Team biologist's subcommittee to review Dr. McKelvey's spatially explicit population simulation model. Recommended structural changes and methods of parameterization.
- 8 August
Mapping session with biologists from the Tahoe NF.
- 9 August
Planning session with cartographers.
- 19-22 August-Third field trip
The first day was spent on the Angeles NF; the San Bernardino NF was visited on the second day; the third day was divided between Mount San Jacinto and Palomar Mountain; and the fourth day was spent on the Cleveland NF in the Laguna Mountains.
- 26-30 August-Sacramento
26 August
Meeting with cartographers to discuss options for producing maps.
- 27-28 August
Biology Workshop with 55 participants from all the NFs in Region 5 to discuss the California spotted owl's current status, habitat use and distribution, and future trends of the owl in each National Forest.
- 30 August
Meeting with Steve Self, Sierra Pacific Industries, Redding, California. Presentation and discussion of Sierra Pacific Industries' owl plan--approach, habitat descriptions, implementation, guidelines, and so on.
- 8-13 September-Sacramento
Formulating working library and gathering data.
- 10 September
Meeting with Jonathan Bart, Northern Spotted Owl Recovery Team Leader, Portland, Oregon. Reviewed recommendations on parameter values for Kevin McKelvey's simulation model.
- 10-11 September
Conservation Biology Workshop with 36 participants from numerous State and Federal agencies, universities, and private industries throughout the U.S.; discussed a variety of issues and concepts from conservation biology as they might relate to planning for the California spotted owl.
- 23-27 September-Sacramento .
25 September
Meeting with History Group to discuss objectives of their contribution to the CASPO report.
- 1 October-Sacramento
Meeting with timber staffs from all Sierran NFs to discuss the kinds of timber inventory information that could be provided, and how soon. Resolved details on instructions to National Forests on maps needed and tabular information to accompany some maps.
- 7-11 October-Sacramento
7 October
Meeting to discuss fuels management.
- 8 October .
Information exchange with representatives of environmental organizations.
- 11 October
Bureau of Land Management presented their potential owl habitat information.
- 12-13 October-Fourth field trip
Team visited Roseburg Resources Company's lands to gain additional firsthand information on owl habitat on industry lands.
- 14-18 October-Sacramento
17 October
Silviculture Workshop; all-day session with 24 agency, academic, and industry silviculturists participating, along with members from the Core Group.
- 28 October-1 November-Sacramento
30 October
Fifth field trip. Visited Michigan-California Timber Company's lands and compared current forests with old, historic photos of forests and land management from the past 80-100 years.
- 4-8 November-Sacramento
Compiling information for library, mapping, and general data.
- 18-22 November-Sacramento
19 November
Meeting with Fuels Management Specialists to have a full review of all habitat photos taken on the field trips. Discussed their use in depicting spotted owl habitat. Also discussed dead-and-downed woody material and forest stands with regard to fire hazards.
- 20 November
Reviewed progress of the History Group. Viewed and picked possible habitat photos for use in Chapter 5.
- 21 November
Met to review cumulative effects analysis used by Region 5 to determine impacts of green timber sales on California spotted owl habitat.
- 2-6 December-Sacramento
2 December
Meeting to discuss ways in which the Technical Assessment Team and the Policy-Implementation Team can interact most efficiently.
- 5 December
Presentation on the influence of fire on forest structure and composition by John Maupin, Fire Management Officer, Plumas NF, Quincy, California.
- 6-10 January 1992-Sacramento
Team working session.

- 20-24 January-Sacramento
Team working session. 24
January
Coordination meeting with Policy-Implementation Team.
- 3-14 February-Sacramento
4 February
Discussion of possible approaches to risk assessment.
- 11 February
Presentation on forest conditions to be expected, over the long-term, if the California Forestry Reform Act of 1992, or something like it, is enacted by the State Legislature.
- 13 February
Briefing for co-chairs of Steering Committee on current status of the Team's discovery process.
- 24-28 February-Sacramento
Team working session.
- 2-6 March-Sacramento
Team working session.
- 9 March-Fresno
Nine of 13 report chapters sent from Fresno to peer reviewers picked by presidents of scientific societies:
- American Ornithologists' Union
Dr. Richard N. Conner, Research Wildlife Biologist, Southern Forest Research Station, USDA Forest Service, Nacogdoches, Texas.
- The Wildlife Society
Dr. David Graber, Research Biologist, Sequoia/Kings Canyon National Parks, Three Rivers, California.
- The Society for Conservation Biology
Dr. Stanley A. Temple, Professor, Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin.
- Ecological Society of America
Dr. Ted Case, Professor, Department of Biological Sciences, University of California, La Jolla, California.
- Society of American Foresters
Dr. Arthur Cooper, Head, Department of Forestry, North Carolina State University, Raleigh, North Carolina.
- 10 March-Arcata
Two additional chapters sent to reviewers.
- 16-18 March-Sacramento
Team working session.
- 23-31 March-Sacramento
Team working on last two chapters of the CASPO report. Vacated Sacramento offices 31 March.
- 1 April-7 May-Fresno and Arcata
Team finishing report with regard to review suggestions and final revisions.
- 8 May-Sacramento
Final report presented to the Steering Committee.

Appendix B-Glossary

Activity center-an area within which an owl or pair of owls finds suitable nesting sites and several suitable roost sites, and in which a substantial amount of their foraging occurs. An activity center can generally be identified by the location of a nest or a primary roost. Other identifiers are recent locations of owls, especially of pairs or reproductive pairs.

Adaptive kernel technique-a method of estimating home-range size in which, first, a bivariate probability distribution is estimated using the observed locations, and then the area of the contour that contains 95 percent of the observed locations is calculated.

Adaptive management-process of implementing policy decisions as scientifically driven management experiments that test predictions and assumptions in management plans.

Algorithm-mathematical rule for solving a problem.

Allee effect-a depression in the encounter rate between males and females resulting from low population densities; the probability of finding a mate drops below that required to maintain the reproductive rates necessary to support the population.

Allowable sale quantity-(ASQ) the maximum quantity of timber that may be sold by a given National Forest from land capable, available, and suitable for timber production for a time period; usually expressed on an average annual basis.

Basal area-the area of the cross-section of a tree stem near its base, generally at breast height and inclusive of bark.

Biological diversity-the variety of life's forms-that is plants, birds, insects, and so on.

Biomass-the total quantity (at any given time) of living organisms of one or more species per unit of space, or of all the species in a biotic community.

Biomass sale-sale of wood fiber such as logging residue (slash), small diameter live trees and cull logs (other than saw logs), for the purpose of energy co-generation or chip production.

Birth-pulse population-a population assumed to produce all of its offspring at an identical, and instantaneous, point during the annual cycle.

Blowdown-trees felled by high winds.

Bonferroni confidence interval-an individual confidence interval constructed about each estimated proportion within a multinomial contingency table. The width of each confidence interval is adjusted downward to account for the estimation of simultaneous intervals.

Bottleneck-see "population bottleneck."

Burning period-the anticipated period of greatest fire activity during a 24-hour period, typically from 1000 until 1800.

Cambium-a layer of formative cells between the wood and bark in woody plants: the cells increase by division and differentiate to form new wood and bark.

Canopy closure-the degree to which the crowns of trees are nearing general contact with one another.

Carrying capacity-the maximum number of animals that can be sustained over the long-term on a specified land area.

Center of activity-owl's nest site or primary roost area.

Checkerboard ownership-a land ownership pattern in which every other section (square mile) is in Federal ownership as a result of Federal land grants to early western railroad companies.

Cohort-individuals all resulting from the same birth-pulse, and thus all of the same age.

Colonization-the act or process of establishing a new colony or population.

Commercial forest land-forest land tentatively suitable for the production of crops of timber and that has not been withdrawn for other reasons.

Confidence interval-a region lying above and below a parameter estimate (for example, the mean) in which the true parameter value is believed to occur with some specified probability.

Connectivity-a measure of the extent to which intervening habitat truly connects habitats for juvenile spotted owls dispersing between them.

Core area-a defined area that includes the center of activity of a pair, including the nest site if known.

Corridor-defined tract of land, usually linear, through which a species must travel to reach habitat suitable for reproduction and other life-sustaining needs.

Cull-a tree that is not healthy (diseased, broken top, stunted, and so on) and is rejected as not being up to standard for regular timber harvest.

D.b.h.-diameter of a tree at breast height, typically measured in inches.

Demographic rescue-see "rescue."

Demographic stochasticity-random fluctuations in birth and death rates.

Density-dependent-process, such as fecundity, whose value depends on the density of animals in the population.

Dispersal-the movement, usually one way, and on any time scale, of plants (seeds) or animals from their point of origin to another location where they subsequently produce offspring.

Dispersal capability-ability of members of a species to move from their area of birth to another suitable location and subsequently to breed.

Dispersal distance-the straight-line distance traveled by an individual from its birth place until it stops dispersing (assumed to be a breeding site) or dies.

Dominant canopy closure (cover)-canopy closure of only the dominant trees in a stand, expressed as a percentage.

Dry ravel-a form of surface erosion in which dry, unconsolidated material moves down slope under the influence of gravity.

Duff-decaying vegetable matter that forms a layer on the forest floor.

Eastside pine forest-general name for a habitat type occurring generally east of the Sierran crest. It is dominated by ponderosa and/or Jeffrey pine.

Ecological integrity-the condition in which all key components of an ecological system are intact and functioning normally.

Ecotone-contact zone between two plant communities, where elements of each intermingle.

Edge effects-differences in microclimate, flora, fauna, stand structure, habitat values, stand integrity (including resistance to being blown down by high winds) that occurs in or as a result of a transition zone where two plant communities or successional stages come together.

Emigration-permanent movement of individuals of a species from a population.

Environmental stochasticity-random variation in environmental attributes such as temperature, precipitation, and fire frequency.

Epigeous fungi-above-ground fruiting bodies of fungi, in the form of mushrooms; these make up part of the diet of spotted owl prey.

Even-aged forest-a forest stand composed of trees with less than a 20-year difference in age between the oldest and youngest.

Extinction rate-the number of elements (individuals, populations, species) lost per unit of time.

Extinction time-predicted period of time for a population to become extinct.

Fecundity-the number of young per breeding-age female. In model formulations, fecundity usually refers to the number of female young per breeding-age female, calculated by assuming a 1:1 sex ratio.

Fire regime-a description of the frequency, severity, and extent of fires that occur in an area.

Floaters-nonbreeding adults and subadults that move and live within a breeding population, often replacing breeding adults that die; nonterritorial individuals.

Foothill riparian/hardwood forest-general name for a habitat type occurring at low elevations in the Sierran foothills. It includes stands of hardwoods immediately adjacent to streams, as well as dense stands of hardwood forests on the adjoining slopes. Tree species along streams include cottonwood, California sycamore, interior live oak, California buckeye, Oregon ash, and occasionally white alder. Tree species on the adjoining slopes include blue oak, interior live oak, and digger pine.

Forest landscape-land presently forested or formerly forested and not currently developed for nonforest use.

Fragmentation-process of reducing the size and continuity of patches of habitat; specifically in this document, fragmentation is used in reference to forests.

Fuel ladder-dead or living fuels that connect surface fuels to tree or brush foliage and promote spread of fire from ground to vegetation crowns.

Fuel loading-the amount of combustible material present per unit area, usually expressed in tons per acre.

Fuels-combustible materials.

Gene flow-movement of genetic material between populations.

Genetic stochasticity-random changes in gene frequencies from such factors as inbreeding.

Genetic variability-the number of different genes possessed by an individual or population.

Habitat capability-capacity of a habitat to support an estimated number of pairs of a species.

Habitat Conservation Area-(as proposed by the ISC), a contiguous block of habitat to be managed and conserved for breeding pairs, connectivity, and distribution of owls; application may vary throughout the range according to local conditions.

Habitat fragmentation-see "fragmentation."

Habitat mosaic-the mix of habitat conditions across a landscape.

Home range-the area to which the activities of an animal are confined during a defined period of time.

Home range of a pair-the sum of the home ranges of each member of a pair, minus the area of home-range overlap.

Home-range overlap-percentages of the home ranges of two individuals that are shared between them.

Hypogeous fungi-below-ground fruiting bodies of fungi, known as true and false truffles; these are an important part of the flying squirrel's diet.

Initial attack-first action taken to suppress a wildfire, via ground or air.

Interbirth interval-the interval between birth pulses.

Internal recruitment-addition of new breeding individuals to a local population that were born within that same population.

Lambda-the finite rate of population change (population size in year 2 divided by the population size in year 1).

Land Management Plan-a plan written for the management of a National Forest unit, as directed by regulations of the National Forest Management Act of 1976, in which the integrated management of all major resources has been determined through an interdisciplinary team process.

Lands not suited for timber production-lands incapable of producing 20 cubic feet of wood fiber per acre per year, or lands withdrawn from commercial forest harvest for other reasons (see reserved lands).

Lands suited for timber production-commercial forest land identified as appropriate for timber production.

Large sawtimber-forest stands that are characterized by trees that are ≥ 21 inches in d.b.h.

Late seral stage forest-near-final stage in development of a forest from grasses and forbs, through shrubs, small trees, and finally to large, old trees.

Leave strips-generally narrow bands of forest trees that are left along streams and rivers to buffer aquatic habitats from upslope forest management activities.

Lefkovich matrix-a two-dimensional array of numbers whose entries represent stage-specific estimates of demographic (birth and death) rates. The matrix is used to project population stage structures through time.

Legacy-remnant trees of original forest stands, both alive and dead.

Leslie matrix-a two-dimensional array of numbers whose entries represent the age-specific estimates of demographic (birth and death) rates. The matrix is used to project population age structures through time.

Life table-mathematical table illustrating the age-specific birth and death rates of a population.

Linear model-a combination of random variables, none of which has exponents that differ from 1.0.

Linear regression model-an equation that explains some amount of the variation in a dependent variable with a linear combination of one or more independent variables.

Live oak/bigcone Douglas-fir forest-general name for a habitat type that occurs in a narrow band, mostly at mid-elevations, in mountains of all four NFs in southern California. Dominant tree species are canyon live oak, coast live oak, and bigcone Douglas-fir.

Locus-the point (for example, along an axis of a graph) at which the shape of a mathematical function changes dramatically.

Long term-here, 50 to 100 years and sometimes beyond.

M2G, M3G, M3N, M3P, M4G, M4N, M4P, M5G, M5N, M6-see timber strata.

Managed forest-forest land that is harvested on a scheduled basis and contributes to an allowable sale quantity.

Medium sawtimber-forest stands that are characterized by trees that are 11-20.9 inches in d.b.h.

Metapopulation-a population comprised of a set of isolated subpopulations that are "linked" by the dispersal of individuals, allowing for recolonization of unoccupied habitat patches after local extinction events.

Mesic-moderately moist, in referring to habitats.

Microenvironment-the sum total of all the external conditions in a small or restricted area that may influence organisms.

Microhabitats-a restricted set of distinctive environmental conditions that constitute a small habitat, such as the area under a log.

Minimum convex polygon technique-a method of estimating home-range size in which the smallest possible convex polygon is drawn around the outermost locations where an animal was observed; the area within the polygon is then calculated.

Mixed-conifer forest-general name for similar habitat types in the Sierra Nevada and southern California. It is the predominant timber-producing forest of the Sierra Nevada, consisting of various mixtures of white fir, ponderosa pine (at lower elevations), incense-cedar, sugar pine, black oak, and red fir (at higher elevations). Douglas-fir is an important component from Yosemite NP northward, and giant sequoia occurs in widely scattered localities. In southern California, this type is best developed at relatively high elevations in the San Gabriel and San Bernardino Mountains, and on Mount San Jacinto. Species composition is similar to that of Sierran mixed-conifer, although Coulter pine occurs, bigcone Douglas-fir occasionally occurs at lower elevations; but red fir, Douglas-fir, and giant sequoia are missing.

Mixed-evergreen forest-a forest community that is dominated by two or more species of broad-leaved hardwoods whose foliage persists for several years; important western species include madrone, tanoak, chinquapin, canyon live oak, and California-laurel.

Model-an idealized representation of reality developed to describe, analyze, or understand the behavior of some aspect of it; a mathematical representation of the relationships under study.

Monitoring-a process of collecting information to evaluate whether or not objectives of a management plan are being realized.

Monitoring program-see "monitoring"; the program used to monitor a population and its habitat.

Natal cluster-a group of adjacent animal territories, in one of which an individual was born.

Network-a particular spatial arrangement of entities (blocks or patches of owl habitat in this case) that are interconnected in some fashion (by dispersal of owls in this case).

Null hypothesis-a supposition of no difference between test comparisons (situation A no different from situation B).

Old growth-forest stand with moderate to high canopy closure; a multilayered, multispecies canopy dominated by large overstory trees; a high incidence of large trees with large, broken tops, and other indications of decadence; numerous large snags; and heavy accumulations of logs and other woody debris on the ground.

Owl site-an area of unspecified dimensions where a single owl or a pair of owls has been located, usually repeatedly. In demographic and radio-tracking study areas, where efforts to locate all owls are more intense than elsewhere, most owl sites with single owls have eventually been found to have a pair. All owl sites have been mapped and given unique spatial references, so they can be tallied. Designation of an owl site makes no assumption about home-range or territory boundaries of the owls, although usually a center of activity can be identified by the location of a nest or a primary roosting area. The terms "owl site" and "site" are general and often used generically to refer to home ranges, territories, or to sites designated by agencies for special owl management.

Owl use area-an irregularly shaped polygon that contains a known or predicted activity center and encompasses the amount of nesting and foraging habitats typically found within home ranges during the breeding season.

Pair site-an area of variable dimensions on the landscape assumed to be large enough to have an amount of habitat capable of supporting one pair of spotted owls; see "owl site."

Paradigm-an underlying model or representation that characterizes a process.

Physiographic province-a geographic region in which climate and geology have given rise to a distinct array of land forms and habitats.

Ponderosa pine/hardwood forest-(montane hardwood) general name for a habitat type that blends with the upper portion of the foothill riparian/hardwood forest. In the southern Sierra Nevada, ponderosa pine at its lowest elevation generally occurs with interior live oak, canyon live oak, and black oak, with incense-cedar and white fir coming into stands at slightly higher elevations. In the northern Sierra Nevada, tanoak and Pacific madrone commonly contribute to the hardwood component of this type.

Population-a collection of individuals that share a common gene pool through interbreeding.

Population bottleneck-the phenomenon experienced by a small population that is susceptible to the deleterious effects of demographic and genetic stochasticity; also a zone of constriction in the distribution of a population.

Population density-number of individuals of a species per unit area.

Population persistence-general term for the capacity of a population to maintain sufficient numbers and distribution over time.

Population viability-probability that a population will persist for a specified period of time across its range, despite normal fluctuations in population and environmental conditions.

Potential habitat-(1) habitat that has been altered (for example, logged or burned) and is not presently suitable for owls but is believed to have the potential to regenerate into suitable habitat; (2) unsurveyed habitat that appears to be suitable based on comparisons with habitat elsewhere that has known owl sites.

Power analysis-a statistical method for estimating the probability of making a type-II error (failure to detect a difference or a trend that actually occurs, such as a decline in a population of spotted owls).

R3G, R3N, R3P, R4G, R4N-see timber strata.

Red fir forest-general name for a habitat type that blends with the higher portions of Sierran mixed-conifer forest. It is dominated by red fir, with increasing amounts of white fir at lower elevations until it becomes mixed-conifer forest. At upper elevations it often includes some lodgepole pine and occasionally quaking aspen.

Redwood/California-laurel forest-general name for a habitat type that is restricted to the central coast range, where coast redwood, California-laurel, tanoak, Pacific madrone, red and white alder, coast live oak, Santa Lucia fir, and bigleaf maple form various mixtures.

Regulated forest-theoretical managed forest from which the same acreage of trees can be removed annually, in perpetuity.

Rescue (rescue effect)-periodic immigration of new individuals sufficient to maintain a population that might otherwise decline toward extinction.

Reserved land-Federal lands unavailable for timber yield or management due to being a National Park or classified as a Wilderness Area in a National Forest.

Reserves-tracts of forest temporarily or permanently set aside from logging.

Restricted harvest-land either withdrawn from logging or where timber production is limited to less than clearcutting.

Riparian/hardwood forest-general name for a habitat type that varies considerably in different parts of southern California. In deep canyons in the Los Padres NF, for example, it occurs in narrow strips adjacent to permanent or near-permanent streams. Common tree species include coast live oak (near coast), canyon live oak (interior locations), California sycamore, white alder, California-laurel, and cottonwood. In shallower canyons in the Cleveland NF, these forests may consist almost exclusively of coast live oak.

Rotation-the planned number of years between the regeneration of an even-aged stand and its final cutting at a specified stage.

Saw kerf-the cut or channel made by a saw.

Scansorial-adapted for climbing.

Search capability-the ability of a dispersing juvenile or adult owl to locate suitable habitat.

Search efficiency-proportion of dispersing juveniles or adults that locate minimally suitable habitat before they die.

Search time-number of days required for an average dispersing individual to locate suitable or better habitat.

Seed-tree cut-an even-aged regeneration cutting in which only a few seed trees per acre (fewer than for a shelterwood cut) are retained until after new tree seedlings are established.

Senescence-state of being old; characterized by having attributes associated with old age.

Sensitivity coefficient-term that measures relative degree of change in outcome of a mathematical expression or equation after a specified change in an individual component.

Shelterwood cut-an even-aged regeneration cutting in which new tree seedlings are established under the partial shelter of seed trees.

Short term-here, 1 to 50 years.

Sink-population whose average reproductive rate is less than its average rate of mortality; area that attracts immigrants not expected to contribute significantly to future populations (see "source").

Site-an area considered from the standpoint of its use for some specified purpose (for example, habitat studies, owl locations-see "owl site," and logging operation).

Small sawtimber-forest stands that are characterized by trees that are <11 inches in d.b.h.

Snag-standing dead tree.

Source-an actively breeding population that has an average birth rate that exceeds its average death rate; produces an excess number of juveniles that may disperse to other areas.

Standards and guidelines-directions generated and followed in management plans.

Stochastic-random, uncertain; involving a random variable.

Stochastic fecundity-random fluctuation in a population's rate of producing offspring.

Subpopulation-a well-defined set of interacting individuals that comprise a proportion of a larger, interbreeding population.

Suitable habitat-here, an area of forest vegetation with the age-class, species of trees, structure, sufficient area, and adequate food source to meet some or all of the life needs of a California spotted owl.

Sustained yield or production-the amount of timber that a forest can produce continuously from a given intensity of management; implies continuous production; a primary goal is to achieve a balance between incremental growth and cutting.

Synoptic weather pattern-large-scale weather pattern.

Territory-the area that an animal defends, usually during the breeding season, against intruders of its own species.

Threshold phenomenon-a pattern or trend, as in population growth rate, that exhibits relatively long periods of slow change followed by precipitous increase or decrease in response to a slight change in an environmental gradient.

Timber strata-M = mixed conifer, R = red fir, P = ponderosa pine; 2 = trees <12 inches in d.b.h., 3 = trees 12-23.9 inches in d.b.h., 4 = trees ≥24 inches in d.b.h.; G = good canopy cover (70+ percent), N = normal canopy cover (40-69 percent), P = poor canopy cover (0-39 percent). Hence, an M4G stand is mixed-conifer with trees ≥24 inches in d.b.h., and canopy cover ≥70 percent; an R2P stand is red fir with trees <12 inches in d.b.h., and 0-39 percent canopy cover.

Torpid-having lost temporarily all or part of the power of sensation or motion, as a hibernating animal.

Total canopy closure (cover)-canopy cover by all vegetation 7 feet or higher above the ground, expressed as a percentage.

Truffles-the below-ground fruiting bodies of hypogeous fungi, which are a major food source for flying squirrels and other small mammals.

Turnover-a term in population analysis that indicates the rate or number of identifiable adults that die and are replaced during a specified period.

Type conversion-conversion of an area from one habitat type to another, such as oak woodland to annual grassland.

Type-I error-statistical term for the error made when a null hypothesis that is true is rejected; for example, concluding that a difference exists between two populations that are identical.

Type-II error-statistical term for the error that is made when a null hypothesis that is false is not rejected; that is, concluding that no difference exists in a comparison between two populations when a difference does exist.

Variance-a statistical term that indicates a measure of variability within a finite population of a sample; the total of the squared deviations of each observation from the arithmetical mean divided by one less than the total number of observations.

Viability-ability of a population to maintain sufficient size so that it persists over time, in spite of normal fluctuations in numbers; usually expressed as a probability of maintaining a specific population for a specified period.

Vital rates-collective term for the age-specific birth and death rates of a population.

Windthrow-a tree or group of trees uprooted by the wind.

Xeric-dry, in referring to habitats.

Appendix C-Species List

Common Name	Scientific name
Lower Plants	
Algae	Division Chlorophyta (various species)
Fungi, epigeous	Divisions Ascomycota and Basidiomycota.
	Common genera in the Sierra Nevada include <i>Boletus</i> , <i>Amanita</i> , <i>Cortinarius</i> , and <i>Armillaria</i>
Fungi, hypogeous	Divisions Ascomycota and Basidiomycota.
	Common genera in the Sierra Nevada include <i>Rhizopogon</i> , <i>Gautieria</i> , <i>Geopora</i> , <i>Melanogaster</i> , and <i>Hymenogaster</i>
Lichens	Division Ascomycota (various species)
Chartreuse	<i>Letharia vulpina</i>
Hair	<i>Bryoria fremontii</i>
Staghorn	<i>Usnea ceratina</i>
Moss	Division Bryophyta, Class Muscopsida, (various species)

Grasses/Forbs

Bitterroot, meadow	<i>Lewisia nevadensis</i>
Brodiaea, golden	<i>Brodiaea lutea</i>
Buckwheat, California	<i>Eriogonum fasciculatum</i>
Chinese nests	<i>Collinsia concolor</i>
Grass	<i>Gramineae</i> spp.
Lupine, broad-leaf	<i>Lupinus latifolius</i>
Trefoil (bird's foot)	<i>Lotus</i> spp.

Shrubs

Blackberry, California	<i>Rubus ursinus</i>
Buckbrush	<i>Ceanothus cuneatus</i>
Buckeye, California	<i>Aesculus californica</i>
Ceanothus	<i>Ceanothus</i> spp.
Chamise	<i>Adenostoma fasciculatum</i>
Cherry, hollyleaf	<i>Prunus ilicifolia</i>
Chinquapin, golden	<i>Castanopsis sempervirens</i>
Chokecherry	<i>Prunus virginiana</i>
Coffeeberry, California	<i>Rhamnus californica</i>
Currants	<i>Ribes</i> spp.
Deerbrush	<i>Ceanothus integerrimus</i>
Elderberry	<i>Sambucus</i> spp.
Gooseberry, rock	<i>Ribes quercetorum</i>
Hazel, California	<i>Corylus cornuta</i> var. <i>californica</i> (Hazelnut)
Jim brush	<i>Ceanothus sorediatus</i>
Juniper, mountain	<i>Juniperus communis</i> var. <i>saxatilis</i>

Common Name	Scientific name
Shrubs	
Manzanita	<i>Arctostaphylos</i> spp.
Mountain mahogany,	<i>Cercocarpus ledifolius</i> curlleaf
Poison oak	<i>Rhus diversiloba</i>
Rose, California wild	<i>Rosa californica</i>
Sage, coastal	<i>Artemisia californica</i>
Sage, White	<i>Salvia apiana</i>
Sagebrush, big	<i>Artemisia tridentata</i>
Sagebrush, California	<i>Artemisia californica</i>
Serviceberry, western	<i>Amelanchier alnifolia</i>
Sumac, lemonade	<i>Rhus integrifolia</i>
Toyon	<i>Heteromeles arbutifolia</i>
Whitethorn, mountain	<i>Ceanothus cordulatus</i>
Willows	<i>Salix</i> spp.
Yerba-Santa	<i>Eriodictyon</i> spp.
Yucca	<i>Yucca whipplei</i>
Other	
Mistletoes, dwarf	<i>Arceuthobium</i> spp.
Trees	
Alder, red	<i>Alnus rubra</i>
Alder, white	<i>Alnus rhombifolia</i>
Ash, Oregon	<i>Fraxinus latifolia</i>
Aspen, quaking	<i>Populus tremuloides</i>
Boxelder, California	<i>Acer negundo</i>
Buckeye, California	<i>Aesculus californica</i>
California-laurel (bay)	<i>Umbellularia californica</i>
Cedar, incense -	<i>Libocedrus decurrens</i>
Chinquapin, giant	<i>Castanopsis chrysophylla</i>
Cottonwood	<i>Populus</i> spp.
Dogwood, Pacific	<i>Cornus nuttallii</i>
Douglas-fir	<i>Pseudotsuga menziesii</i>
Douglas-fir, bigcone	<i>Pseudotsuga macrocarpa</i>
Fir, red (Shasta)	<i>Abies magnifica</i>
Fir, Santa Lucia	<i>Abies bracteata</i>
Fir, white	<i>Abies concolor</i>
Hazelnut, California	<i>Corylus cornuta</i> var. <i>californica</i> (hazel)
Hemlock, mountain	<i>Tsuga mertensiana</i> (black)
Incense-cedar	<i>Libocedrus decurrens</i>
Juniper, California	<i>Juniperus californica</i>
Juniper, western	<i>Juniperus occidentalis</i> , <i>J. australis</i>
Laurel, California- (bay)	<i>Umbellularia californica</i>
Madrone, Pacific	<i>Arbutus menziesii</i>

Common Name	Scientific name
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Trees

Maple, bigleaf	<i>Acer macrophyllum</i>
Oak, black	<i>Quercus kelloggii</i>
Oak, blue	<i>Quercus douglasii</i>
Oak, California scrub	<i>Quercus dumosa</i>
Oak, canyon live	<i>Quercus chrysolepis</i>
Oak, coast live	<i>Quercus agrifolia</i>
Oak, interior live	<i>Quercus wislizenii</i>
Oak, shrub live	<i>Quercus turbinella</i>
Oak, valley	<i>Quercus lobata</i>
Pine, Coulter	<i>Pinus coulteri</i>
Pine, digger	<i>Pinus sabiniana</i>
Pine, foxtail	<i>Pinus balfouriana</i>
Pine, Jeffrey	<i>Pinus jeffreyi</i>
Pine, lodgepole	<i>Pinus contorta</i>
Pine, pinyon	<i>Pinus monophylla</i>
Pine, ponderosa	<i>Pinus ponderosa</i>
(yellow)	
Pine, sugar	<i>Pinus lambertiana</i>
Pine, western white	<i>Pinus monticola</i>
Redwood (coast)	<i>Sequoia sempervirens</i>
Sequoia, giant	<i>Sequoiadendron giganteum</i>
Sycamore, California	<i>Platanus racemosa</i>
Tanoak	<i>Lithocarpus densiflorus</i>
Willows	<i>Salix</i> spp.

Invertebrates

Beetle, bark	<i>Dendroctonus</i> spp., <i>Ips</i> spp., <i>Scolytus</i> spp.
Beetle, fir engraver	<i>Scolytus ventralis</i>
Beetle, June	<i>Ploecoma hoppingi</i>
Cricketer	<i>Gryllus</i> spp.
Fly, hippoboscids	<i>Icosta americana</i> , <i>Ornithomya anchineuria</i>
Worm, flat	<i>Cestoda</i>
Worm, round	<i>Nematoda</i>
Worm, spiny-headed	<i>Acanthocephala</i>

Birds

Goshawk	<i>Accipiter gentilis</i>
Hawk, Cooper's	<i>Accipiter cooperi</i>
Hawk, red-tailed	<i>Buteo jamaicensis</i>
Hawk, sharp-shinned	<i>Accipiter striatus</i>
Mallard	<i>Anas platyrhynchos</i>
Owl, barn (common)	<i>Tyto alba</i>
Owl, barred	<i>Strix varia</i>
Owl, boreal (Tengmalm's)	<i>Aegolius funereus</i>

Common Name	Scientific name
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Birds

Owl, California spotted	<i>Strix occidentalis occidentalis</i>
Owl, eagle	<i>Bubo bubo</i>
Owl, great gray	<i>Strix nebulosa</i>
Owl, great horned	<i>Bubo virginianus</i>
Owl, long-eared	<i>Asio otus</i>
Owl, Mexican spotted	<i>Strix occidentalis lucida</i>
Owl, northern hawk	<i>Surnia ulula</i>
Owl, northern spotted	<i>Strix occidentalis caurina</i>
Owl, pygmy (Eurasian)	<i>Glaucidium passerinum</i>
Owl, short-eared	<i>Asio flammeus</i>
Owl, snowy	<i>Nyctea scandiaca</i>
Owl, tawny	<i>Strix aluco</i>
Owl, ural	<i>Strix uralensis</i>
Partridge, gray	<i>Perdix perdix</i>
Raven	<i>Corvus corax</i>
Sparrowhawk (Eurasian)	<i>Accipiter nisus</i>
Woodpecker, acorn	<i>Melanerpes formicivorus</i>
Woodpecker, red-cockaded	<i>Picoides borealis</i>

Mammals

Bats	<i>Chimera</i>
Chipmunk	<i>Eutamias</i> spp.
Gopher, Great Basin pocket	<i>Thomomys talpoides</i>
Gopher, mountain pocket	<i>Thomomys monticola</i>
Gopher, southwestern pocket	<i>Thomomys bottae</i>
Mole	<i>Scapanus</i> spp.
Mouse, brush	<i>Peromyscus boylii</i>
Mouse, cactus	<i>Peromyscus eremicus</i>
Mouse, California	<i>Peromyscus californicus</i>
Mouse, California pocket	<i>Perognathus californicus</i>
Mouse, deer	<i>Peromyscus maniculatus</i>
Mouse, house	<i>Mus musculus</i>
Mouse, pinyon	<i>Peromyscus truei</i>
Mouse, western harvest	<i>Reithrodontomys megalotis</i>
Mouse, western jumping	<i>Zapus princeps</i>
Mouse, white-footed	<i>Peromyscus</i> spp.
Pika	<i>Ochotona princeps</i>
Rabbit	<i>Sylvilagus</i> spp.
Rabbit, brush	<i>Sylvilagus bachmani</i>
Rabbit, cottontail	<i>Sylvilagus audubonii</i>
Shrew	<i>Sorex</i> spp.
Squirrel, ground	<i>Spermophilus</i> spp.
California	<i>Spermophilus beecheyi</i>
Golden-mantled	<i>Spermophilus lateralis</i>

Common Name	Scientific name
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Mammals

Squirrel, northern flying	<i>Glaucomys sabrinus</i>
Squirrel, southern flying	<i>Glaucomys volans</i>
Squirrel, tree	<i>Sciurus</i> spp.
Vole	<i>Microtus</i> spp.
Vole, California	<i>Microtus californicus</i>
Vole, long-tailed	<i>Microtus longicaudus</i>
Woodrat	<i>Neotoma</i> spp.
Woodrat, bushy-tailed	<i>Neotoma cinerea</i>
Woodrat, desert	<i>Neotoma lepida</i>
Woodrat, dusky-footed	<i>Neotoma fuscipes</i>

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The Pacific Southwest Research Station

- Represents the research branch of the Forest Service in California, Hawaii, American Samoa and the western Pacific.

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Color Photo Section

Habitat from throughout the
range of the California
spotted owl

5-1-Foraging habitat. Note the extensive downed wood and abundant staghorn lichen on tree trunks. Dominant trees, in order, were red fir, white fir, and Jeffrey pine; some sugar pines were present but not visible in the photo.

Habitat type: -----Sierran Red Fir
Location: -----Lassen National Forest
Elevation: -----6,170 feet
Date: -----24 June 1991
Photographer: -----John S. Senser

5-2-Typical red fir canopy. This site was occupied by owls 5 of the 6 years surveyed, 3 of these years by pairs.

Habitat type: -----Sierran Red Fir
Location: -----Eldorado National Forest
Elevation: -----6,000 feet
Date: -----24 June 1991
Photographer: -----John S. Senser



5-3-Probable nest tree with adult and two juvenile owls. The nest may have been the cavity in the bole of the tree, above the owls.

Habitat type: -----Sierran Red Fir
Location: -----Tahoe National Forest
Elevation: -----7,000 feet
Date: -----26 June 1991
Photographer: -----John S. Senser

5-4-The forest floor in a foraging area showing a thick mat of decomposing organic matter. The fallen trees progress from recognizable trunks (background) to a spongy mass of organic matter (foreground).

Habitat type: -----Sierran Red Fir
Location: -----Lassen National Forest
Elevation: -----6,170 feet
Date: -----29 June 1991
Photographer: -----John S. Senser



5-5—A foraging habitat in red and white fir showing the multi-storied nature of the stand and the presence of natural snags (left center).

Habitat type: ----- Sierran Red Fir
 Location: ----- Tahoe National Forest
 Elevation: ----- 6,800 feet
 Date: ----- 26 June 1991
 Photographer: ----- John S. Senser

5-6—Mixed-conifer canopy 50 feet north of a spotted owl nest site in the cavity of a giant sequoia. Trees represented here were white fir, sugar pine, and giant sequoia.

Habitat type: ----- Sierran Mixed-conifer
 Location: ----- Sequoia National Park
 Elevation: ----- 6,200 feet
 Date: ----- 10 July 1991
 Photographer: ----- John S. Senser



5-7-Ground litter 100 feet east of a nest tree. Observe the extensive decomposing deadwood, which may provide shelter and nurture food resources (such as hypogeous fungi) for the owl's prey.

Habitat type: -----Sierran Mixed-conifer
Location: -----Sequoia National Park
Elevation: -----7,000 feet
Date: -----10 July 1991
Photographer: -----John S. Senser

5-8-Nest snag. Overstory canopy cover around the nest was about 30 percent, and about 40 percent in the surrounding forest. The pair at this site produced two young in 1991; they were found roosting nearby in a dense stand of ponderosa pine and incense-cedar. The area was logged for large pines during the railroad logging era of the 1920s, selectively cut in 1980, and re-entered for additional salvage logging in 1989 and 1990. Today, the forest is composed mostly of a mosaic of height classes and trees not more than 70 years old (with scattered 120-year-olds).

Habitat type: -----Sierran Mixed-conifer
Location: -----Fiberboard Timber Company
(within Stanislaus National Forest)
Elevation: -----4,400 feet
Date: -----8 July 1991
Photographer: -----John S. Senser

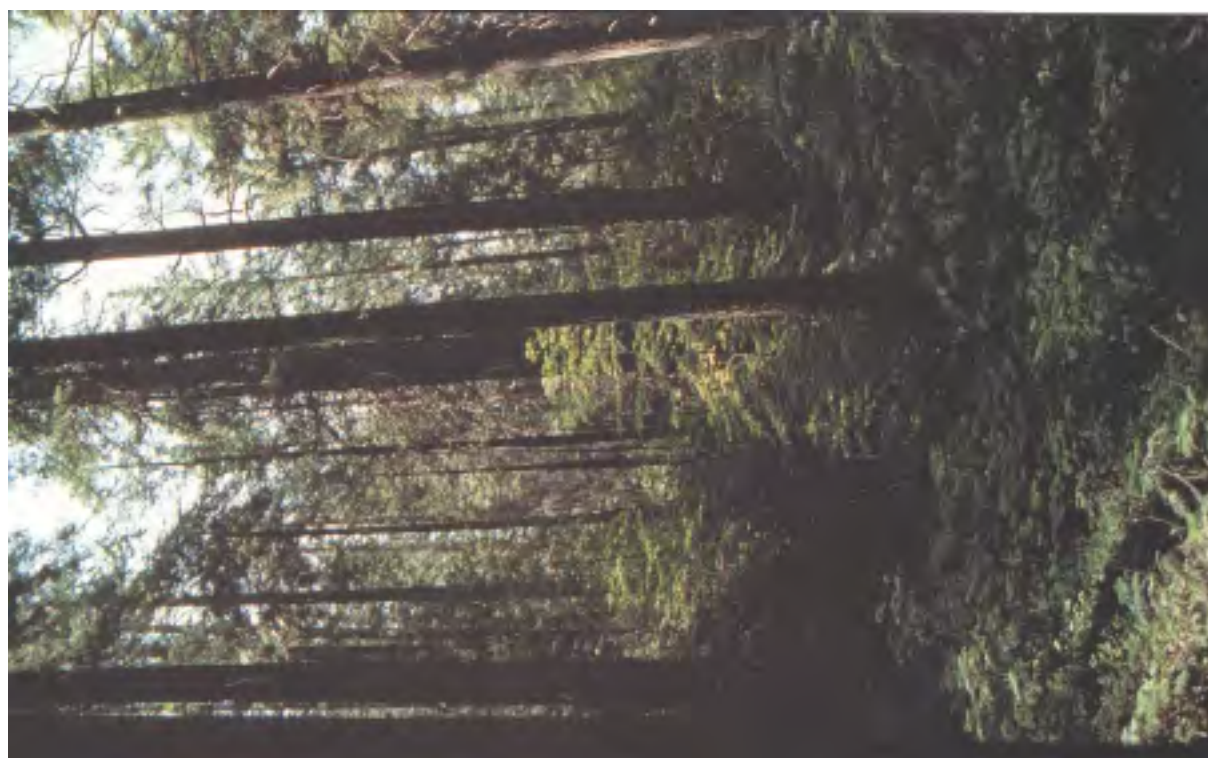


5-9—Foraging area in a site where owl young were produced in 1990 and 1991. This site was mainly white fir with a crown closure of 70 percent and a dense understory of Pacific dogwood and California hazelnut.

Habitat type: ----- Sierran Mixed-conifer
 Location: ----- Sequoia National Park
 Elevation: ----- 5,000 feet
 Date: ----- 10 July 1991
 Photographer: ----- John S. Senser

5-10—Foraging habitat composed of dispersed, large ponderosa pines and a dense understory of white fir and Douglas-fir saplings and pole-sized trees. Note extensive downed wood and forest litter.

Habitat type: ----- Sierran Mixed-conifer
 Location: ----- Eldorado National Forest
 Elevation: ----- 2,800 feet
 Date: ----- 24 June 1991
 Photographer: ----- John S. Senser



5-11—Adult spotted owl at roost in a mixed-conifer stand of white fir and incense-cedar, with a thick understory of Pacific dogwood.

Habitat type: -----Sierran Mixed-conifer
Location: -----Eldorado National Forest
Elevation: -----4,300 feet
Date: -----24 June 1991
Photographer: -----John S. Senser

5-12—Nest stand of mixed-conifer showing canopy of white fir, Douglas-fir, and incense-cedar. The nest cavity is about half way up the center incense-cedar. This site has high fidelity by spotted owls, with pair occupancy for the last 6 years of survey.

Habitat type: -----Sierran Mixed-conifer
Location: -----Eldorado National Forest
Elevation: -----4,300 feet
Date: -----24 June 1991
Photographer: -----John S. Senser





5-15—Foraging area showing a mixture of conifers (mostly Douglas-fir) and black oak.

Habitat type: ----- Sierran Conifer/Hardwood
Location: ----- Eldorado National Forest
Elevation: ----- 3,200 feet
Date: ----- 25 June 1991
Photographer: ----- John S. Senser

5-16—This area was logged during the railroad logging era of the 1920s and selectively cut since. The oldest conifers are 70-120 years old. The photo shows a foraging area in a mixture of conifers (mostly white fir and sugar pine) with black oak. Note the multi-storied nature of the stand and the ground cover of broad-leaf lupine in the foreground.

Habitat type: ----- Sierran Conifer/Hardwood
Location: ----- Stanislaus National Forest
Elevation: ----- 3,700 feet
Date: ----- 8 July 1991
Photographer: ----- John S. Senser

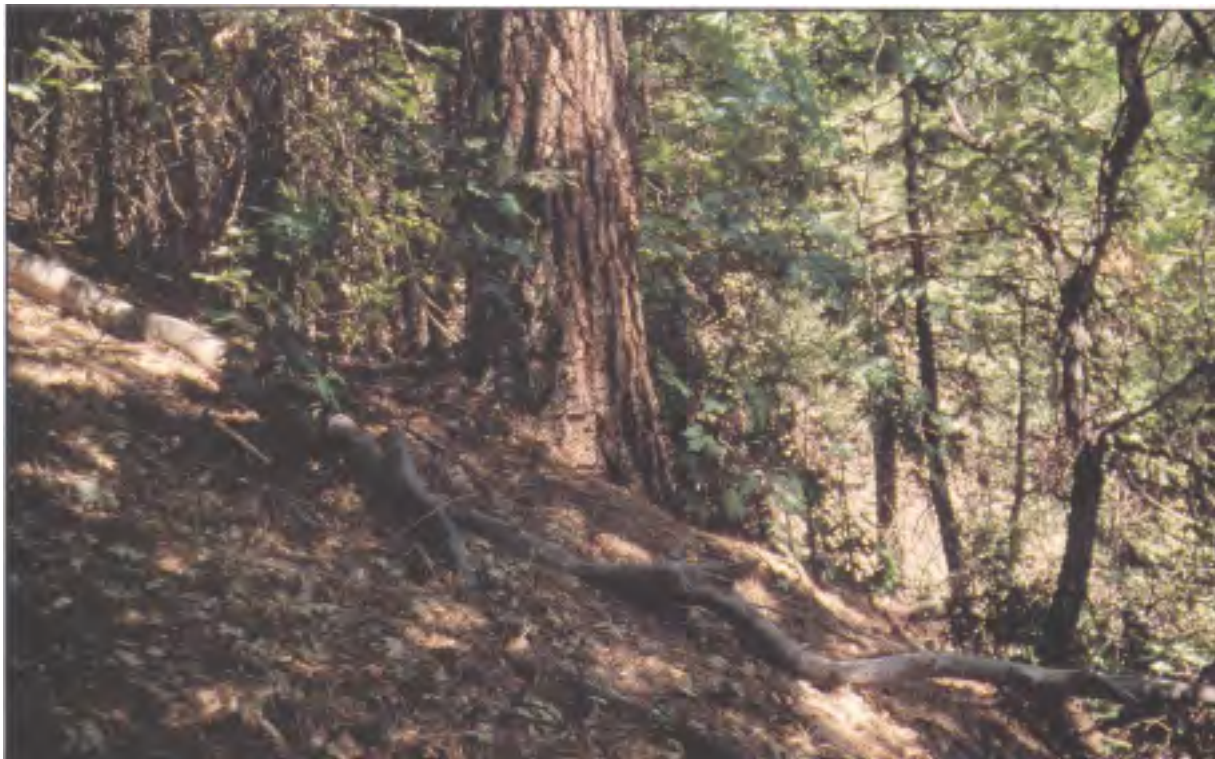


5-17-Canopy typical of the Sierran Conifer/Hardwood type, showing a 60-70 percent closure of white fir and black oak.

Habitat type: -----Sierran Conifer/Hardwood
Location: -----Stanislaus National Forest
Elevation: -----3,700 feet
Date: -----8 July 1991
Photographer: -----John S. Senser

5-18-Ground cover 30 feet west of a nest tree, showing a dense understory of bigleaf maple and conifer saplings. Note the extensive layer of needle/cone litter and presence of large downed limbs, such as the black oak limbs seen here.

Habitat type: -----Sierran Conifer/Hardwood
Location: -----Eldorado National Forest
Elevation: -----4,200 feet
Date: -----25 June 1991
Photographer: -----John S. Senser



5-19—Black oak nest tree in 1991 (to left of group). The nest was in a cavity in one of the large limbs.

Habitat type: -----Sierran Conifer/Hardwood
 Location: -----Fiberboard Timber Company
 (within Stanislaus National Forest)
 Elevation: -----4,400 feet
 Date: -----8 July 1991
 Photographer: -----John S. Senger

5-20—Tanoak nest tree in 1991. Note extensive understory of young pines, Pacific madrone, and tanoak. This area has seen considerable disruption in the past 100 years. At least three fires and extensive mining have impacted this habitat.

Habitat type: -----Sierran Conifer/Hardwood
 Location: -----Plumas National Forest
 Elevation: -----2,880 feet
 Date: -----20 June 1991
 Photographer: -----John S. Senger

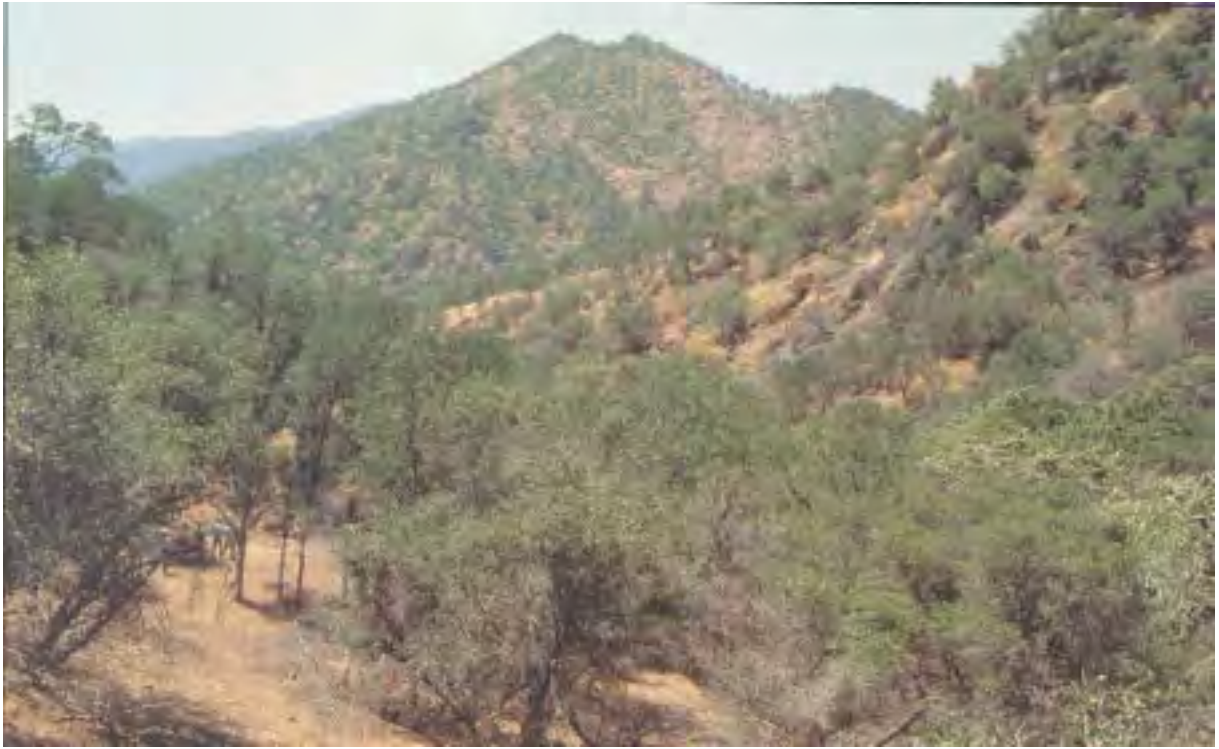


5-21-Overview of owl foraging habitat showing the live oaks that are typical of the area.

Habitat type: -----Sierran Foothill Hardwood
Location: -----Sierra National Forest
Elevation: -----1,360 feet
Date: -----9 July 1991
Photographer: -----John S. Senser

5-22-Roost area in a streamside location. The photo shows dense stands of California sycamore and live oak. A roosting owl is visible on a limb in the upper-center of the photo. Nearby Cooper's hawk nests in canopies of interior live oaks provided nesting platforms in 1989 and 1990.

Habitat type: -----Sierran Foothill Hardwood
Location: -----Sierra National Forest
Elevation: -----1,360 feet
Date: -----9 July 1991
Photographer: -----John S. Senser



5-23—Owl wintering site in interior live oak habitat. Note the abundance of downed wood. Researcher Barry Noon is examining a woodrat nest in the live oak canopy.

Habitat type: -----Sierran Foothill Hardwood
 Location: -----Sierra National Forest
 Elevation: -----1,000 feet
 Date: -----9 July 1991
 Photographer: -----John S. Senser

5-24—Interior live oak canopy at owl wintering site. Observe woodrat nest in canopy (right center).

Habitat type: -----Sierran Foothill Hardwood
 Location: -----Sierra National Forest
 Elevation: -----1,000 feet
 Date: -----9 July 1991
 Photographer: -----John S. Senser



5-25-Woodrat nests in owl foraging area showing distribution of nests in oak woodland.

Habitat type: -----Sierran Foothill Hardwood
Location: -----Sequoia National Forest
Elevation: -----3,300 feet
Date: -----11 July 1991
Photographer: -----John S. Senser

5-26-Overview of a north-facing slope with typical owl habitat as it occurs in the central coastal region. The slope shows a mix of conifers (mostly coast redwood, Douglas-fir, Coulter pine, and sugar pine) and hardwoods (live oak, Pacific madrone, and California-laurel). Chamise, sagebrush, other chaparral species, yucca, and grasses are dispersed along the well-grazed, south-facing slopes.

Habitat type: -----Central Coastal Redwood/
California-laurel
Location -----Los Padres National Forest
Elevation: -----3,000 feet
Date: -----13 July 1991
Photographer: -----John S. Senser

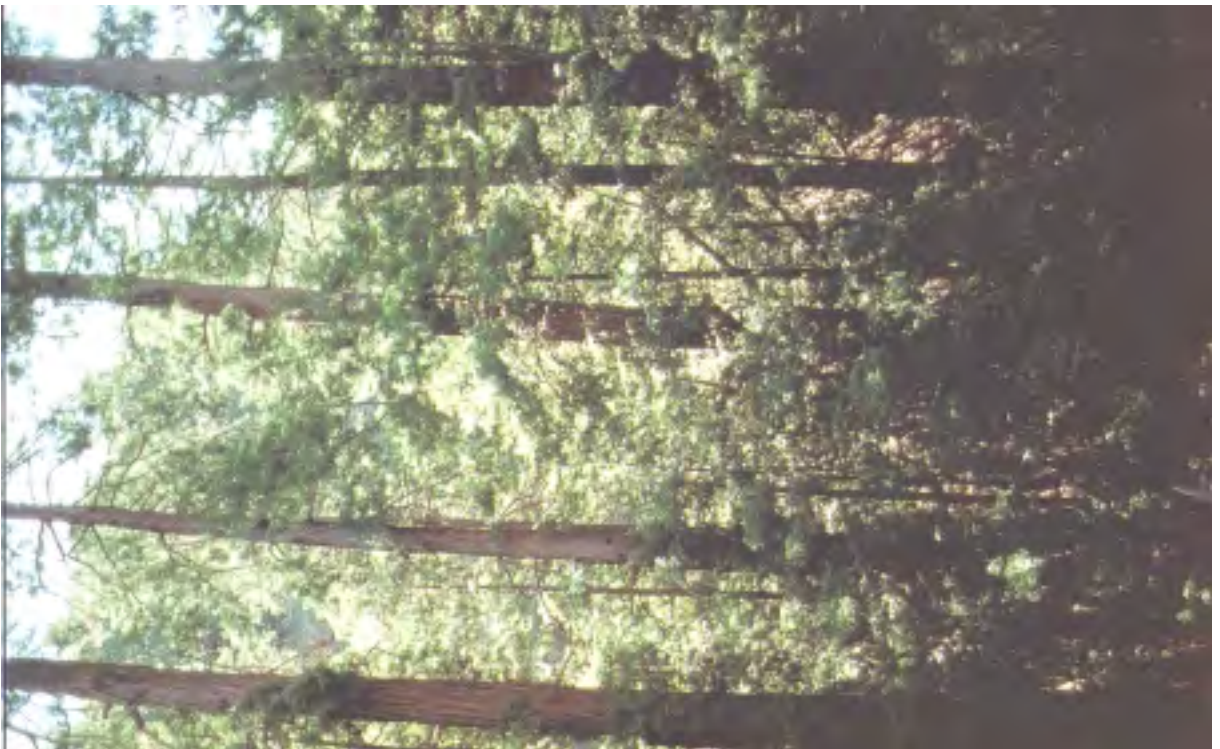


5-27—Overview of coastal redwoods showing multi-storied stand. The large trees here measured 46 inches in diameter at breast height and were 300-400 years old.

Habitat type: ----- Central Coastal Redwood
Location: ----- Los Padres National Forest
Elevation: ----- 2,100 feet
Date: ----- 13 July 1991
Photographer: ----- John S. Senger

5-28—Riparian area 300 feet downstream from a nest grove, showing the creekside California-laurel and white alder typical of these owl foraging areas.

Habitat type: ----- Riparian/Mixed Hardwood
Location: ----- Angeles National Forest
Elevation: ----- 3,860 feet
Date: ----- 19 August 1991
Photographer: ----- John S. Senger



5-29-Foraging area typical of riparian/hardwood habitat. The roost site is farther up-canyon (upper center of photo). The dense chaparral cover on the slopes blends with the thick white alder, live oak, and California-laurel along the stream channel, making it difficult to trace its course in the photo.

Habitat type:-----Riparian/Mixed Hardwood
Location: -----Los Padres National Forest
Elevation: -----2,400 feet
Date: -----12 July 1991
Photographer: -----John S. Senser

5-30-Roost area showing good cover composed of coast live oaks, California-laurel, and streamside white alder.

Habitat type: -----Riparian/Mixed Hardwood
Location: -----Los Padres National Forest
Elevation: -----2,520 feet
Date: -----12 July 1991
Photographer: -----John S. Senser



5-31-Stream diversion to a reservoir for domestic use. Future water demands, especially in southern California, may have a marked negative impact on spotted owl habitat.

Habitat type:-----Riparian/Mixed Hardwood
Location: -----Los Padres National Forest
Elevation: -----2,250 feet
Date: -----12 July 1991
Photographer: -----John S. Senser

5-32-Canopy typical of riparian/mixed-hardwood habitats. Trees pictured include bigleaf maple, California-laurel, and white alder. California sycamore was also present but not visible in this photo.

Habitat type:-----Riparian/Mixed Hardwood
Location: -----Los Padres National Forest
Elevation: -----2,290 feet
Date: -----12 July 1991
Photographer: -----John S. Senser



5-33-Overview of foraging habitat showing stands of bigcone Douglas-fir and canyon live oak on the moister north-facing slopes and various species of shrubs from the chaparral community on the drier, more south-facing slopes.

Habitat type: -----Bigcone Douglas-fir
Location: -----Angeles National Forest
Elevation: -----3,400 feet
Date: -----19 August 1991
Photographer: -----John S. Senser

5-34-Ground view 60 feet west of a nest tree. Observe the extensive dead wood, which can provide shelter for owl prey.

Habitat type: -----Mixed-conifer/Black Oak/Live Oak
Location: -----San Bernardino National Forest
Elevation: -----5,920 feet
Date: -----21 August 1991
Photographer: -----John S. Senser



5-35-Within a nest grove. The dominant tree species here were canyon live oak, incense-cedar, white fir, and assorted pines. Canopy closure was about 75 percent.

Habitat type: -----Mixed-conifer
Location: -----San Bernardino National Forest
Elevation: -----5,920 feet
Date: -----September 1988
Photographer: -----William S. LaHaye

5-36-Looking north from a nest tree. Note the open character of the canopy but relatively dense lower vegetative cover, composed here of curlleaf mountain mahogany. Only two of 131 nest sites and four of 134 owl territories found in the San Bernardino Mountains were in these open habitats (LaHaye et al. 1992).

Habitat type:-----Mixed-conifer with Pinyon Pine
and Mountain Juniper
Location: -----San Bernardino National Forest
Elevation: -----8,100 feet
Date: -----21 August 1991
Photographer: -----John S. Senser



5-37—In the vicinity of a nest site. Tree species found here were white fir, Jeffrey pine, incense-cedar, and black oak. Canopy closure was about 70 percent.

Habitat type: Southern California Mixed-conifer
 Location: San Bernardino National Forest
 Elevation: 7,200 feet
 Date: October 1988
 Photographer: William S. LaHaye

5-38—White slider nest tree. Typical riparian/hardwood habitat providing good canopy cover.

Habitat type: Riparian/Mixed Hardwood
 Location: Los Padres National Forest
 Elevation: 2,500 feet
 Date: 12 July 1991
 Photographer: John S. Senser



5-39—This habitat burned in 1987 but has recovered quickly. Crown sprouting by the black oak (left) and bigcone Douglas-fir (right) has hastened the recovery. An owl pair was found here 2 years after the fire.

Habitat type: ----- Bigcone Douglas-fir
Location: ----- Cleveland National Forest
Elevation: ----- 4,680 feet
Date: ----- 21 August 1991
Photographer: ----- John S. Senger

5-40—Canopy at an owl foraging area showing bigcone Douglas-fir, live oak, and black oak.

Habitat type: ----- Bigcone Douglas-fir
Location: ----- Cleveland National Forest
Elevation: ----- 4,680 feet
Date: ----- 21 August 1991
Photographer: ----- John S. Senger





5-43—Owls have nested twice in this canyon live oak, once in the top of the tree and once in a cavity.

Habitat type: ----- Mixed-conifer/Black Oak/Live Oak
Location: ----- San Bernardino National Forest
Elevation: ----- 5,920 feet
Date: ----- 21 August 1991
Photographer: ----- John S. Senser

5-44—Nest in 1991 in solitary sugar pine (center). It was a cavity nest located about two-thirds of the way up the tree. The cavity was probably created by a limb breaking away.

Habitat type: -----Mixed-conifer/Black Oak/Live Oak
Location: -----San Bernardino National Forest
 (Mount San Jacinto)
Elevation: -----6,200 feet
Date: -----21 August 1991
Photographer: -----John S. Senner

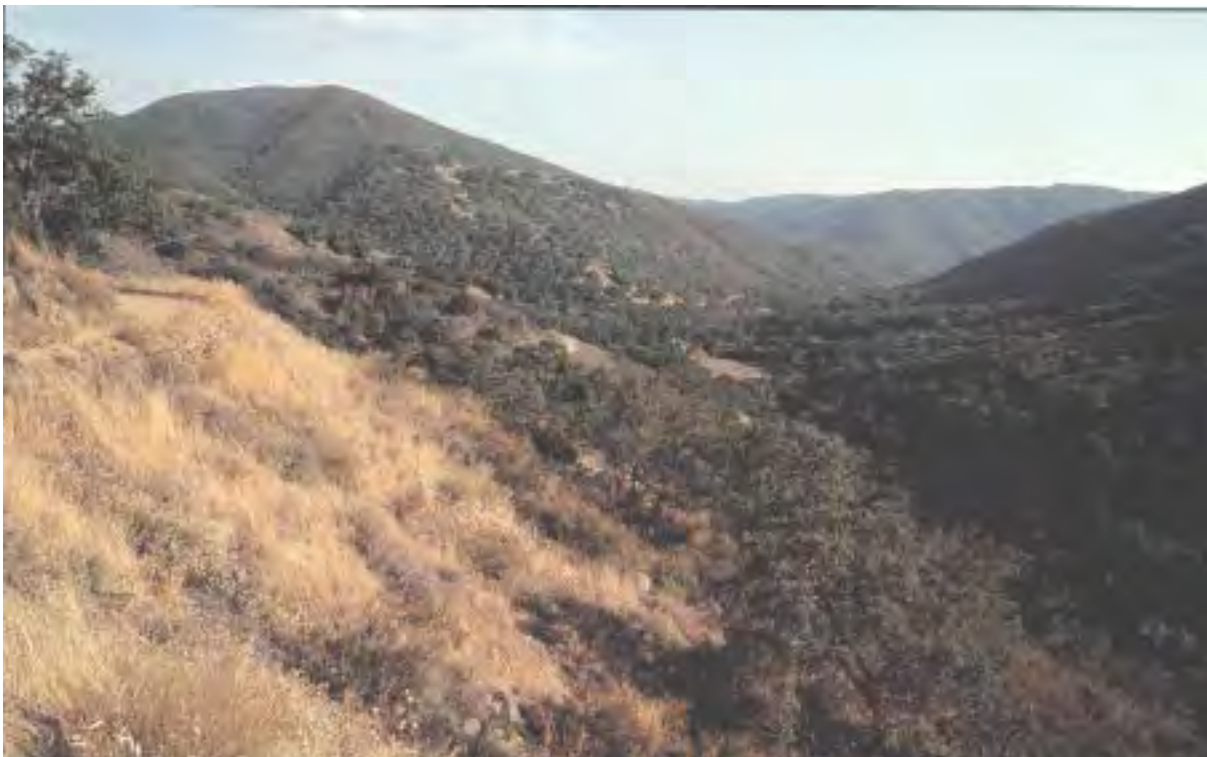


5-45-Overview of a hardwood ravine habitat. Note the dense hardwood stands in ravines, valleys, and on north aspects, with chaparral and grasses dominating the dryer slopes.

Habitat type: -----Hardwood Ravines
Location: -----Cleveland National Forest
Elevation: -----2,100 feet
Date: -----21 August 1991
Photographer: -----John S. Senser

5-46-Part of the study group "hooting" their way through a beautiful stand of live oaks and grassland. Moments after this photo was taken, a male owl responded from a hardwood stand/poison oak thicket just to the left of this view.

Habitat type: -----Hardwood Ravines
Location: -----Cleveland National Forest
Elevation: -----2,100 feet
Date: -----21 August 1991
Photographer: -----John S. Senser



5-47—Trail down Noble Canyon showing a stand of well-spaced, medium-aged live oaks. This is owl foraging habitat. A pair was found roosting nearby in a live oak with good canopy, and pellets were found along the trailside.

Habitat type: ----- Hardwood Ravines
 Location: ----- Cleveland National Forest
 Elevation: ----- 4,640 feet
 Date: ----- 22 August 1991
 Photographer: ----- John S. Senser

5-48—Canopy typical of these hardwood ravines, showing the excellent cover provided by black and live oaks.

Habitat type: ----- Hardwood Ravines
 Location: ----- Cleveland National Forest
 Elevation: ----- 4,640 feet
 Date: ----- 22 August 1991
 Photographer: ----- John S. Senser



RESEARCH ARTICLE

Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls

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ABSTRACT

Predators are among the most threatened animal groups globally, with prey declines contributing to their endangerment. However, assessments of the habitat conditions that influence the successful capture of different prey species are rare, especially for small, cryptic predators. Accordingly, most predator conservation plans are based on the relative importance of habitats inferred from coarse-scale studies that do not consider habitat features contributing to hunting success, which can vary among prey species. To address this limitation, we integrated high-resolution global positioning system tracking and nest video monitoring to characterize habitat features at prey capture locations during the nestling provisioning stage for the Spotted Owl (*Strix occidentalis*) a small, cryptic predator that has been at the center of a decades-long forest management conflict in western North America. When all prey species were considered collectively, males provisioning nests tended to capture prey: (1) in areas with more large-tree forest, (2) in areas with more medium trees/medium canopy forest, and (3) at edges between conifer and hardwood forests. However, when we considered the owl's two key prey species separately, males captured woodrats (*Neotoma fuscipes*) and Humboldt flying squirrels (*Glaucomys oregonensis*) in areas with markedly different habitat features. Our study provides clarity for forest management in mixed-ownership landscapes because different prey species achieve high densities in different habitat types. Specifically, our results suggest that promoting large trees, increasing forest heterogeneity, and creating canopy gaps in forests with medium trees/high canopy cover could benefit Spotted Owls and their prey, which has the ancillary benefit of enhancing forest resilience. Combining high-resolution global positioning system tagging with video-based information on prey deliveries to breeding sites can strengthen conservation planning for small predators by more rigorously defining those habitat features that are associated with successful prey acquisition.

Keywords: forest heterogeneity, large trees, predator–prey interactions, prey availability, Sierra Nevada, Spotted Owl, young forest

LAY SUMMARY

- Predators capture their prey where prey are both present and available for capture. Therefore, mapping and analyzing habitat at capture locations can aid management of quality habitat for predator conservation.
- It is difficult to find the exact places where predators capture their prey. This is especially challenging for smaller, cryptic predators that do not leave behind obvious kill sites.
- We attached global positioning system (GPS) tags to Spotted Owls and placed video cameras at their nests. We assessed the GPS movements to identify places they captured prey, which we then classified into species based on the video data.
- Spotted Owls captured prey in places with big trees, with medium trees and medium canopy cover, and with a greater mixture of forest types (heterogeneity) and forest edge.
- Forest management that promotes big trees, increases forest heterogeneity, and creates canopy gaps in forests will likely result in greater foraging success by owls, as well as increase forest resilience.

Los grandes árboles y la heterogeneidad del bosque facilitan la captura de presas por parte de *Strix occidentalis* de California

RESUMEN

Los depredadores se encuentran entre los grupos de animales más amenazados a nivel mundial, y la disminución de presas contribuye a su peligro. Sin embargo, las evaluaciones de las condiciones del hábitat que influyen en la captura exitosa de diferentes especies de presas son raras, especialmente para depredadores pequeños y crípticos. En consecuencia, la mayoría de los planes de conservación de depredadores se basan en la importancia relativa de los hábitats inferidos a partir de estudios de escala gruesa que no consideran las características del hábitat que contribuyen al éxito de la caza, las cuales pueden variar entre las especies de presa. Para abordar esta limitación, integramos el seguimiento por GPS de alta resolución y el monitoreo mediante grabaciones de video de los nidos, para caracterizar las características del hábitat en las ubicaciones de captura de presas durante la etapa de aprovisionamiento de polluelos de *Strix occidentalis*, un depredador pequeño y críptico que ha estado en el centro de un conflicto de manejo forestal que lleva décadas en el oeste de América del Norte. Cuando todas las especies de presas fueron consideradas colectivamente, los machos que aprovisionaban los nidos tendieron a capturar presas: (1) en áreas de bosques con árboles grandes, (2) en áreas con más árboles medianos/bosques de dosel mediano, y (3) en los bordes entre coníferas y bosques de maderas duras. Sin embargo, cuando consideramos las dos especies de presa clave de *S. occidentalis* por separado, los machos capturaron ratas (*Neotoma fuscipes*) y ardillas (*Glaucomys oregonensis*) en áreas con características de hábitat marcadamente diferentes. Nuestro estudio proporciona claridad para el manejo forestal en sitios de propiedad mixta porque diferentes especies de presas alcanzan altas densidades en diferentes tipos de hábitat. Específicamente, nuestros resultados sugieren que la promoción de árboles grandes, el aumento de la heterogeneidad del bosque y la creación de huecos en el dosel en bosques con árboles medianos/cobertura de dosel alta podría beneficiar a *S. occidentalis* y sus presas, lo que tiene el beneficio adicional de mejorar la resiliencia del bosque. La combinación del seguimiento por GPS de alta resolución con información basada en grabaciones de video de la entrega de presas a los sitios de reproducción puede fortalecer la planificación de la conservación para los pequeños depredadores, al definir de manera más rigurosa aquellas características del hábitat que están asociadas con la adquisición exitosa de presas.

Palabras clave: árboles grandes, bosque joven, disponibilidad de presas, heterogeneidad forestal, interacciones depredador-presa, Sierra Nevada, *Strix occidentalis*

INTRODUCTION

Predators are among the most endangered animal groups (Estes et al. 2011). Many anthropogenic factors threaten predators, but prey depletion resulting from habitat degradation is an important source of endangerment (Manlick and Pauli 2020). Recent work suggests that habitat conditions can mediate trophic interactions between predators and their prey through a variety of processes (Smith et al. 2019). This recognition, coupled with the fundamental importance of prey to predators (Mitchell and Powell 2004), suggests bolstering prey populations through habitat management could contribute to the recovery of imperiled predators.

Management that seeks to enhance prey populations will benefit from understanding how habitat influences predator-prey relationships. First, prey vary in both quality (e.g., nutritional content) and habitat needs, with different species reaching different densities in different habitats. Thus, in heterogeneous landscapes, promoting high-quality habitat for populations of more energetically valuable prey might benefit predator populations (Hobart et al. 2019a). Alternatively, when populations of prey species fluctuate asynchronously, ensuring habitat for multiple or alternative prey could buffer predators from declines in any one species (Sinclair et al. 2013). Second, prey can achieve high densities in habitats that do not constitute high-quality hunting habitat for the predator because of

a lack of suitable foraging structures (Dubey et al. 2019). Mismatches between predator-foraging habitats and high-density prey habitats can reduce predator access to prey but can also create prey refuges that indirectly benefit predators by producing source populations that disperse into predator-foraging habitat (Klecka and Boukal 2014). Thus, while the mechanisms by which habitat mediates predator-prey interactions are complex, understanding these processes can facilitate the development of more effective habitat-based conservation plans for endangered predators.

Studies of the interplay between habitat and predator-prey relationships have focused primarily on large mammalian predators because prey capture locations can be characterized based on the remains of kills made by global positioning system (GPS) or very high frequency (VHF) tagged individuals (Anderson and Lindzey 2003). However, identifying prey capture sites is much more difficult for smaller-bodied, more cryptic predators because discernable remains at kill sites are typically either absent or difficult to locate. For these reasons, studies of habitat selection by small or cryptic species typically “assume” foraging behavior using locations of tagged individuals during periods when foraging activities normally occur (e.g., during nocturnal hours), when in reality few of those locations are likely to represent actual prey capture locations (Marsh et al. 2014). Thus, logistical and technological limitations associated with studying foraging ecology

of small or cryptic predators have challenged a mechanistic understanding of prey habitat and conservation of predator–prey relationships.

Recent advances in GPS tagging technology such as the design of lightweight tags that record fine-scale movements with very high spatial and temporal resolution have facilitated identification of prey capture locations of small-bodied predators (Studd et al. 2021, Wood et al. 2021). For example, Marsh et al. (2014) integrated GPS dataloggers and digital video recorders to study the nocturnal foraging ecology of Burrowing Owls (*Athene cunicularia*) and identified successful captures based on (1) clusters of GPS locations followed by a straight-line movement back to a nest or den; and (2) video observation of prey delivery to the nest or den simultaneous with the arrival determined via GPS. This integrative approach can thus provide otherwise impossible insights into the successful hunting locations (and habitats) of adult individuals provisioning dependent offspring during this critical life history phase. However, to our knowledge, no previous study has characterized differences in habitat associated with the successful acquisition of different prey species in small-bodied predators.

We leveraged these new technologies to gain a more mechanistic understanding of how forest conditions influenced foraging strategies and the successful capture of prey species during the nestling-provisioning phase for the Spotted Owl (*Strix occidentalis*), a mature forest nesting species of conservation concern that is experiencing population declines across many parts of its range (e.g., Franklin et al. 2021). Concern about the Spotted Owl and its habitat has placed this species at the center of forest management planning in many forests of western North America, with substantial implications for both timber harvesting on private lands and forest management efforts intended to curb the spread of unprecedented large severe fires on public lands (Peery et al. 2017). Additionally, Spotted Owls are known to be nest site specialists, but GPS-tagging and VHF telemetry studies suggest that nocturnal activities (and therefore, inferred foraging activities) by Spotted Owls may occur in a broader range of forest types than nesting (e.g., Call et al. 1992, Atuo et al. 2019, Kramer et al. 2021). However, these nocturnal locations likely represent a range of activities besides foraging such as territory defense, pair bonding, and resting, and thus do not necessarily provide insights into the forest conditions that promote successful prey acquisition and associated fitness benefits. Given the profound effects prey availability has on Spotted Owl population dynamics (e.g., Franklin et al. 2000, Hobart et al. 2019a), an improved understanding of how forest conditions relate to the acquisition of primary prey and how habitat conditions differ among prey could substantially enhance forest management intended to benefit this species and meet other management and conservation objectives.

Two of the primary prey of Spotted Owls in California's Sierra Nevada—Humboldt flying squirrels (*Glaucomys oregonensis*) and woodrats (*Neotoma* spp.) (Gutiérrez et al. 2020)—tend to occur in different forest types. Woodrats, which are typically large in body size (mean woodrat consumed by owls = 187 g; C. Zulla personal communication) and more energetically profitable (1,205 kJ; Weathers et al. 2001), can be particularly abundant in some younger forests and brushy areas and are positively related to the presence of large oaks (Sakai and Noon 1993). Conversely, flying squirrels, which are typically smaller in body size (mean flying squirrel consumed by owls = 98 g; C. Zulla personal communication) and less energetically profitable (592 kJ; Weathers et al. 2001), tend to be more abundant in mature coniferous forests that have more arboreal lichens and tree cavities (Meyer et al. 2005). Thus, flying squirrels are more common in forest types considered to be Spotted Owl nesting habitat, while woodrats occur at high densities in areas that may be less suitable for Spotted Owl nesting (North et al. 1999). When brushy areas or some younger forest types having high woodrat density occur adjacent to mature coniferous forests, the resulting edge may provide foraging opportunities for Spotted Owls (Sakai and Noon 1993, 1997), although this hypothesis has not been tested. The consumption of woodrats, facilitated by the juxtaposition of older forest with other vegetation types (i.e. heterogeneous forest) may, in some ecological contexts, promote high territory occupancy rates, fitness, and landscape-scale density in Spotted Owls (Franklin et al. 2000, Hobart et al. 2019a).

We tested the hypothesis that forest type and structure (including edges) are related to acquisition of prey by Spotted Owls. Under this hypothesis, we predicted that Spotted Owls would tend to capture prey in mature forests overall, but that forest structure would differ between successful woodrat and flying squirrel capture sites. Specifically, we predicted that owls would capture woodrats at the edge between mature forests and areas dominated by younger forest, hardwoods, or shrubs—as well as in areas with a high diversity of vegetation types—compared to what is available within owl home ranges. Conversely, we predicted that Spotted Owls would tend to capture flying squirrels in mature forests without selecting for edges or a diversity of vegetation types. Gathering data to assess this long-standing hypothesis could substantially enhance opportunities to promote habitat for prey species that support stable owl populations.

MATERIALS AND METHODS

Study Area

Our study took place in the central and northern Sierra Nevada in 2019 and 2020 on or immediately adjacent to two long-term California Spotted Owl monitoring areas,

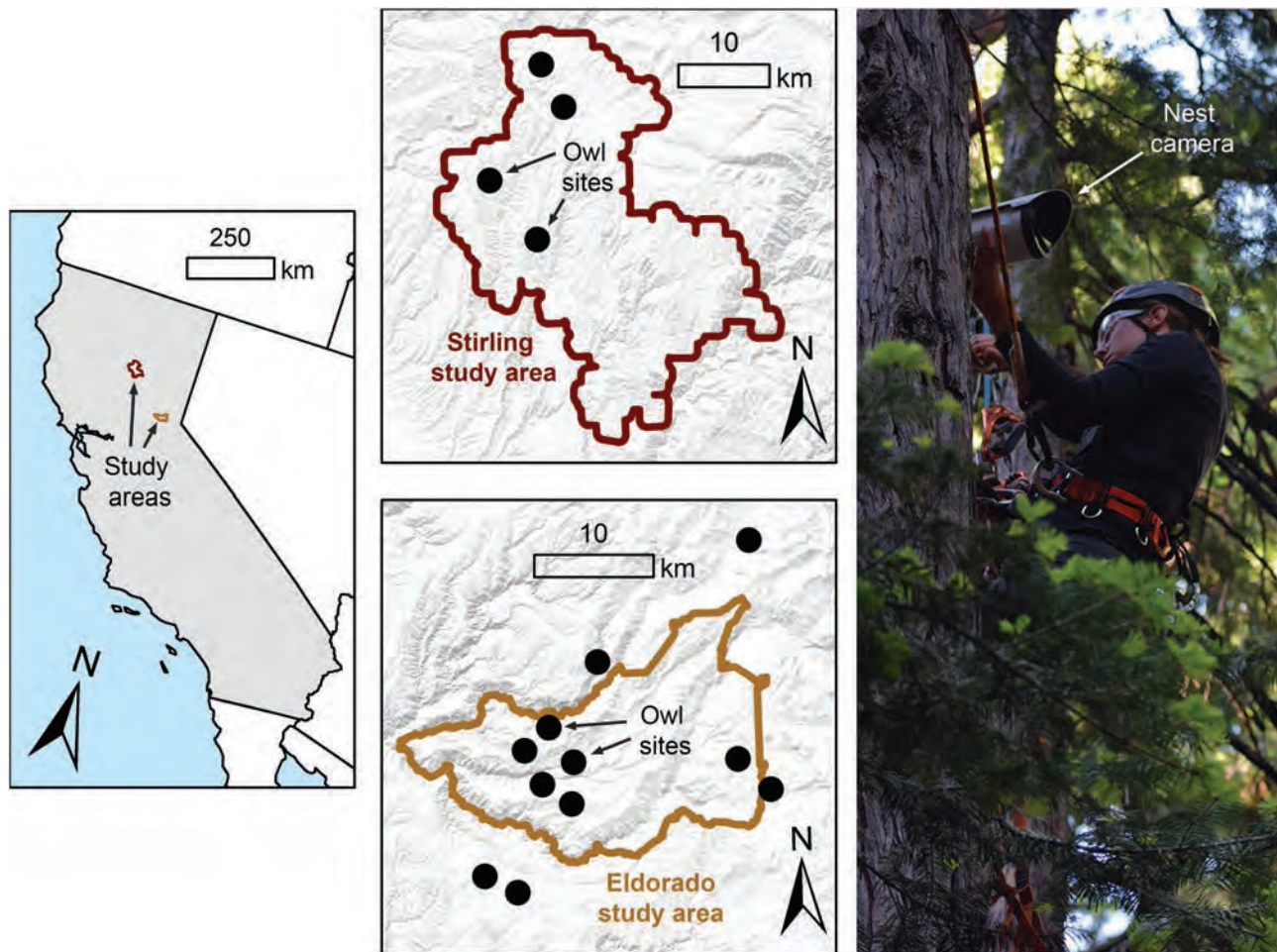


FIGURE 1. Map depicting the 15 locations where Spotted Owls were GPS tagged and video cameras were deployed in the Sierra Nevada, California, USA. Image on the right illustrates a camera installation adjacent to a California Spotted Owl nest.

the Eldorado Demography Study Area (EDSA) and Sierra Pacific Industries' Stirling Study Area (SSA) (Roberts et al. 2017, Hobart et al. 2019b; Figure 1). Elevation in the EDSA ranged from 366 to 2,257 m across 355 km² and elevations in the SSA ranged from 424 to 2,080 m across this 648 km² study area in mountainous terrain. The EDSA area was composed of ~60% public land managed by the U.S. Forest Service (USFS) and ~40% private land managed largely for commercial timber production, whereas the SSA was predominantly privately owned (81%). Forests on USFS-managed lands were typically a mix of mature forests and homogenous/dense forests dominated by small to medium-sized trees, sometimes containing residual large trees, owing to a history of fire-suppression and selective logging of large trees. Conversely, privately owned forests were a mixture of recent clear-felled areas (open and shrubby areas), tree plantations (densely stocked conifer stands), and forests similar to those on public lands. The vegetation on both study areas was typical of Sierran mixed-conifer forest dominated by the following

tree species: Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Tanoak (*Lithocarpus densiflorus*) formed a dense understory in some areas.

GPS Tagging

We located territorial breeding Spotted Owls as part of our routine monitoring surveys conducted annually on the EDSA and SSA (e.g., Roberts et al. 2017, Hobart et al. 2019b). Briefly, owls were located during call-based surveys at night and found during dawn/dusk surveys the following day to ascertain their reproductive status and locate nests (Franklin et al. 1996). Owls were fed live mice during follow-up surveys, which breeding owls then typically delivered to nest sites (Franklin et al. 1996).

We captured 15 nesting males (5 in 2019 and 10 in 2020) for GPS tagging using noose poles and "hand capture" (Wood et al. 2021). Females were not tagged

because they spend most of their time incubating eggs and brooding nestlings while nesting and relatively little time foraging (Forsman et al. 1984). Males were selected opportunistically for tagging based on the accessibility of the nest for video-monitoring (see below) throughout the nesting months (May to July) and the likelihood of recapture to remove transmitters. We affixed GPS tags (Alle-300, Ecotone, Poland) weighing 10 g and with remote downloading capability as tail mounts following methods described in Kramer et al. (2021) (Figure 1). We programmed tags to collect locations at 2-min intervals to characterize Spotted Owl nocturnal movements and ultimately identify prey capture locations (described below). We recaptured 5 individuals for a second deployment to increase the number of observations of prey captures. Following the final deployment, we attempted to recapture all owls to remove GPS tags; 2 individuals that were not recaptured were expected to molt during that season or the following season, thus shedding the GPS tag.

Nest Video Monitoring

We monitored prey deliveries using infrared (IR) video cameras placed at the nest sites of the 15 GPS-tagged males concurrent with the collection of GPS locations. To do so, we climbed a nearby adjacent tree (10–50 m from the nest tree) using a single rope technique and secured a video camera across from the nest tree (Figure 1). We monitored nests using AXIS Q1786–LE 4 megapixel outdoor IR video cameras that continuously recorded high-quality video throughout the nocturnal foraging period that coincided with GPS tag data collection (2000 to 0630 Pacific Daylight Time). We reviewed each video to detect and identify the different prey species delivered to each nest.

Identifying Prey Capture Locations

We located successful foraging sites (hereafter “prey capture locations”) by visually identifying tight clusters of GPS points followed immediately by a straight flight path back to the nest tree (Marsh et al. 2014, Wood et al. 2021). We defined a prey capture location as a cluster of up to 10 GPS points (within the 20 min prior to movement back to the nest), all within 250 m of one another based on that likely being the maximum hunting radius of a perched owl (S. A. Whitmore personal observation). If the two farthest points were >250 m apart, we removed the oldest point (the first point that defined the prey capture location) and continued to remove the points until they were all within 250 m of one another. Each cluster of points was transformed into a minimum convex polygon (mean: 0.38 ha, range: 0.002–2.713 ha) surrounding the cluster and assumed to represent the prey capture location. Although this approach, including the criterion of <250 m among pairs

of points, was somewhat subjective in that it was based on field observations, it was repeatable and typically yielded tight, defined clusters of points (compared to the distribution of owl GPS points overall) followed by distinct straight-line movements back to the nest site (Figure 2). We then matched the time stamp of the video with the time stamp of the GPS return to the nest to link the species of prey to its putative capture location (Figure 2). The area contained by the minimum convex polygon of these GPS points that matched with a prey delivery caught on video was defined as a prey capture location. Three prey capture locations were excluded from the analysis because they likely represented the retrieval of prey from a cache site. We suspected these deliveries to be from a cache location because of their close proximity to the nest site (within 50 m) and the early timing of the delivery (all 3 instances were the first delivery of the night and occurred before sunset), which both indicated a cache delivery (S. A. Whitmore, personal observation).

Vegetation Classification

We visually interpreted aerial imagery from the National Agriculture Imagery Program (NAIP) collected in 2018 and 2020 to characterize vegetation conditions within prey capture locations (as well as random locations, see below) following methods developed and described by Tempel et al. (2014) that typically results in >80% classification accuracy. Specifically, we considered 10 possible vegetation classes based on species composition, canopy cover, and the size of the dominant trees that was largely based on the California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988) (Table 1). Areas classified as hardwood typically represented patches of black oaks, with tanoaks in the understory typically being obscured by overstory conifer trees and thus not measured. We digitized polygons around relatively homogenous areas of vegetation with a minimum mapping unit of 20 m² and then classified the area within the polygon as 1 of the 10 vegetation classes.

Prey Capture Analysis

We used mixed-effects resource-selection functions (RSFs) to test for the selection of forest structural characteristics (Table 1) and several derived covariates, described below. First, we fit a model that included data from all prey (species pooled together) to examine habitat characteristics of prey capture locations and whether and how these locations differed in forest structure compared to random locations within the home range. Second, we fit models that included only data from either of the owl's 2 primary prey items—flying squirrels and woodrats (see below)—to characterize

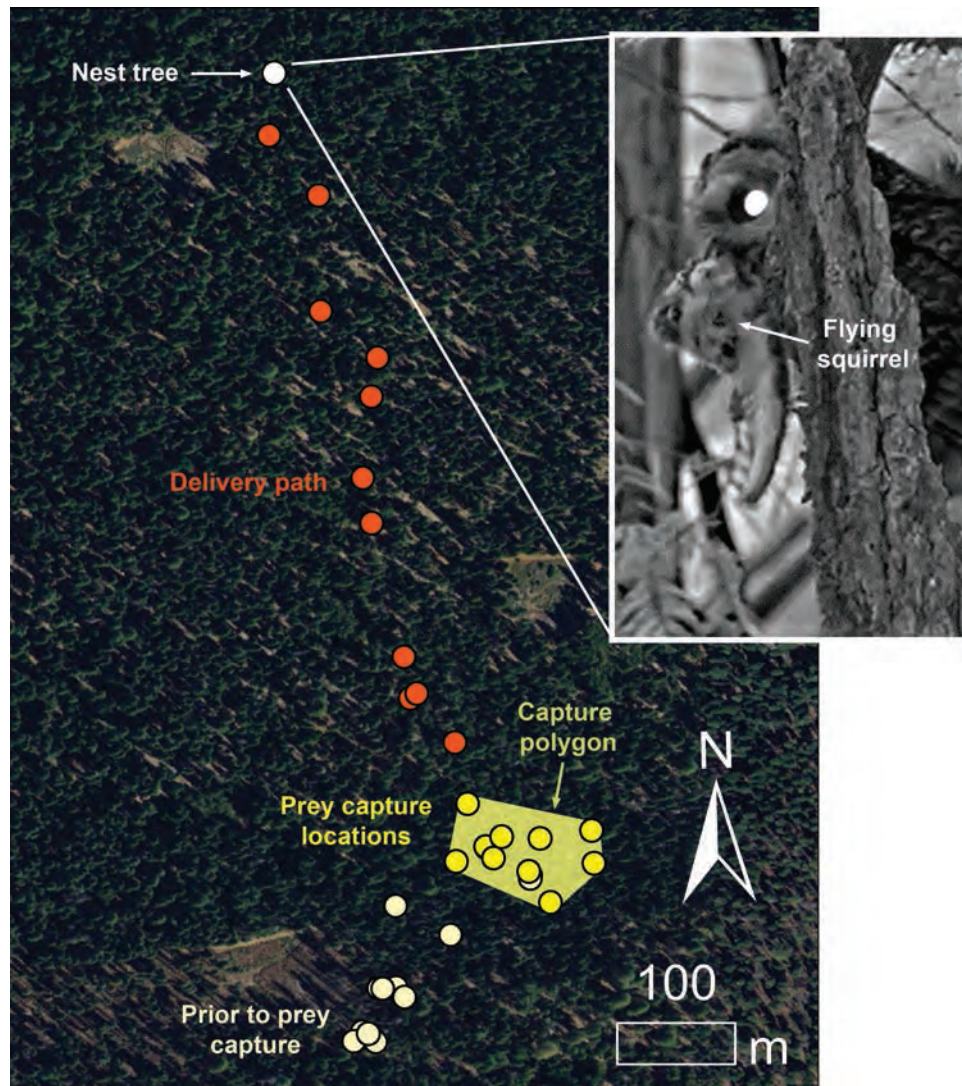


FIGURE 2. Map showing a sequence of Spotted Owl GPS locations preceding a prey delivery, and an image of the subsequent prey delivery at the nest. The prey delivery image is a single frame from an infrared camera mounted in a tree 10 m from the nest tree and shows the delivery of a flying squirrel to the nest. The approximate location of the capture can be inferred from the cluster of GPS locations before the owl's nearly direct flight back to the nest.

the forests where owls caught these 2 important prey species.

The RSFs relied on a use-availability framework to compare habitat characteristics at used locations to randomly generated available locations within a Spotted Owl's home range (Manly et al. 2002). Intercepts within the model varied by individual to account for correlation and unequal sample sizes (Muff et al. 2020). Models with random slopes (Muff et al. 2020) failed to converge; therefore, our models included only fixed covariate effects. For this analysis, a used location refers to the area within a prey capture location (explained above). We generated 5 corresponding available areas for each used area, where the size and shape of the available polygon were identical to that of the used

polygon. Spotted Owl home ranges were estimated using 95% fixed-kernel density estimators (KDE; Seaman and Powell 1996). Each available polygon was centered on a random location within the given owl's home range and rotated to a random orientation. To account for GPS error and potential neighborhood effects of surrounding habitat, we buffered all used and available polygons by 50 m. Available polygons were assigned a high weight ($W = 1000$) to facilitate approximate convergence to the inhomogeneous Poisson process likelihood (following Muff et al. 2020). We fitted RSFs using the R package "glmmTMB," version 3.6.3 (Brooks et al. 2017).

Our model covariates (fixed effects) included the proportion of each polygon containing various vegetation

TABLE 1. Vegetation classes used to characterize forest conditions used by Spotted Owls in the Sierra Nevada, California, USA.

Vegetation class	Description	Diameter at breast height (cm)	Canopy cover (%)
1	Hardwoods	N/A	>50 hardwood
2	Shrubs	<15.2	N/A
3	Young forest	15.2–30.4	N/A
4	Medium trees/medium canopy cover	30.5–60.9	30–69
5	Medium trees/high canopy cover	30.5–60.9	≥70
6	Large trees/medium canopy cover	≥61.0	30–69
7	Large trees/high canopy cover	≥61.0	≥70
8	Water or barren rock ^a	N/A	N/A
9	Medium or large trees/low canopy cover ^a	≥30.5	<30
10	Road ^a	N/A	N/A

^aNot included in resource selection models.

characteristics derived from NAIP imagery (Table 1) and the Shannon diversity index of the proportional contribution of those vegetation characteristics (i.e. heterogeneity). We excluded 3 vegetation classes (water or barren rock, medium/large trees with very sparse canopy cover, and road) given their rarity. We also included the total length of edges between hardwood, young forest, and shrubs with the other adjacent forest cover classes used in the analysis (Table 1) because these ecotones may provide owls with access to their most energetically profitable prey, the dusky-footed woodrat (*Neotoma fuscipes*), which are often most common in these 3 habitat types (Sakai and Noon 1993, 1997). Distributions of covariate values for both used and available prey capture locations are presented in Supplementary Material Figures S1 and S2. The size of buffered prey capture locations varied from 0.93 to 6.77 ha, so we also included a covariate for polygon area to control for potential area effects. We included an interaction term between percent public land and large trees/high canopy cover within owl home ranges to examine whether selection of this key forest type differed as a function of ownership given the different forest management approaches on public and private land.

We tested for collinearity among model covariates using the Pearson's correlation coefficient with a threshold of $r = 0.6$. If 2 variables were correlated where $r > 0.6$, we retained the variable that we assumed was more biologically informative. We z -standardized all continuous covariates. When making inferences about statistical relationships, we evaluated the direction of the effect (positive or negative), the effect size (biological magnitude), and uncertainty (95% confidence intervals [CIs]). However, we did not interpret the "statistical significance" of effects because the use of arbitrary thresholds based on P -values is problematic (Amrhein et al. 2019). Therefore, we sometimes made inferences about statistical relationships with P -values greater than 0.05 (but not greater than 0.1) to avoid accepting a false null hypothesis and therefore ignoring variables that were potentially biologically meaningful (Fidler et al. 2006).

We used odds ratios to aid our interpretation of the effects of vegetation classes on Spotted Owl prey capture location selection. For vegetation classes (i.e. non-edge categories), we scaled the odds ratio to represent a change in odds of selection for a 10% increase in that vegetation class. For edge categories, we scaled odds ratios to represent the change in odds of selection for an increase of 10 m ha⁻¹ of edge. For example, we interpreted an odds ratio of 1.2 for "medium trees/medium canopy cover" as follows: each 10% increase in medium tree/medium canopy cover forest was associated with a gain in the odds of prey capture by a factor of 1.2 (or a 20% increase in the odds).

RESULTS

We acquired 33,056 usable nocturnal GPS locations from the 15 tagged males after culling locations taken below 3.7 voltage that typically have greater positional error (S. A. Whitmore personal communication). We identified 127 prey capture locations, of which we were able to identify specific prey species using video monitoring for 91 (72%). Spotted Owls captured 43 dusky-footed woodrats, 29 Humboldt flying squirrels, 11 white-footed mice (*Peromyscus* spp.), 3 voles (*Microtus* spp.), 2 moles (*Scapanus* spp.), 2 Botta's pocket gophers (*Thomomys bottae*), and 1 bird (Order: Passeriformes). These patterns reinforced the importance of woodrats and flying squirrels as primary Spotted Owl prey and supported only conducting species-specific resource selection analyses for these 2 prey species.

All Prey Capture Analysis

All vegetation classes were present in prey capture locations, but Spotted Owls tended to capture more prey in areas with forests characterized by more medium trees/medium canopy cover forest ($\beta = 0.41$, 95% CI: 0.10 to 0.71, $P = 0.009$), more large trees/medium canopy cover forest ($\beta = 0.41$, 95% CI: 0.18 to 0.64, $P = 0.0004$), more large trees/high canopy cover forest ($\beta = 0.61$, 95% CI: 0.07 to 1.14, $P = 0.02$) and along hardwood edges

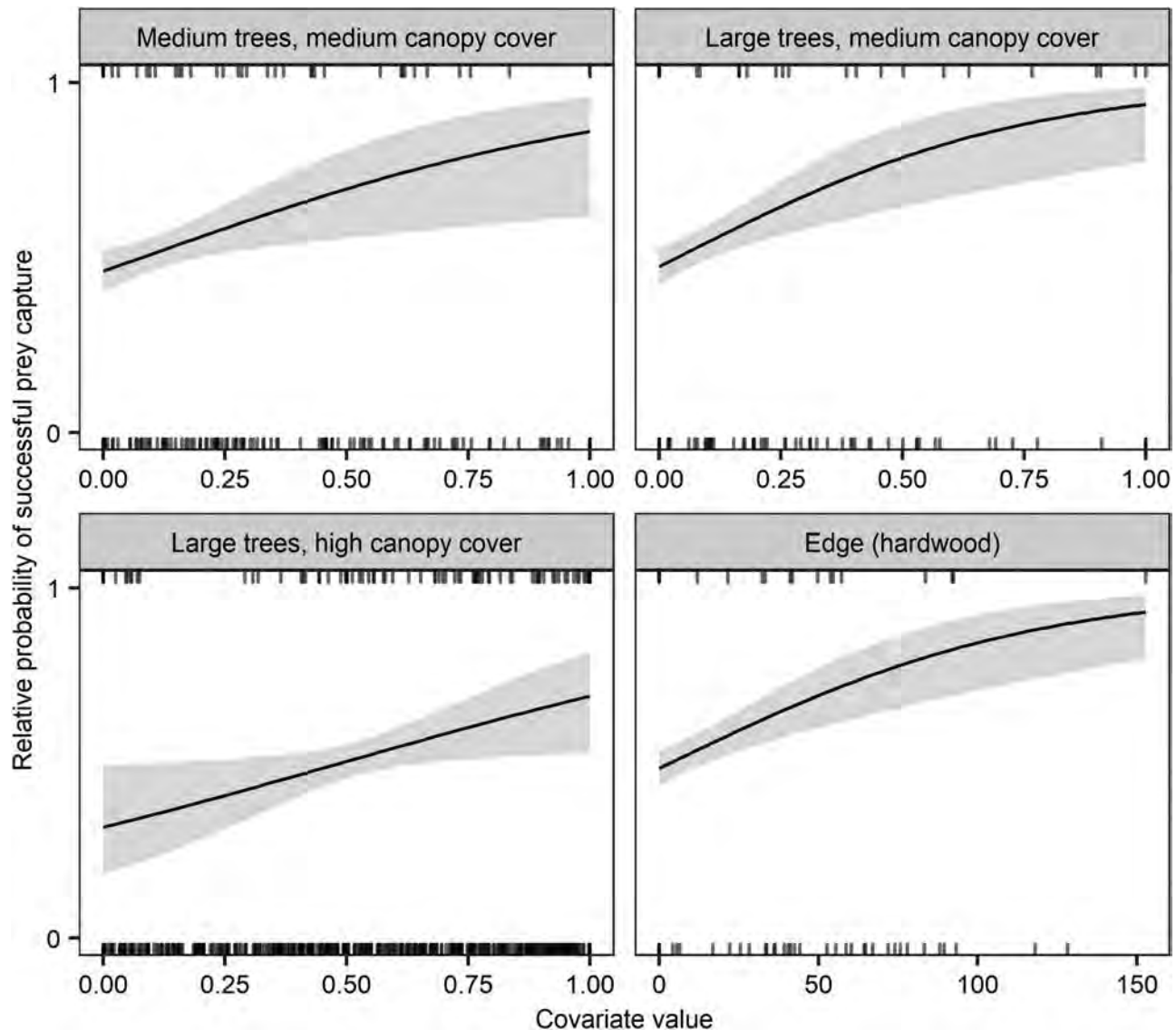


FIGURE 3. Relative probability of prey captures (with shaded areas representing 95% confidence intervals) as a function of habitat conditions for foraging Spotted Owls. Covariate values for prey capture and random polygons are visualized as rug plots at the top and bottom of each panel, respectively.

($\beta = 0.27$, 95% CI: 0.13 to 0.40; $P < 0.0001$) (Figure 3). Odds ratios indicated that with each 10% increase in medium trees/medium canopy cover forest, the odds of prey capture increased by a factor of 1.20 (i.e. a 20% increase in odds). The odds of prey capture increased by a factor of 1.30 and 1.16 with each 10% increase in large trees/medium canopy cover forest and large trees/high canopy cover forest, respectively. Lastly, odds of prey capture increased by a factor of 1.12 with every additional 10 m ha⁻¹ of hardwood edge.

Woodrat Capture Analysis

Spotted Owls tended to capture woodrats in areas with more young forest ($\beta = 0.55$, 95% CI: -0.01 to 1.12,

$P = 0.056$), more medium trees/medium canopy cover forest ($\beta = 0.62$, 95% CI: -0.02 to 1.27, $P = 0.06$), more large trees/medium canopy cover forest ($\beta = 0.71$, 95% CI: 0.24 to 1.19, $P = 0.003$), more large trees/high canopy cover forest ($\beta = 1.96$, 95% CI: 0.83 to 3.09, $P = 0.0007$), in areas with a higher density of hardwood edges ($\beta = 1.29$, 95% CI: 0.53 to 2.04, $p = 0.0008$), and areas with higher forest heterogeneity ($\beta = 0.48$, 95% CI: -0.02 to 1.00, $P = 0.06$; Figure 4). Odds ratios indicated that the odds of prey capture increased by a factor of 1.39 with every 10% increase in young forest and by a factor of 1.33 with every 10% increase in medium trees/medium canopy cover forest. The odds of prey capture increased by a factor of 1.60 with every 10% increase in large trees/medium canopy cover forest and 1.61 with

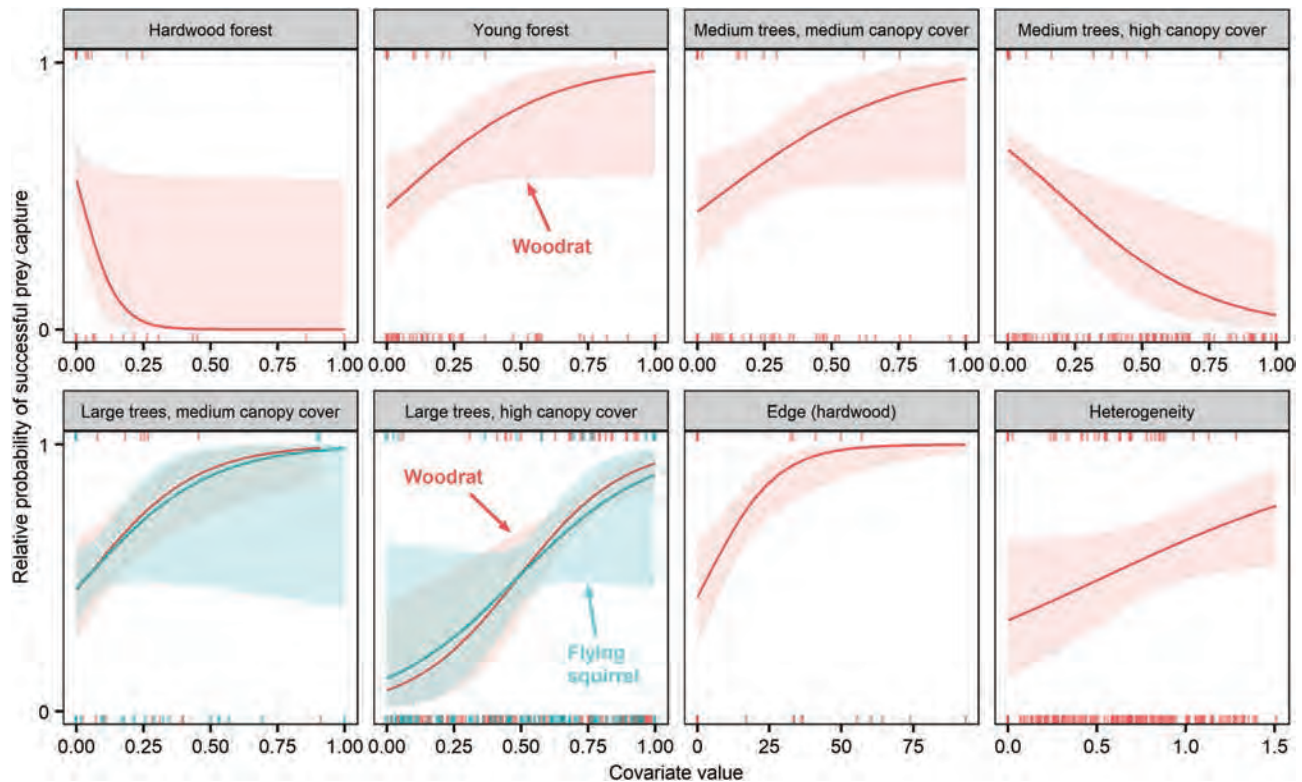


FIGURE 4. Relative probability of woodrat and flying squirrel captures (with shared areas representing 95% confidence intervals) as a function of habitat conditions for foraging Spotted Owls. Covariate values for prey capture and random polygons are visualized as rug plots at the top and bottom of each panel, respectively.

every 10% increase in large trees/high canopy cover forest. Each 10 m ha⁻¹ increase in hardwood edge increased the odds of prey capture by a factor of 1.73, and each 10% increase in cover type heterogeneity increased the odds of prey capture by a factor of 1.22.

Spotted Owls were less likely to capture woodrats in areas with more hardwoods ($\beta = -1.27$, 95% CI: -2.47 to -0.06 , $P = 0.049$; Figure 4). The odds of prey capture decreased by a factor of 0.24 (or a 4.2-fold decrease) with each 10% increase in hardwood forest. Spotted Owls also tended to avoid areas characterized by medium trees/high canopy cover forest when capturing woodrats ($\beta = -1.13$, 95% CI: -1.85 to -0.41 , $P = 0.002$; Figure 4). The odds of prey capture decreased by a factor of 0.71 (or a 1.4-fold decrease) with each 10% increase in medium trees/high canopy cover forest.

Flying Squirrel Habitat Selection Analysis

Spotted Owls tended to capture flying squirrels in areas with more, large tree/medium canopy cover forest ($\beta = 0.63$, 95% CI: -0.09 to 1.36 , $P = 0.09$) and more large tree/high canopy cover forest ($\beta = 1.56$, 95% CI: -0.23 to 3.36 , $P = 0.09$; Figure 4). The odds of prey capture increased by a factor of 1.51 with every 10% increase in large trees/medium canopy cover forest and increased by a factor of

1.65 times for each 10% increase in larger trees/high canopy cover forest. Unlike the “all prey” and “woodrat” analyses, we found evidence of a negative interaction between ownership and large trees/high canopy cover forest for flying squirrels ($\beta = -0.42$, 95% CI: -0.91 to 0.06 , $P = 0.09$). The odds of flying squirrel prey capture increased by a factor of 1.65 with each 10% increase in large trees/high canopy cover forest when no public land was present, but weakened by a factor of 1.25 when all land in an owl’s home range was public. Example capture locations illustrating areas with high values for selected covariates are provided in Figure 5.

DISCUSSION

We leveraged recently developed GPS tagging technologies to identify capture sites of different prey species for Spotted Owls, which led to novel inferences and implications for species conservation and forest management. Importantly, several of the habitats that promoted the capture of one prey species (woodrats), such as forest heterogeneity and young forests, were not identified as informative covariates in RSFs when all prey species were considered jointly. Thus, our work builds on the findings of Marsh et al. (2014) who found that RSFs for predators including all GPS points do

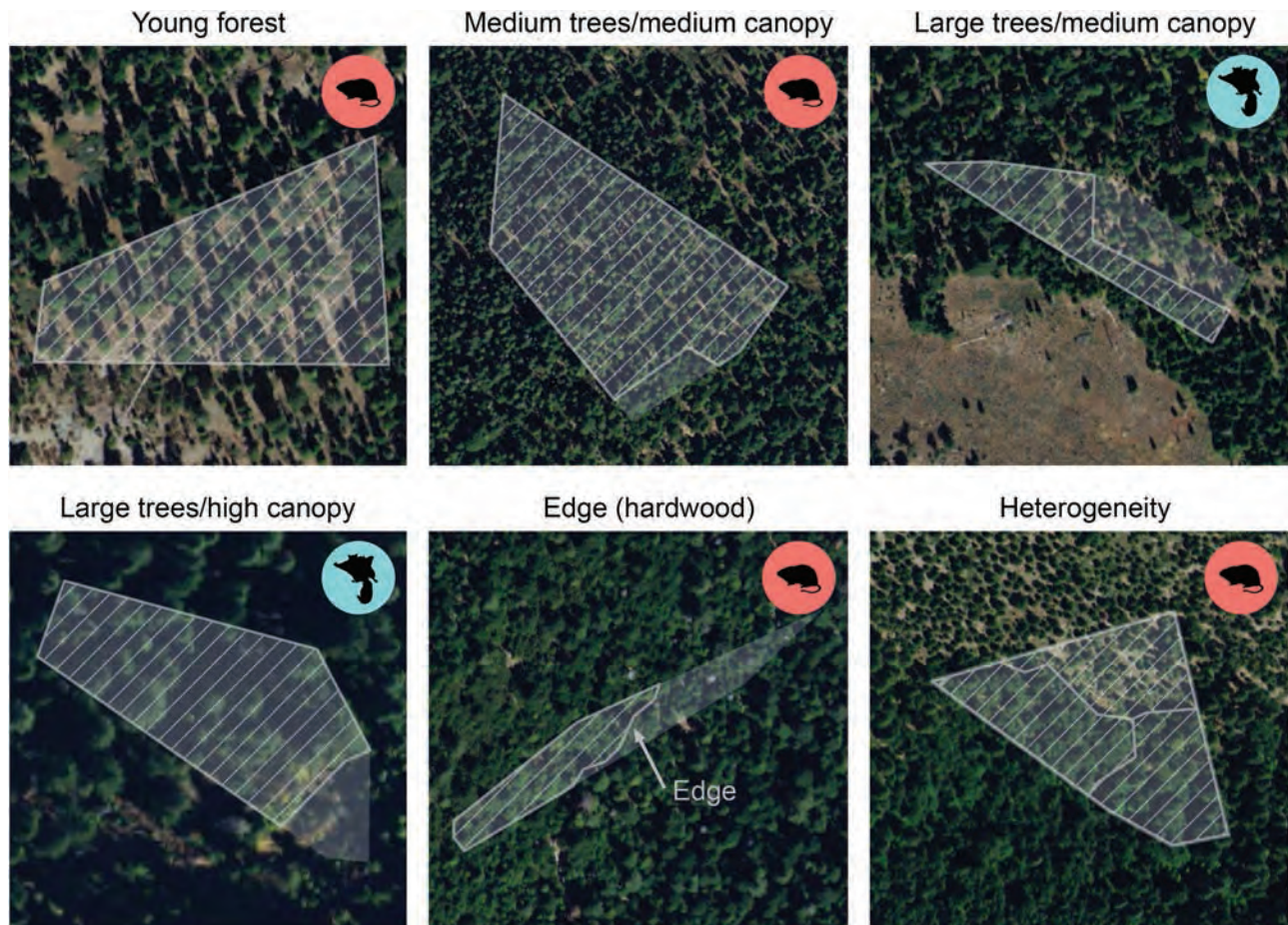


FIGURE 5. Example polygons where Spotted Owls captured either a woodrat or flying squirrel. The capture polygon is the entire shaded area, while the areas in each capture polygon containing the focal covariate (noted above each panel) are illustrated with cross-hatching. The relevant covariate value for the “edge (hardwood)” panel is the length of the internal line between the cross-hatched area (representing hardwood forest) and the shaded area (other cover types). The “heterogeneity” panel shows a mixture of three cover types (separated by thick lines) within a single capture polygon.

not necessarily reveal habitat types that confer successful prey capture. Had we not ascertained the species identity of individual prey items using nest video monitoring, we would not have identified young forests as an important habitat type, nor forest heterogeneity as important for the capture of woodrats by Spotted Owls. Such a limitation could lead to sub-optimal habitat management, given that the consumption of woodrats—a large and energetically profitable prey species—has been closely and positively linked to population-level density, reproductive rates, and territory occupancy rates of Spotted Owls (Smith et al. 1999, Hobart et al. 2019a). Indeed, the fact that previous GPS and VHF telemetry studies of Spotted Owls have been conducted without specifically accounting for prey capture locations, or linking the capture locations to the species of those prey, could account for the fact that these features are often not found to be selected by owls (Call et al. 1992). Accordingly, when practical, we encourage future studies of predator habitat selection to not only distinguish

successful prey capture from other locations (e.g., resting, commuting, territorial defense) but also to discriminate among the capture of different prey species so key ecological relationships are not obscured. Studies of prey delivery rates and/or biomass of different prey types are critical to building a more complete picture of the foraging needs and tradeoffs of nesting Spotted Owls.

Whereas we have known for many decades that Spotted Owls preferentially use mature forest for nesting, roosting, and foraging (Gutiérrez et al. 2020), more recent work has indicated the importance of other habitat types (e.g., Call et al. 1992, Atuo et al. 2019, Kramer et al. 2021). These different habitat preferences can perhaps be explained by our results, which demonstrate that successful hunting—particularly for woodrats—tends to occur in a broad range of conditions, including in areas with more young forest and higher heterogeneity. Thus, our results may partially explain observations of high owl densities on some private lands (which include young forest and higher

heterogeneity; Roberts et al. 2017), as well as the potential for life-history tradeoffs hypothesized to occur owing to forest heterogeneity (Franklin et al. 2000). In addition, the finding that Spotted Owls tended to not capture woodrats in areas with medium trees and high canopy cover supports previous stable isotope analyses demonstrating that owls with relatively high proportions of this forest type in their territories consume fewer woodrats, which can lead to lower territory occupancy rates and landscape-scale density (Hobart et al. 2019a). Similarly, the higher likelihood of woodrat capture in areas of high heterogeneity and young forests supports stable isotope analyses suggesting that these conditions promote woodrats that are then more available to owls (Hobart et al. 2019a)—and that young forests with a hardwood component can increase Spotted Owl reproductive success presumably because they promote populations of this energetically valuable prey species (Hobart et al. 2019b). Thus, our resource selection analysis appears to provide a mechanistic explanation for previously observed population-level phenomena in Spotted Owls.

Habitats that conferred successful prey captures by Spotted Owls likely did so by promoting hunting efficiency, high prey densities, access to areas with high prey densities, or some combination of these processes. Spotted Owls, as ambush predators, may have increased hunting efficiency due to a prevalence of suitable perching structures characteristic of mature forests with substantial vertical heterogeneity in tree height that conferred relatively high hunting success for multiple prey species (North et al. 1999). Further, forests with larger trees, and thus taller canopies, can harbor higher densities of flying squirrels due to accessibility to denning options and suitable microclimate conditions for lichen and hypogeous fungi—key food resources of flying squirrels (Waters and Zabel 1995). Spotted Owls may have rarely captured woodrats in medium tree forests with high canopy cover because of sparse shrub cover (due to reduced sunlight reaching the understory), which represents a key feature of woodrat habitat; conversely, owls may have selected for medium tree forests with medium canopy cover because of a more robust shrub component and denser woodrat populations. Furthermore, higher landscape heterogeneity in cover types may increase flying squirrel densities in remnant mature forests (Sollmann et al. 2016) and therefore might increase hunting success by owls in those areas. This could partly explain our result (Figure 6) of a stronger selection of large tree forests with high canopy cover in areas with more private lands, where mature forests occur in more discrete units and are surrounded by a greater variety of cover types. High woodrat capture success in young forests was likely the result of what can be very high woodrat densities in this forest type (Sakai and Noon 1993, Hamm and Diller 2009). While we originally predicted that edges between young forests and

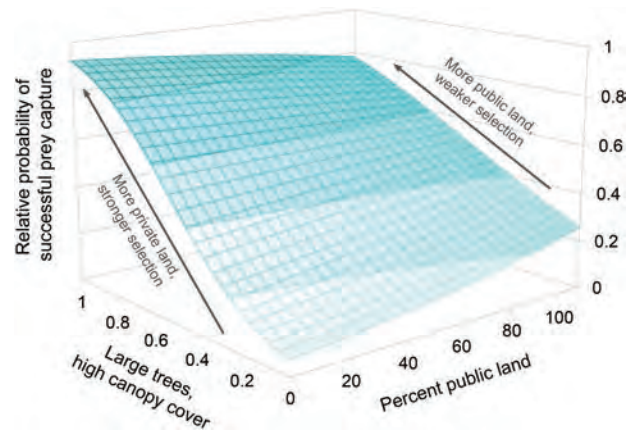


FIGURE 6. Relative probability of flying squirrel capture as a function of an interaction between large trees/high canopy cover forest and percentage of public land in a home range. The interaction term shows that positive selection for large tree forests with high canopy cover tends to weaken (though remains positive) for owls that have more public land in their 95% kernel density estimated (KDE) home range.

forests with medium and large trees would confer higher woodrat capture success by providing owls access to high-density woodrat areas (Sakai and Noon 1993), some young forests perhaps contained sufficient perching structures in the form of residual old trees or other structures (Atuo et al. 2019). Conversely, woodrats were captured less frequently in hardwood forests, which can also contain high densities of woodrats (Sakai and Noon 1993), whereas edges between hardwood and coniferous-dominated forests promoted woodrat captures by owls—consistent with our predictions. This finding suggests that hardwood forests may not provide suitable foraging structures but do appear to provide a source of woodrats for Spotted Owls foraging along the edge of hardwood and conifer forests as was hypothesized several decades ago (Sakai and Noon 1993). In this study, areas of forest classified as hardwood were generally patches of black oaks, with tanoaks in the understory typically being obscured by overstory conifer trees and thus not measured—yet are also likely potential sources of woodrats for Spotted Owls (Sakai and Noon 1993).

Our study demonstrates the opportunity to promote the conservation of Spotted Owls through habitat management. By understanding the specific habitat types and configurations that confer hunting success during a critical life-history period (the provisioning of young in nests and dens), management actions can promote higher prey densities in areas where capture is likely. Numerous predators have become endangered because of direct exploitation (Carter et al. 2017), yet declines in prey resources that reduce reproduction (Becker and Beissinger 2006), as well as indirect effects associated with anthropogenic habitat change (Hanski 2011),

can also cause species declines. Hence, enhancing the habitat of key prey species, especially large-bodied or nutritionally important ones that promote individual fitness components and population density, hold promise for recovering endangered predators. Recent advances in very small GPS packages with high accuracy, combined with video-based breeding site monitoring, now make fine-scale studies practical for a broader suite of predators, including small-bodied and cryptic ones (Studd et al. 2021, Wood et al. 2021). Such investigations will certainly be fruitful in forested systems such as the one studied here, but similar opportunities also exist in other terrestrial and aquatic ecosystems.

Several findings in this study point to co-benefits between Spotted Owl conservation and forest management activities intended to reduce forest fuels, two objectives often seen as diametrically opposed in a region experiencing megafires without modern precedent that can lead to Spotted Owl population losses (Jones et al. 2016, 2021). First, the selection of forests with large trees for the capture of both key prey species underscores that these structures are both “ecological backbones” of dry forests and a key component of foraging habitat for mature forest species such as Spotted Owls (Hessburg et al. 2015). Second, Spotted Owls tended not to capture woodrats in forests characterized by medium trees and high canopy cover, a forest type that is often synonymous with the historical legacy of fire exclusion and selective large tree removal in the dry forest ecosystems in western North America, which are now at great risk of large severe fires (Peery et al. 2017). Thus, promoting large tree recruitment and creating canopy openings in such forests as part of management activities could enhance the ability of Spotted Owls to capture and consume woodrats and lead to population-level benefits. Such forests could benefit Spotted Owls even prior to large tree recruitment given that medium tree forests with medium canopy cover tended to promote successful woodrat hunting. Further, promoting heterogeneous forests characterized by a mosaic of mature and younger forests, as well as a mixture of conifer and hardwood species, could both reduce severe fire risk and benefit Spotted Owls and other taxa.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement: Data collectors were trained in the responsible handling of birds following our IACUC (Institutional Animal Care and Use Committee) protocol # A005367-R02 and were authorized from California Department of Fish and Wildlife’s scientific collection permit (S-193180001-19324-001) and under USGS Bird Banding Lab permit # 23685 before undertaking the work. We also adhered to the University of Wisconsin–Madison Responsible Conduct of Research policy in carrying out this work.

Conflict of interest statement: The authors declare no conflict of interest.

Author contributions: J.J.K., K.N.R., B.P.D., S.C.S., and M.Z.P. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). C.J.Z. performed the experiments (collected data, conducted the research). C.J.Z., H.A.K., G.M.J., and M.Z.P. developed or designed statistical methods. C.J.Z., H.A.K., G.M.J., A.K.W., and M.Z.P. analyzed the data. All authors contributed to writing the or substantially editing the paper.

Data availability: Analyses reported in this article can be reproduced using the data provided by Zulla et al. (2022).

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Forest heterogeneity outweighs movement costs by enhancing hunting success and reproductive output in California spotted owls

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Abstract

Context The concept of landscape heterogeneity is central to species conservation; yet understanding the processes by which heterogeneity affects species can be challenging in practice. Complex and sometimes difficult-to-measure responses of species may reflect the outcome of life-history trade-offs shaped by different landscape properties.

Objectives We tested the hypothesis that a mosaic of forest stand types affected hunting and breeding success for California spotted owls (*Strix occidentalis occidentalis*).

Methods We integrated high-temporal-resolution GPS tags, video monitoring of nest sites, long-term assessments of reproductive status, and high-resolution remotely sensed vegetation data in a

mixed-ownership landscape in the Sierra Nevada, California to test our hypothesis.

Results Spotted owls made shorter nocturnal movements in homogenous territories with large areas of medium-aged forest apparently because this forest type allowed direct movement paths to foraging sites. However, spotted owls delivered prey at a higher rate to nest sites when they had more forest edge in their territory, which presumably provided greater access to large-bodied woodrat (*Neotoma* spp.) prey. Further, spotted owl reproductive output was relatively high in heterogenous territories containing a mix of mature and open forest.

Conclusions The benefits heterogenous forests provide to hunting success appeared to outweigh costs associated with additional commuting distance to foraging sites and provided potential fitness benefits to spotted owls. We suggest that the effects of landscape heterogeneity can vary not only among,

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but also within, species and can reflect the outcome of trade-offs among different life history activities. Understanding the effects of landscape properties on biological communities will benefit from additional empirical and mechanistic studies of individual species.

Keywords Habitat fragmentation · Habitat heterogeneity · Hunting success · Movement · Reproductive output · Spotted owl

Introduction

Landscape heterogeneity is a fundamental concept in basic ecology and promoting landscape heterogeneity is often a guiding principle in applied conservation science (Rosenzweig 1995; Katayama et al. 2014). Landscape heterogeneity can be often defined as the occurrence of multiple habitat types distributed in a mosaic of patches with different characteristics (Turner and Gardner 2015). Such mosaics can promote the persistence of species using different habitat and thus benefit species diversity (MacArthur 1958; MacArthur and MacArthur 1961). Moreover, individual species can also benefit from heterogeneous environments, particularly when individuals use different habitat types for different life-history needs such as breeding, foraging, and concealment (Vickery and Arlettaz 2012).

Responses to landscape heterogeneity, however, will depend on the size, configuration, and the juxtaposition of patch types (Tilman et al. 1997; Hanski et al. 2013; Loke et al. 2019) and will vary both within and among species (Stein et al. 2015; Wilson et al. 2016; Crooks et al. 2017; Chesson 2018). While some life-history traits can influence a species' responses in predictable ways (Cote et al. 2016), the manner in which the arrangement of habitat types influences individual fitness and populations may be the result of complex outcomes involving interactions between landscape properties and a suite of traits. Indeed, trade-offs can occur where one trait responds positively and another responds negatively to a specific landscape feature, with the nature of trade-offs differing among landscape features (Hanski et al. 2006). Consequently, there is a need for more empirical, mechanistic studies evaluating how life-history traits—and particularly potential trade-offs among

traits—are shaped by landscape properties to understand how anthropogenic habitat change affects species. An enhanced focus on responses by individual species to landscape patterns may reveal mechanisms that contribute to a greater understanding of community-level responses (Jones and Tingley 2022).

The California spotted owl (*Strix occidentalis occidentalis*) provides a high profile example of the challenges associated with understanding how landscape heterogeneity and changes to landscape heterogeneity impacts a species. Spotted owls—which are a major consideration in the management planning of many western forests—typically nest and roost in large patches of mature forest and some studies have found that fitness components and territory occupancy benefit from extensive relatively contiguous areas of closed canopy and mature forests in their home ranges (Tempel et al. 2014, 2016; Jones et al. 2018). Moreover, the Humboldt flying squirrel (*Glaucomys oregonensis*), a primary prey species for many spotted owl populations (Munton et al. 2002), is often associated with dense canopy cover in mature forests (Meyer et al. 2005; Smith and Person 2007). However, in some parts of their range, spotted owls also forage in landscapes characterized by a mix of mature, young, and open forests (Waters and Zabel 1995; Irwin et al. 2007; Williams et al. 2011; Atuo et al. 2019; Gallagher et al. 2019; Zulla et al. 2022). Notably, woodrats (*Neotoma* spp.), on average are more energetically profitable than flying squirrels (1205 kJ versus 592 kJ; Weathers et al. 2001), can achieve higher densities in open/younger forests (Lee and Tietje 2005; Innes et al. 2007; Slowik 2015), and may be particularly accessible to owls along the edges of mature and open/younger forests where the combination of prevalent perching structures and dense prey create favorable hunting conditions (Sakai and Noon 1997). Both the consumption of woodrats and presence of open/young forest that promote woodrat populations, when intermixed with more mature forest (i.e., spotted owl nesting habitat), have been shown to benefit spotted owl populations in some studies (Franklin et al. 2000; Hobart et al. 2019a, b). Nevertheless, the dispersion of more mature forests created by the interspersed of open and younger forests could increase travel distances for spotted owls while foraging given that owls often tend to prefer mature forest during nocturnal activities (Atuo et al. 2019; Blakey et al. 2019; Kramer et al. 2021a), and thus

may be restricted to such forests when commuting to more heterogeneous foraging areas. Potential increases in movement distances in heterogeneous forests could both increase the energetic costs of foraging and the risk of nest predation while adults are hunting, thus reducing reproductive output. To date, however, studies linking spotted owl population metrics, habitat, and prey conditions are typically coarse in scale and correlational—with no mechanistic, integrative assessments of the behavioral, trophic, and fitness consequences of the potential trade-offs associated with different arrangements of forest types.

Here, we tested the hypothesis that the benefits to California spotted owls (henceforth spotted owl) of capturing larger prey (such as woodrats) outweigh the costs of potentially greater nocturnal movements when their mature forest foraging habitat is patchily distributed or intermixed with open forest and younger forest within their home ranges. We developed several predictions that, if supported, would provide evidence for this hypothesis. First, we predicted that spotted owls would travel farther distances to foraging sites when habitat characteristics were more patchily distributed within their home ranges (prediction 1). Second, we predicted that spotted owls would deliver prey items and biomass to nests at higher rates when their home ranges encompassed greater forest heterogeneity and edge (prediction 2). Finally, we predicted that spotted owl reproductive success would be related to the degree of forest heterogeneity and edge in home ranges as a consequence of these trade-offs (prediction 3). Understanding these potential trade-offs and the effects of landscape properties on spotted owls is particularly important given that much of their habitat occurs in mixed-ownership landscapes experiencing commercial timber harvesting and planting, and secondly, that forest managers are attempting to promote more heterogeneous forest conditions to create more resilient landscapes and reduce large severe wildfires in a region experiencing unprecedented change (Jones et al. 2020, 2021; Koontz et al. 2020).

Materials and methods

Study system

Our study took place in the northern and central Sierra Nevada, California (Fig. 1). Field work was

conducted in a mix of private and public land to characterize spotted owl space use, trophic ecology, and fitness consequences across a gradient of composition and configuration of forested stands of different ages. Specifically, we studied spotted owls in and adjacent to (1) the Eldorado Demography Study Area (EDSA; all predictions); (2) Sierra Pacific Industries' (SPI) Stirling Study Area (SSA; all predictions), and (3) within SPI's five Watershed Study Areas (WSAs; prediction 3 only; Hobart et al. 2019b). All of these areas were characterized by mixed coniferous forests containing both patches of mature forest dominated by large trees and forests where the selective harvesting of large trees has produced relatively homogenous stands dominated by medium-aged trees (Fig. 2). Forests where selective harvest had occurred typically contained high densities of trees resulting from over a century of fire suppression (Parsons and DeBenedetti 1979). Other forest types in the study areas included patches of open (often times containing a brushy understory) naturally regenerating young forests, and timber plantations (primarily on private land; Fig. 2). Past wildfires also shaped forest structure in our study areas and ranged from mixed severity fires that created a mosaic of forest types across the landscape to primarily large, severe fires that created extensive areas of snag forest (see also below). The vegetation was typical of Sierran mixed-conifer forest dominated by Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Tanoak (*Lithocarpus densiflorus*) formed a dense understory in some areas. Mountain whitethorn (*Ceanothus cordulatus*), common manzanita (*Arctostaphylos manzanita*), and sierra gooseberry (*Ribes roezlii*) are commonly found in open areas across the landscape as well.

Owl surveys

We surveyed for owls from March 15 to August 31, 2013–2020 in all three study areas. EDSA and WSA territory locations were part of a long-term monitoring program (Tempel et al. 2016; Roberts et al. 2017). Owls were located during call-back surveys at night and found during dusk or dawn surveys the following day to determine their reproductive status and roost and nesting locations (Franklin et al. 1996). Owls

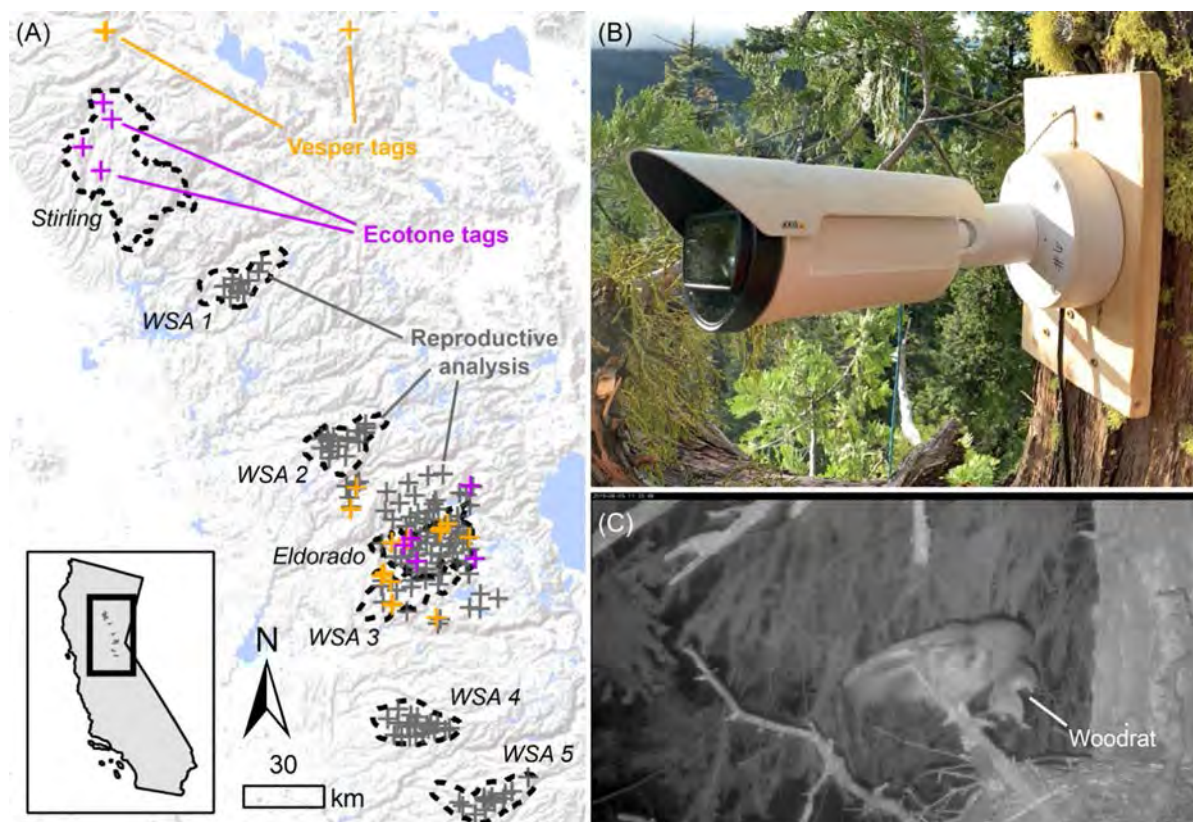


Fig. 1 **A** Map of Sierra Nevada, USA depicting locations of California spotted owl territories sampled in the study. **B** Video camera adjacent to a spotted owl nest. **C** Prey delivery of dusky-footed woodrat (*Neotoma fuscipes*) recorded on the video camera

were fed live mice during follow-up surveys to determine nesting status and number of juveniles fledged (Franklin et al. 1996).

GPS tagging

We captured 31 spotted owls (24 males and 7 females) for GPS tagging in 2019 and 2020, using noose poles, pan traps and hand capture methods (Wood et al. 2021). Owls were selected opportunistically for tagging based on the accessibility of the nest for video-monitoring (see below) and the likelihood of recapture to remove transmitters. We affixed GPS tags (Alle-300, Ecotone, Poland, 10 g) to 15 of these owls as tail mounts following methods in previous research (Kramer et al. 2021a, b). We affixed a different tag model (Vesper 3.2 tag manufactured by ASD, Haifa, Israel; 11.6 g) to the remaining 16 individuals also as tail mounts. The second set of tags collected vocalization data as part of another

study in addition to the GPS data (Reid et al. 2022). Ecotone tags averaged a 45 m median spatial error and Vesper tags averaged a 23 m median spatial error when tested in various forested conditions (open, medium-aged, and mature forest; Kramer and Whitmore, *unpublished data*). For Ecotone GPS units, we removed locations below 3.7 voltage because they typically have greater positional error; and with Vesper GPS we removed locations with horizontal dilution of precision (HDOP) < 10 and satellites < 6 (S. Whitmore *unpublished data*). We programmed tags to collect locations at two-minute intervals throughout the nocturnal foraging period (2000 to 0600 Pacific Daylight Time) to characterize spotted owl movements during the nestling period in May and early June. Following the final deployment, we attempted to recapture all owls to remove GPS tags. Two individuals were not recaptured but were expected to molt during that season or the following, thus shedding the GPS tag.

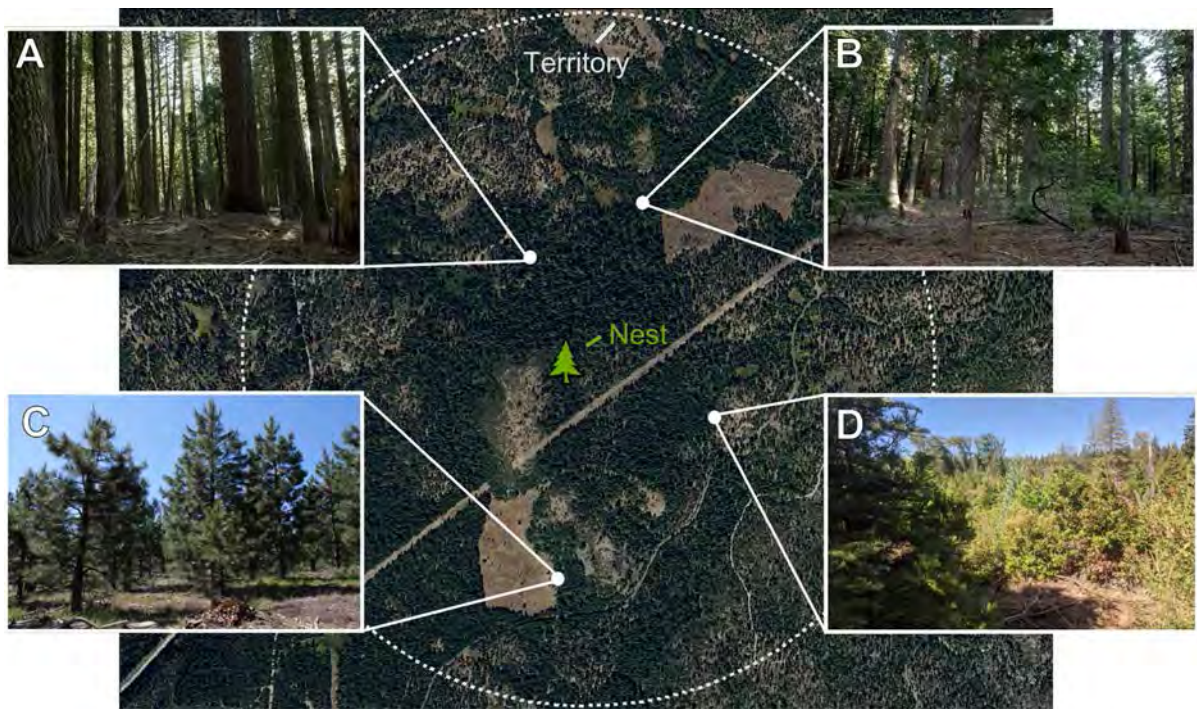


Fig. 2 Example images of vegetation types used in analyses (refer to Table 1 for definitions) overlaid on top of a spotted owl territory. **A** mature forest, **B** medium-aged forest, **C** young forest, and **D** open forest

Nest video monitoring

We monitored prey deliveries using infrared (IR) video cameras placed at the nest sites of 15 GPS-tagged males concurrent with the collection of GPS locations. To do so, we climbed a nearby adjacent tree (10–50 m from the nest tree) using a single rope technique and secured a video camera across from the nest tree. We monitored nests using AXIS Q1786—LE 4 megapixel outdoor infrared video cameras that continuously recorded high quality images throughout the nocturnal foraging period (2000 to 0630 Pacific Daylight Time). The video cameras were powered by a deep cycle lithium battery, both the battery and the video camera were connected to a Power over Ethernet (PoE) switch. The camera was programmed (using AXIS Companion manufactured by Canon Inc., Lund, Sweden) to specify image quality and recording period. Video recordings were saved to an onboard SD card, downloaded, and reviewed to detect and identify prey delivered to each nest.

Characterizing habitat composition and configuration

To understand the effects of habitat composition and configuration on spotted owl movements and prey deliveries, we characterized vegetation conditions within individual GPS-tagged spotted owl home ranges as well as in a large number of spotted owl home ranges in our study to understand effects on reproductive output (see below). For each GPS-tagged owl, we estimated the home range using 95% kernel density estimators (KDE) with all GPS location points (Seaman and Powell 1996). This unbiased method of home range estimation does not represent an individual's total territory nor its total home range size, as that would require months of tracking each individual owl (Forsman et al. 1984). Instead, the 95% KDE provides a relative measure of space use during the 2-to-15-night tracking period. Additionally, this method generates a utilization distribution that estimates the amount of time an owl spends in one location and then creates the smallest area containing 95% of the distribution. Within the calculated

home range, we characterized the landscape into measures of both habitat composition (forest stand type) and configuration (spatial arrangement of forest stand types).

We classified habitat composition based on four forest stand types: mature, medium-aged, young, and open forest (Table 1) based on canopy cover and quadratic mean diameter thresholds consistent with previous work on owl-prey relationships (Hobart et al. 2019b). We defined open forest as areas where canopy cover was less than 40% and divided other forested areas with a canopy cover of 40% or greater into several classes based on tree sizes: (i) mature forest, where the quadratic mean diameter (QMD) of dominant and codominant trees was at least 60 cm, (ii) medium-aged forest, when QMD was between 30 and 60 cm, and (iii) young forest, when QMD was less than 30 cm. We then calculated the proportional area of each habitat class within each 95% KDE home range.

Our classification was based on 30 m resolution gradient nearest neighbor (GNN) data, which interpolates information from an extensive forest-inventory plot network across the landscape using Landsat imagery at a resolution of 30 m (Ohmann and Gregory 2002). Given that owl data spanned from 2013–2020, we used GNN data from an intermediate date of 2017. While timber harvesting did occur in some territories both before and after 2017, temporal changes in habitat composition based on remotely-sensed data were very small (on average < 1% of territories) relative to the degree of spatial variation in habitat composition among territories (Table 1; Tempel et al. 2016; Jones et al. 2018) and our analyses were focused on variation in owl behavior, diet, and reproduction that occurred among territories. Our study area experienced a large, severe fire in 2014 (the King fire) which substantially changed habitat conditions in several territories. However, on average, less than 1% of the area of the 95% KDE home range

Table 1 Metrics used to characterize habitat composition and configuration within individual spotted owl home ranges

Metric	Data source	Definition	Mean (SD)	Min–max
Mature forest	GNN	Proportion of home range with forests with QMD $\geq$ 60 cm and canopy cover $\geq$ 40%	0.09 (0.08)	0.00–0.43
Medium-aged forest	GNN	Proportion of home range with forests with QMD 30–60 cm and canopy cover $\geq$ 40%	0.55 (0.16)	0.08–0.90
Young forest	GNN	Proportion of home range with forests with QMD < 30 cm and canopy cover < 40%	0.19 (0.10)	0.02–0.74
Open forest	GNN	Proportion of home range with forests with < 40% canopy cover	0.14 (0.15)	0.00–0.78
Medium/mature patch distance*	CFO	Mean distance to nearest neighboring patch, for each medium/mature core forest patch (height > 20 m). To delineate each medium/mature core forest patch (i) identify all areas of medium/mature forest, (ii) remove all area within 50 m of young or open forest patches (of > 3600 m ²), and (iii) delineate patches using the 4-neighbor rule, and removing patches $\leq$ 3600m ²	71.8 (40.3)	2–141
Woodrat-prevalent edge	CFO	Relative woodrat-prevalent edge area in each territory, where edge is defined as the area between forests with 2–10 m canopy height and > 20 m canopy height (classified using a 90 m moving window across 10 m CFO-generated canopy height)	0.013 (0.010)	0–0.058
Forest heterogeneity	CFO	Canopy texture (SD of SD, using a 90 m moving window across 10 m CFO-generated canopy height)	0.80 (0.19)	0.23–1.29

Habitat composition metrics were derived from 30 m resolution 2017 Gradient Nearest Neighbor (GNN) data (Ohmann and Gregory (2002) and habitat configuration metrics were calculated using 10 m 2017 California Forest Observatory data [CFO; California Forest Observatory (2020)]

QMD quadratic mean diameter, SD standard deviation

*Some territories lacked medium/mature patches, which prevented computation of this variable because patch distance was greater than home range size. In these cases, we estimated patch distance as the maximum observed value plus one standard deviation

for each of the 15 tagged spotted owls included in the movement and prey delivery analyses was affected by severe fire since 1986 and less than 4% of open forests in spotted owls 95% KDE home ranges overlapped with severe fire. Thus, the vegetation features in the home ranges of GPS tagged owls (including measures of spatial configuration described below) were mostly created by forest management on private lands rather than by severe fire.

We characterized three metrics of spatial configuration of forests within owls 95% KDE home ranges: (i) the distance between patches of medium-aged and mature forest (medium/mature patch distance), (ii) relative amount of edge where woodrats would likely be prevalent (woodrat prevalent edge; Sakai and Noon 1993, 1997), and (iii) forest heterogeneity (Table 1). We did so using finer-scale 2017 California Forest Observatory data [CFO; California Forest Observatory (2020)] describing vegetation height and canopy cover at 10 m resolution because fine-scale habitat configuration may be driving prey abundance and ease of capture. To calculate medium/mature patch distance, we first defined the core patch area as patches (defined using the four-neighbor rule; Turner & Gardner 2015) of at least 3600 m² in area where canopy height was over 20 m and which were located at least 50 m from shorter forest patches (defined as patches at least 3600 m² in area and with canopy height at or below 20 m; see Fig. 3). We then calculated the average distance between these patches within each 95% KDE home range. We approximated woodrat-prevalent edge as areas where shorter vegetation (small trees and brushy areas that we presumed to be woodrat source habitat; Sakai and Noon 1993, 1997) was in close proximity to tall vegetation (where woodrats may have been less abundant but easier to capture by owls because of more perching locations for owls and less cover for woodrats). We calculated this metric using a 90 m moving window to identify all pixels where at least 30% of pixels within the moving window were between 2 and 10 m in height [where 10 m was the maximum vegetation height in the woodrat abundant younger forest considered by Sakai and Noon (1997)] and at least 30% of the remaining pixels were over 20 m in height (see Fig. 3). Finally, we estimated forest heterogeneity using the standard deviation of vegetation height. We first calculated the standard deviation of canopy height within a 90 m moving window. In

heterogeneous forests composed of a patchwork of clear cuts and mature forest, this produced a raster with both very high values (on clear cut edges) and very low values (within clear cuts or in even-aged stands), whereas in homogeneous forests that were more contiguous, values were mostly intermediate. While this delineation differentiated between these landscapes visually, a summary statistic could not capture this pattern. Thus, we measured the standard deviation of the standard deviation raster using another 90 m moving window. As shown in Fig. 3, this clearly resulted in values that were higher in heterogeneous areas and lower in more homogeneous forests.

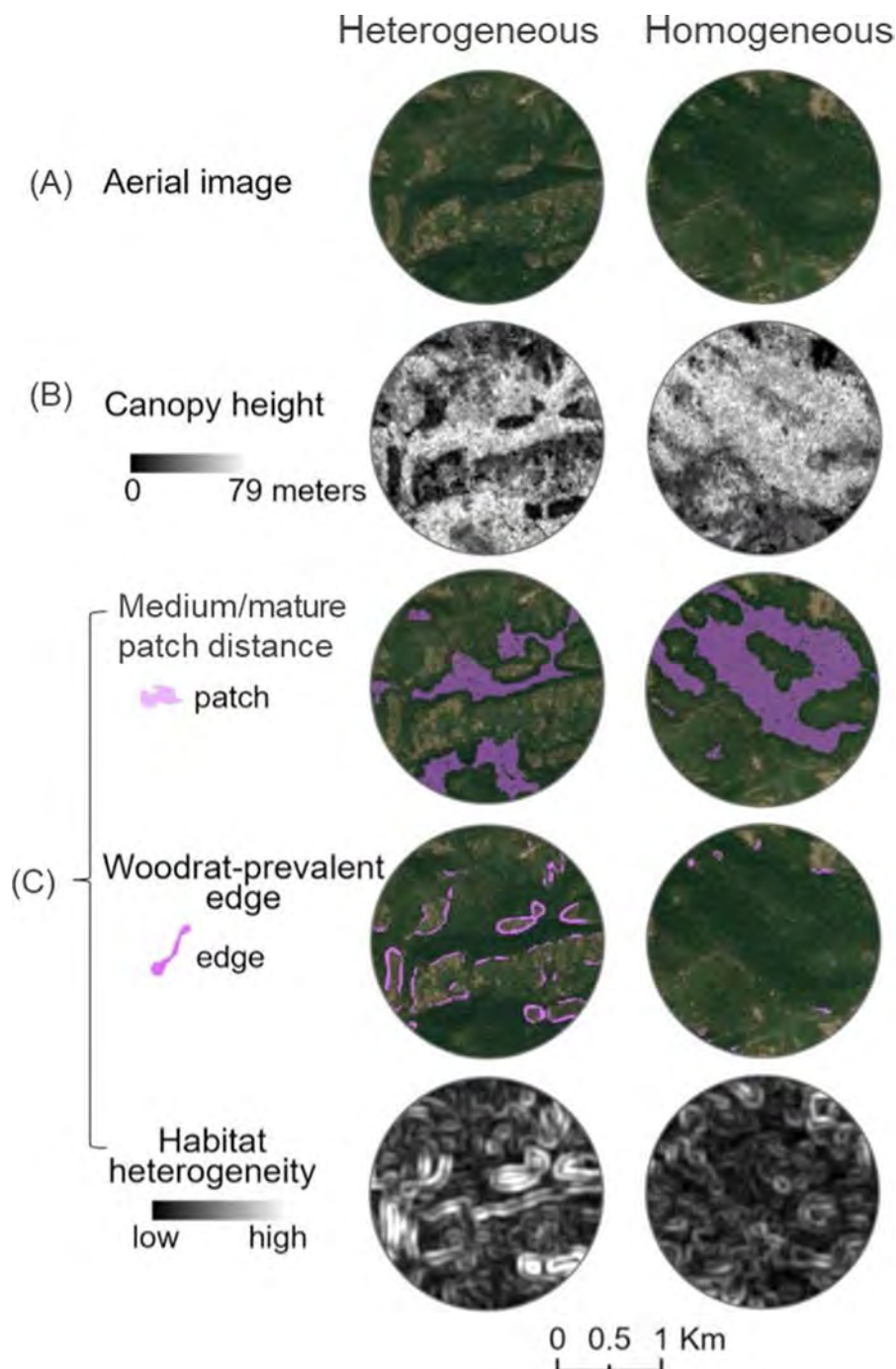
Estimating distance travelled

We used sequential GPS locations to estimate the total nocturnal flight distance each night for each individual owl. Because energetic cost is strongly correlated to distance traveled, we considered this estimate likely to be a reasonable proxy for nightly energy expenditure (Shepard et al. 2013). To account for GPS error (again 45 m and 23 m median spatial error for the Ecotone and Vesper tags, respectively; Kramer and Whitmore, *unpublished data*) we removed any point that was farther from both the previous and subsequent points than the distance between the previous and subsequent points, a process that removed 10% of the GPS points. We then smoothed the line using a polynomial approximation with an exponential kernel algorithm to better approximate the actual distance flown by each owl each night. Finally, we calculated the mean nightly distance travelled for each tagged individual for analyses of movements in relation to habitat conditions, as described in more detail below.

Estimating prey and biomass delivery rates

For each nest monitored with video recorders, we estimated both the mean nightly prey delivery rate (number of prey items delivered per hour) and the mean nightly biomass delivery rate (grams delivered per hour) based on prey deliveries identified from the nest video data. Calculating prey biomass delivery rate required that we estimate the body mass of each prey item delivered. For the largest and most common prey, dusky-footed woodrats and Humboldt flying squirrels, we assumed that the mean

Fig. 3 **A** NAIP imagery for a heterogeneous and homogenous spotted owl territory. **B** Canopy heights for the same two territories based on 2017 California of Forest Observatory (CFO) data. **C** Derived measures of habitat configuration for these territories calculated from CFO tree height data



body mass of individuals delivered to nests were equal to the body mass of individuals consumed by spotted owls as ascertained from regurgitated pellets that we collected as a part of previous field work in these areas (Peery, *unpublished data*). To calculate the mean body mass of these two species in

spotted owl pellets, we collected at least one and up to six skull and mandible measurements (depending on the condition of the prey remains) from 26 flying squirrel and 31 dusky-footed woodrat skulls or skull fragments (Table S1). We then collected the same measurements from museum specimens using

available mass measurements from the University of Washington's Burke Museum for flying squirrels ($n=86$) and the University of California, Berkeley's Museum of Vertebrate Zoology for woodrats ($n=50$). For the museum specimens, we developed predictive relationships between body mass and skull and mandible measurements using a set of univariate linear regressions of body mass against the skeletal measurements. We did not use a multiple regression approach as measurements could not be taken on all skull and mandible parts for all museum specimens or pellet samples. We estimated body mass for remains within pellets based on these predictive relationships and measurements of skull and mandible parts in museum specimens (Table S1). For each of the two species, we averaged body mass estimates from each prediction to determine an average mass. Using this approach, we estimated that the mean body mass of woodrats and flying squirrels consumed by spotted owls was 187.4 g (range 110.9 to 271.2 g) and 98.8 g (range: 80.2 to 117.2 g), respectively. We estimated the mass of the secondary and generally smaller species delivered to nests according to the midpoint of body mass ranges for species presented in the literature (Reid 2006). For example, if an owl delivered a mouse (body mass range 15–25 g) to their nest, the assigned body mass would be 20 g. When we were unable to identify the species delivered, we assigned the body mass based on the observed size class (large, medium, small, or extra small). Thus, in the small class that included mice (15–25 g), montane voles (30–80 g), and passerines (20–120 g), the prey mass estimate was 47.5 g. In instances where we were able to identify that there was indeed a prey delivery but were unable to estimate the size of the prey item due to the view being obstructed by the owl or an object in frame, we used the mean body mass of all other prey deliveries at that territory. To calculate the mean nightly biomass delivery rate and the mean nightly delivery rates, we averaged nightly values of these rates for each tagged spotted owl.

Estimating reproductive output

We related reproductive success estimated from spotted owl surveys conducted from 2013 to 2020 to the metrics of vegetation composition and configuration in Table 1. This analysis included the same 151 spotted owl territories used in Hobart et al. (2019b)

but over a longer time period (Fig. 1). We treated the number of juveniles fledged (0, 1, 2, or 3) as the response variable where territorial pairs that did not attempt to nest were excluded such that 0 young fledged in this case represented the outcome of failed nesting attempts. Our rationale for this approach was that analyses of prey delivery rates to nests (i.e., prediction 2) were, by definition, constrained to pairs that attempted to nest and our objective was, collectively, to understand how the habitat-mediated variation in prey deliveries influenced the number of young fledged.

Because we lacked GPS tagging data for spotted owls within all of 151 territories considered in reproductive analyses, we calculated measures of vegetation composition and configuration (2017 GNN and CFO vegetation data) within circular areas approximating the size and location of owl territories. We calculated the geometric center for each territory based on the geometric mean of nest and roost locations over the study period following Hobart et al. (2019b). We then calculated the $\frac{1}{2}$ nearest-neighbor distance for each territory (1.12 km) to create a radius centered on the territory's activity center and subsequently summarized the vegetation data within the circle.

We excluded reproductive data from the breeding seasons of 2013 and 2014 (pre-fire) to ensure that there were no substantial temporal mismatches between mapped vegetation conditions and owl data collection. Almost all of these severely burned territories remained unoccupied for the remainder of our study (2015–2020) and therefore generated no reproductive data. We included one territory in our reproductive analysis that experienced > 50% of severe burn and remained an occupied territory post fire. However, we did exclude pre-fire reproductive data for this territory because the mapped vegetation conditions did not reflect those present prior to the King Fire.

Statistical analyses

We used generalized linear models (GLMs) and generalized linear mixed-effects models (GLMMs) to evaluate our three predictions in program R with the packages 'glmulti' version 1.0.8 (Calcagno and de Mazancourt 2010) and 'lme4' version 1.1-27 (Bates et al. 2015). We selected the most parsimonious

model for each prediction using an all-subsets approach in which all combinations of covariates in Table 1 were evaluated as competing models and did not consider interactions among variables (but see below). All covariates were z-standardized to improve model fitting routines and interpretation (Schielzeth 2010). We selected models using Akaike's information criterion with sample size correction (AICc). Models within 2 AICc of the top model were considered competitive (Burnham and Anderson 2002). Models containing pairs of variables with correlation coefficients greater than 0.70 were not considered. We report the 85% confidence interval for model coefficients because this interval is more compatible with AIC approaches than a 95% confidence interval (Arnold 2010). We estimated a pseudo- R^2 for GLMs and GLMMs using a corrected likelihood ratio-based approach (Nagelkerke 1991) with the R package 'rsq' version 2.2 (Zhang 2021). All-subsets selection was conducted using package 'glmulti' for GLMs and the 'dredge' function in the package 'MuMin' version 1.43.17 (Barton 2020) for GLMMs. For each prediction, we selected the distributional family a priori before model fitting and selection. All models were fitted using maximum likelihood estimation.

For prediction 1 (mean nightly distance traveled as a function of patchiness; $n=31$), we specified a Gamma distribution with a log link. For the sake of parsimony, prior to considering the habitat covariates in Table 1, we first modeled "nuisance" effects that included sex, reproductive status, and tag type (because of differences in locational precision) as categorical fixed effects without any random effects. We then included supported terms from this modeling stage in all models incorporating habitat covariates in a second modeling stage. For prediction 2 (mean nightly prey biomass and mean nightly prey item delivery rates as a function of patchiness; $n=15$) we specified a Gamma distribution with a log link. Similar to prediction 1, this model contained only fixed effects. For prediction 3 (reproductive output), we specified a Gaussian distribution. The number of young fledged followed a positive discrete distribution ranging from 0 to 3. Although the data distribution for young fledged was not Gaussian, applying normal regression procedures (or a GLM procedure with Gaussian error) was less biased than GLM alternatives that followed positive discrete error distributions, such as Poisson (McDonald and White 2010).

Territories were repeatedly visited across 8 years, so we treated 'territory' as a random effect. Reproductive output can also vary substantially among years in spotted owls (Franklin et al. 2004), so we treated 'year' as a random effect.

Results

Distance travelled

We acquired 33,056 usable nocturnal locations from the 15 spotted owls tagged with Ecotone GPS units and an additional 45,460 usable nocturnal GPS locations from the 16 spotted owls tagged with Vesper GPS units. We also deleted any partial nights from the estimates of distance travelled for both GPS tags. For analyses purposes, we collected a mean of 1466 locations per owl (range 553–4327) over a mean of 5.3 nights (range 2–15). The average size of the 95% KDE for these 31 individuals was 400 ha ($SD=377$).

Our "nuisance" analysis suggested that the mean nightly distance travelled differed as a function of breeding status and tag type, but not sex or month—and we therefore carried over the former two effects into the second stage of modelling that included habitat covariates. Based on this model, spotted owls travelled shorter distances when there was more medium-aged forest available within their territory ($\beta_{\text{medium-aged forest}} = -0.14$, 85% CI $[-0.20, -0.08]$) based on the top model following all-subsets selection in the second stage (AICc=115.88; pseudo- $R^2=0.87$; Table 2). Breeding owls traveled over twice as far as non-breeders (breeders mean nightly distance=7375 m and non-breeders mean nightly distance=3648 m; Fig. 4). Models containing measures of configuration (medium/mature patch distance, woodrat prevalent edge, or forest heterogeneity) all received relatively little support ($\Delta\text{AICc}=0.267$ to 3.07) and, indeed, all three measures were considered uninformative parameters (Table 2).

Prey biomass and prey delivery rates

Based on the video recordings, we observed 348 potential prey deliveries by spotted owls to their 15 nests. Of these, 62.6% were identified to species, 18.7% were identified according to size, 6.4% were of unknown species and size, and it was uncertain

Table 2 Most supported generalized linear models from each of three predictions

Model	AICc	$\Delta AICc$	w	K
Prediction 1				
“Nuisance” analysis for distance traveled				
Breeding + tag type	122.07	0.00	0.433	3
Breeding + tag type + nights	123.46	1.38	0.217	4
Sex + breeding + tag type	124.89	2.81	0.106	4
Breeding + tag type + month tag deployed	124.91	2.83	0.105	4
Sex + breeding + tag type + nights	126.20	4.12	0.055	5
Breeding + tag type + nights + month tag deployed	126.45	4.37	0.049	5
Distance traveled				
Breeding + medium-aged forest + tag type	115.88	0.00	0.247	4
Breeding + medium-aged forest + mature + tag type	118.52	2.64	0.066	5
Breeding + medium-aged forest + young forest + tag type	118.55	2.66	0.065	5
Breeding + medium-aged forest + woodrat prevalent edge + tag type	118.56	2.67	0.065	5
Breeding + medium-aged forest + medium/mature patch distance + tag type	118.73	2.85	0.059	5
Breeding + open forest + medium forest + tag type	118.94	3.06	0.053	5
Breeding + medium-aged forest + heterogeneity + tag type	118.95	3.07	0.053	5
Prediction 2				
Prey biomass without potential influential territory				
Open forest + woodrat prevalent edge	107.66	0.00	0.167	3
Open forest	108.25	0.58	0.125	3
Open forest + woodrat prevalent edge + medium/mature patch distance	108.46	0.79	0.112	4
Open forest + medium/mature patch distance	109.67	2.00	0.061	3
Intercept-only	110.01	2.34	0.052	1
Prey biomass with potential influential territory				
Heterogeneity	131.85	0.00	0.194	2
Intercept-only	132.84	0.98	0.118	1
Mature forest	133.93	2.07	0.069	2
Woodrat prevalent edge	134.46	2.60	0.053	2
Young forest	134.55	2.69	0.050	2
Prey delivery rate				
Intercept-only	– 11.07	0.00	0.190	1
Heterogeneity	– 10.34	0.73	0.131	2
Woodrat prevalent edge	– 9.54	1.53	0.088	2
Mature forest	– 8.68	2.39	0.057	2
Young forest	– 8.56	2.51	0.054	2
Prediction 3				
Reproductive success*				
Mature forest + open forest + mature forest * open forest	543.2	0	0.135	6
Mature forest + open forest	543.4	0.14	0.126	5
Mature forest	543.8	0.6	0.100	4
Medium-aged forest + young forest	544.7	1.47	0.065	5
Woodrat prevalent edge + mature forest + open forest	544.8	1.59	0.061	6

AICc Akaike information criterion, ΔAIC difference between AIC and the top model in the set, *w* Akaike weight, *K* number of parameters. Depending on the degree of model selection uncertainty, we display models within 2 (denoted with *) or 5 AICc of the top model. Intercept-only (null) models were included in each set. *K* for Prediction 3 includes two random effects (year and territory)

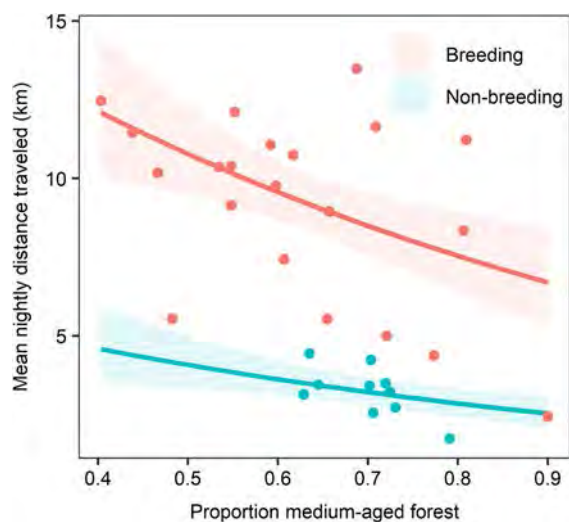


Fig. 4 Mean nightly distance traveled for breeding and non-breeding owls as a function of the proportion of their home range containing medium-aged forest

whether prey was delivered in 12.3% of cases. We identified eight different species delivered to nests, of which dusky-footed woodrats and Humboldt flying squirrels were the most common (41.5% and 40.2%, respectively). The less common species were bats (*Myotis* spp., 0.4%), mice (*Peromyscus* spp., 13.8%), montane voles (*Microtus montanus*, 1.8%),

Townsend's mole (*Scapanus townsendii*, 0.9%), pocket gophers (*Thomomys* spp., 0.9%) and passerines (*Passeriformes* (order), 0.4%).

The null model for the mean number of prey items delivered per night, ($AIC_c = -11.08$) outperformed all other models indicating that delivery rates by spotted owls were unrelated to the measures of vegetation composition and configuration we considered (Table 2). The top model for the mean nightly prey biomass delivery analysis ($AIC_c = 107.7$; $\text{pseudo-}R^2 = 0.50$) suggested that spotted owls delivered prey biomass at a slower rate when there was a higher proportion of open forest within their 95% KDE home range ($\beta_{\text{open}} = -0.16$, 85% CI $[-0.26, -0.07]$; Fig. 5A) and at a higher rate to nests when more woodrat-prevalent edge occurred within their 95% KDE home range ($\beta_{\text{woodrat-prevalent edge}} = 0.12$, 85% CI $[0.04, 0.21]$; Fig. 5B). This relationship was derived after excluding a single observation with a high rate of biomass delivery (117 g per hour) at a nest for which we only collected 10.5 h of data before the juveniles fledged and for which a relatively high proportion of prey (8 of 9 deliveries) were not identified to species. Including this data point, spotted owls delivered prey biomass at a faster rate to nests when their territories contained more heterogeneous forest conditions ($\beta_{\text{habitat heterogeneity}} = 0.22$ $[0.05, 0.41]$); based

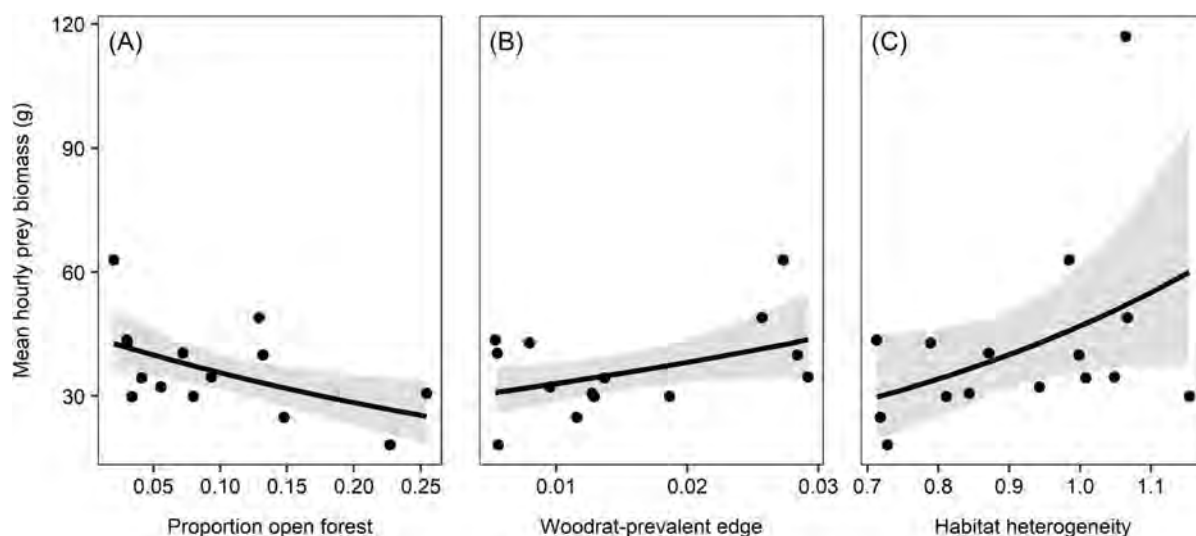


Fig. 5 Effects of habitat composition and configuration on prey biomass delivery rates to nests by spotted owls in the Sierra Nevada, California

on the top model ($AICc = 131.9$; $\text{pseudo-}R^2 = 0.24$; Fig. 5C); this was the only model to outperform the null model ($AICc = 132.8$).

Reproductive output

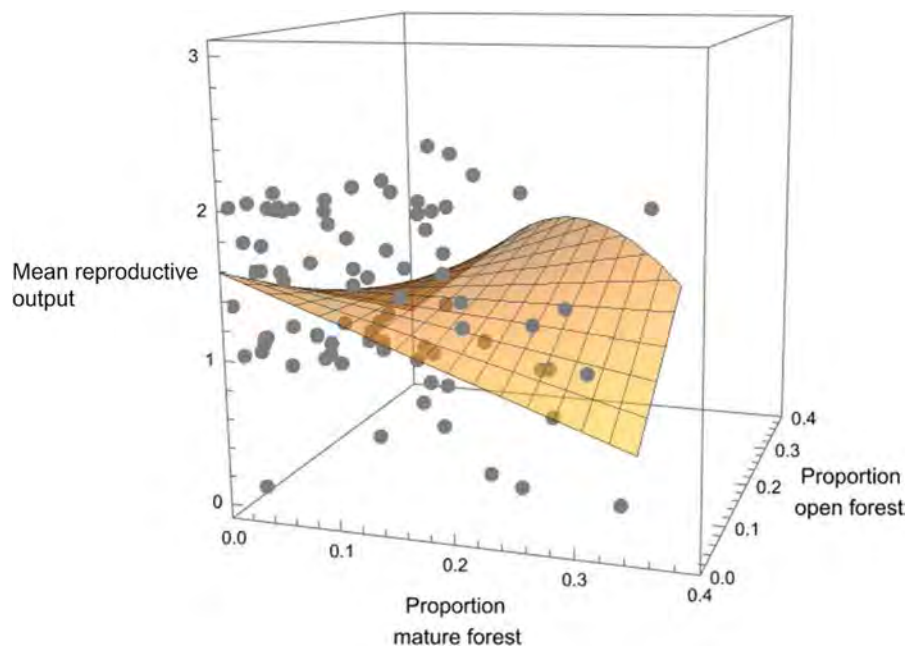
Reproductive output was lower for owls in territories with more mature forest ($\beta_{\text{mature forest}} = -0.11$, 85% CI $[-0.19, -0.04]$) and open forest ($\beta_{\text{open}} = -0.17$, 85% CI $[-0.33, -0.02]$) based on the most supported model ($AICc = 543.4$; Table 2). However, given that edges (or heterogeneity in vegetation conditions) increased biomass delivery rates to nests (prediction 2), we also examined a post-hoc model to explore a potential interaction between mature and open forest. This post hoc model ($AICc = 543.2$) was slightly more supported than the additive model and indicated that the effect of mature forest on reproductive output was conditional on the amount of open forest in a territory ($\beta_{\text{mature forest} \times \text{open}} = 0.27$, 85% CI $[0.01, 0.54]$). Specifically, the benefits of mature forest on reproductive output were only realized when territories also had a high proportion of open forest (Fig. 6). Collectively, open forest, mature forest, and their interaction explained 33% of the variance

in reproductive output among territories following the variance components approach of Franklin et al. (2000).

Discussion

Improved understanding of the mechanisms by which species respond behaviorally and demographically to landscape heterogeneity is needed to mitigate the potential effects of land use change and develop informed conservation plans. Here, we demonstrate that the effects of habitat configuration on a species considered to be a barometer of mature forest conditions are complex, where (i) the prevalence of medium-aged forest reduced nocturnal movements, (ii) edges between older and younger forests increased rates of biomass delivered to nests; and (iii) a mixture of mature and open forest increased reproductive output. Medium-aged forests may help reduce energy expenditures during nocturnal activities that include foraging, but a mixture of forest types provide the greatest benefit to prey acquisition and ultimately fitness (as measured by reproductive output). These findings are broadly consistent with previous studies demonstrating that heterogeneous forest conditions can, in some circumstances, benefit spotted owl fitness by increasing the abundance or availability of

Fig. 6 Mean reproductive output as a function of interacting effects of the proportion of mature and the proportion of open forest within territories for nesting spotted owls in the Sierra Nevada, California



prey (Franklin et al. 2000; Hobart et al. 2019a). We provide a mechanistic and integrative explanation of how habitat configuration benefits spotted owls by shaping their movement patterns, prey capture success, and fitness.

Spotted owls made shorter nightly movements when there was more medium-aged forest available within their 95% KDE home range. This presumably resulted in lower energetic expenditures for owls when more medium-aged forest was available. While movement distances were not associated with the medium-aged and mature forest patch distance or other measures of habitat configuration we considered, the negative association between movement distance and medium-aged forest was generally consistent with our expectation that heterogeneity might increase movement distances. Medium-aged forest was the most prevalent forest type within spotted owl 95% KDE home ranges, on average exceeding half of the 95% KDE home range area (Table 1), such that 95% KDE home ranges containing a high portion of this forest type can be considered relatively homogenous. We suggest that high proportions of medium-aged forest afforded more direct paths to foraging sites at more heterogeneous locations (Fig. 7) and potentially more direct paths to locations used to meet other life history demands such as territorial defense (Wood et al. 2019). Our previous work suggests that successful prey capture sites, particularly

for woodrats, often occur in more open and heterogeneous areas (Zulla et al. 2022). Further, spotted owls often selected medium-aged forests (and mature forests) for nocturnal activities based on GPS and VHF tagging agnostic to activity (Atuo et al. 2019; Kramer et al. 2021b). The frequent use of this forest type in our study may reflect commuting to more high-quality foraging sites while providing concealment from predators associated with open habitats such as great-horned owls (*Bubo virginianus*). While medium-aged forests reduced nightly movement distances in general, we note that spotted owl 95% KDE home ranges with large areas of this forest type have the potential to increase commuting distances to edges with open/younger forests where owls tend to capture woodrats. In addition, breeding individuals exhibited greater nightly movement distances than non-breeders, likely because of the additional movement necessary to deliver prey from foraging sites to nests (Zulla et al. 2022). However, breeding status and medium-aged forest were not correlated ($r = -0.30$), such that tests of these two effects in the most supported model should have been independent.

While medium-aged forests reduced nocturnal movements and potentially benefited spotted owls energetically, edges between older forests (typically considered spotted owl habitat) and younger forests (more likely to constitute woodrat habitat) increased the rate at which adults (Fig. 5B) delivered prey to

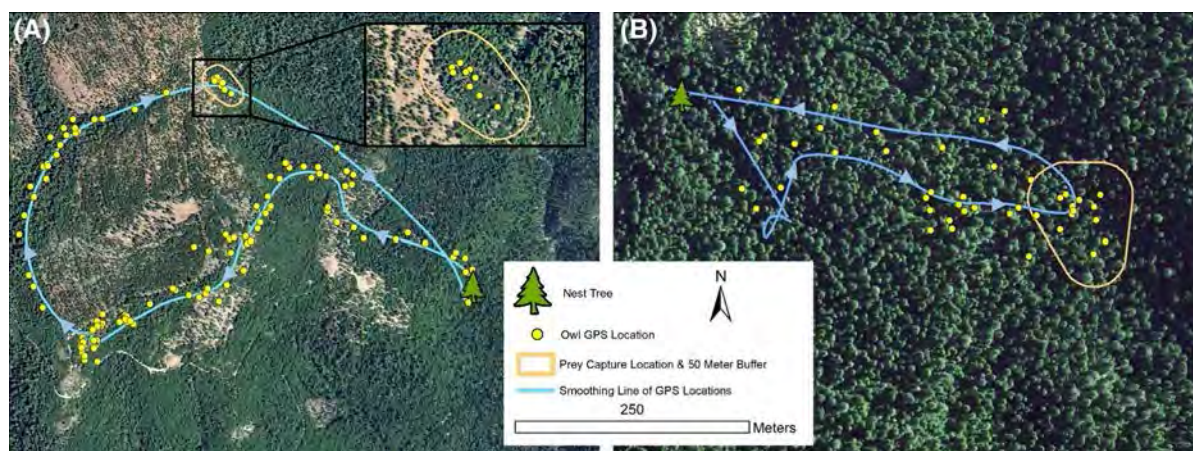


Fig. 7 Two examples of spotted owl movement paths away from and back to nest sites following successful prey captures in the Sierra Nevada, California. **A** a more circuitous path in areas with less medium-aged forest and **B** a more direct path

in areas with more medium-aged forests. Note the prey capture sites are shown with tan shaded polygons (see Zulla et al. 2022 for methods)

nesses. This result supports previous stable isotope work in the Sierra Nevada demonstrating that, in some mixed-ownership landscapes, heterogeneity can increase woodrat consumption in adult spotted owls, which in turn increases territory occupancy rates and landscape-scale population densities (Hobart et al. 2019a). This result is also consistent with spotted owls having higher fitness in territories characterized by higher levels of forest heterogeneity (Franklin et al. 2000), although we did not evaluate the mechanisms linking fitness and heterogeneity. Indeed, we provide long-sought support for the hypothesis that the juxtaposition of older forests and woodrat habitat promotes hunting success for spotted owls (Sakai and Noon 1993). The juxtaposition of these two habitats could both (i) promote the dispersal of individual woodrats from high-density populations in shorter (younger) forests into taller (more mature) forests, and (ii) allow spotted owls to capture woodrats at these ecotones (Sakai and Noon 1997). While we also found that spotted owls delivered prey biomass at a faster rate to nests when our measure of habitat heterogeneity was high, we caution that this result was strongly influenced by a single nest that was only monitored for a short period of time and for which it was unclear whether prey were delivered in several instances. While it may seem reasonable that fine-scale variation in forest age (as proxied by tree heights) could promote woodrat captures, we suggest that stronger evidence exists for the importance of edges between taller (older) and shorter (younger) forests. We note the edges promoting prey deliveries were typically the result of commercial timber management rather than wildfire in our study (e.g., Fig. 3C). None of the four territories with large values for edge in Fig. 5B experienced any recent severe fire. Importantly, however, the rate at which spotted owls delivered prey biomass to nests declined with the proportion of open forest in their territories (Fig. 5A). While some open areas, particularly those with substantial brush cover, likely harbor dense woodrat populations, large expanses are unlikely to be sources of prey to spotted owls unless sufficient taller (mature) forest is present in the vicinity.

Spotted owl reproductive output unexpectedly decreased with increasing proportions of mature forest and open forest, based on the most supported a priori model (Table 2). We expected that a greater proportion of mature forest would provide better

opportunities for nest site selection, concealment from predators, and protection from inclement weather conditions (Franklin et al. 2000) particularly since this forest type constituted a relatively small proportion of spotted owl 95% KDE home ranges (0.09, Table 1). However, a *post-hoc* interactive model suggested that reproductive output was relatively high when territories contained greater proportions of *both* mature and open forests. In the absence of a positive main effect for mature forest, we suggest that a more likely explanation for higher reproductive output in territories containing a mix of mature and open forest involves enhanced foraging success—particularly considering the benefits of edge habitat to prey deliveries to nests. A faster rate of prey biomass delivery by adult spotted owls to nests afforded by greater edge between mature and open forests is likely to reduce nestling mortality and nest abandonment by breeding females. Although we acknowledge that woodrat-prevalent edge did not explain appreciable variation in reproductive output, we suggest that landscapes characterized by an interspersed mature and open forest are likely to contain forest structural characteristics promoting the capture of woodrats, but we were unable to quantify these characteristics. Flying squirrels can be more abundant in mature forests, so that territories containing greater amounts of both forest types may harbor a greater diversity of prey types and overall prey availability. While the exact mechanism behind higher reproductive output in territories containing a mix of open and mature forest is uncertain, we suggest that enhanced prey access, hunting success, and deliveries to nests in territories with a mosaic of forest stand ages can lead to emergent benefits to spotted owl fitness in some ecological settings. Further, even if the association between reproductive output and mature and open forests were negative, as suggested by the top ranked a priori model, there was no evidence of greater commuting distances in territories with less medium-aged forest (and presumably greater heterogeneity).

Large scale loss and fragmentation of northern spotted owl (*S. o. caurina*) habitat from commercial timber harvesting appears to have contributed to population declines in the Pacific Northwest, where the Humboldt flying squirrel is the primary prey species (U.S. Department of Interior 1990). However, our results indicate that enhanced foraging opportunities in landscapes containing heterogeneous forest

conditions—with stands 10 s of ha in size—resulting largely from timber harvesting may benefit some fitness components (e.g., reproduction)—although we acknowledge that fire created some of this heterogeneity in 47 of the 151 territories (of these 47 territories, 33 were affected by less than 10% of fire across the territory). Previous work in the Sierra Nevada similarly suggested owls can have high reproduction and territory occupancy rates, as well as smaller home ranges, in such landscapes (Hobart et al. 2019a, b). Benefits of mosaics of forest of different ages are most likely to benefit spotted owls when younger and open forests retain the denser shrub cover and hardwood species (i.e., oaks) that promote dense woodrat populations. Moreover, there likely exists a threshold in terms of habitat modification where heterogeneous landscapes become fragmented by large expanses of open areas, reducing at least some fitness components and ultimately population density. However, further research is needed to understand the nature of such thresholds with respect to the composition and configuration of forest types not just within spotted owl home ranges, but at landscape scales as well. We also acknowledge that our results likely only apply to California spotted owls occurring in landscapes such as the low- to mid-elevation forests of the Sierra Nevada and higher elevation forests of southern California where woodrats can occur in high densities in younger forests and brushy open forests. Responses to changes in habitat composition and configuration are likely to differ in landscapes where flying squirrels are the primary prey of spotted owls, such as higher elevation forests in the Sierra Nevada (Hobart et al. 2019a). Finally, while our focus on reproductive output was appropriate given the tight linkage between prey availability and breeding often observed in owls (Dawson and Bortolotti 2000), other fitness components—such as individual survival and recruitment—can respond differently to habitat conditions (Franklin et al. 2000; Tempel et al. 2014). Nevertheless, while further work is needed to understand the relationship between habitat heterogeneity and spotted owl behavior, foraging success, and population dynamics in other forested landscapes, our study highlights new, integrative approaches (e.g., high temporal resolution GPS tags and nest video monitoring) that can yield novel insights into such questions.

Our results also have implications for the management of fire-suppressed forests on public land (i.e.,

national forests) where land managers are increasingly striving to reintroduce frequent, lower-severity fire regimes to promote forest heterogeneity and ultimately forest resilience to large, severe fires and droughts. While the benefits of forest heterogeneity to spotted owl foraging that we and previous studies have observed (e.g., Franklin et al. 2000; Atuo et al. 2019) was largely the result of commercial timber harvesting, lower-severity wildfire that creates fine-scale heterogeneity similarly benefits spotted owl foraging (Kramer et al. 2021a). In the evolutionary environment of spotted owls, patterns of forest heterogeneity were produced by fire, and owls appear to have become behaviorally adapted to such heterogeneity (Jones et al. 2020). Yet, from the perspective of the owl, the process generating heterogeneity may not be particularly critical. Hobart et al. (2019a) demonstrated using stable isotope analysis that spotted owl diets were similar (high proportion of woodrats) on both national parks and industrial timberlands, and that this similarity in diet was driven by landscape heterogeneity, albeit produced by different processes (fire and timber harvesting, respectively). Natural frequent-fire regimes create small patches of severely burned forests that become open (brushy) areas containing high woodrat densities in the early stages of regeneration (Converse et al. 2006); similar patterns of heterogeneity can be produced through forest management practices (North and Keeton 2008). Forest management that produces landscape heterogeneity, therefore, may result in the dual benefits of providing prey resources for spotted owls and increasing ecosystem resilience to drought and fire (North et al. 2021). Further research must downscale this broad generality to understand the landscape patterns, configurations, and scales that allow these two objectives to be achieved.

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Authors' contributions MZP, SCS, BPD, KNR, and JJK conceived the study; CJZ, RJG, BPD, and KNR led data collection, with contributions from KGK, WJB and SAW; CJZ, GMJ, HAK, JJK, and MZP designed the analysis; CJZ, GMJ, HAK, and MZP analysed the data; CJZ, GMJ, HAK and MZP wrote

the manuscript. All authors provided critical feedback and gave final approval for publication.

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Data availability Data and R code is available from CJZ on request.

Declarations

Competing interests The authors declare no conflict of interest.

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Severe fire has impacted populations of the California spotted owl more than fuels management or drought-related tree mortality

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ABSTRACT

Reducing fuel densities is the primary tool available to improve forest resilience to intensifying disturbance, but implementation is constrained by concern of effects to mature-forest associated species, such as spotted owls (*Strix occidentalis*). While the negative effects of severe fire on spotted owls are well studied, the influence of drought and fuels management on populations is uncertain, impeding fuels management. We integrated a novel dataset of California disturbance history with passive acoustic monitoring to compare the effects of severe fire, drought, and fuels management over 13 years on spotted owl occupancy across the Sierra Nevada, California, USA. Spotted owls were less likely to occupy 4 km² survey sites with a greater proportion of forest that burned at high severity and sites with a greater proportion of “heavier” fuels management (>25 % canopy reduction) but were insensitive to the proportion of “lighter” fuels management (<25 % canopy reduction) at sites. Across 7161 sites in the Sierra Nevada, severe fire resulted in an estimated loss of 482 occupied sites compared to only 65 lost from heavier treatments, owing to the limited implementation of fuels management in the region. Conversely, spotted owls were more likely to occur at sites containing a greater proportion of drought or other canopy reducing disturbance, presumably because of foraging opportunities facilitated by heterogeneous forest conditions. Thus, recent severe fire has had a greater negative effect on spotted owls than fuels management, underscoring the potential benefits of increasing the pace and scale of fuels management for promoting both forest resilience and conserving mature-forest species.

1. Introduction

Around the globe, forests are rapidly changing due to resource extraction and climate-induced shifts in disturbance regimes (Hansen et al., 2013; Hughes, 2003; Seidl et al., 2017). In turn, changes in forest structure and composition are having profound effects on mature-forest-associated species (Bonnot et al., 2018; Wich et al., 2003; Williams et al., 2003). Species reliant on mature forests are among the most affected by compositional and structural forest changes given their dependence on elements of forest structure that can take decades to centuries to regenerate, such as large trees (Lindenmayer et al., 2012; Lindenmayer and Laurance, 2017). In addition, as mature-forest species are often restricted to relatively narrow habitat conditions, yet may be

locally abundant within those conditions, effects of change in their habitat can be difficult to attribute over broad spatial scales. Given clustered abundance of mature forest specialists in suitable habitat, localized surveys may not capture small, but meaningful, changes in the broader population. Therefore, mitigating the effects of shifting disturbance regimes and land use on mature-forest species at broad scales can be challenged by uncertainties in which changing environmental factors are impacting populations, and how.

The spotted owl (*Strix occidentalis*), which uses mature forests for nesting, roosting, and often foraging (Jones et al., 2018; Ward and Noon, 1998; Zulla et al., 2022) is among the most well-studied wildlife species globally (Löhms, 2004; Gutiérrez, 2008). As such, the spotted owl resides at the center of many forest planning efforts across western North

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America. Within seasonally dry forests, such as those in the Sierra Nevada, California, California spotted owl (*Strix occidentalis occidentalis*) habitat has experienced substantial change over the past century due to shifting disturbance regimes and land use changes. Post-colonial exclusion of Indigenous fire and suppression of natural ignitions, coupled with the selective harvesting of large trees, has resulted in forest densification and homogeneity biased toward smaller, shade-tolerant and fire-intolerant trees (Collins et al., 2017; Taylor et al., 2016). This densification, combined with climate warming, has increased the intensity, frequency, and magnitude of fire and drought (Crockett and Westerling, 2018; Stephens et al., 2018; Westerling et al., 2006). Large, severe fires now define forest structure across the Sierra Nevada (Cova et al., 2023) killing a high proportion of mature trees and converting forest to shrubland over increasingly large areas (Steel et al., 2022). Indeed, several recent studies have demonstrated that large patches of severe fire have persistent negative impacts on spotted owl habitat and populations (Jones et al., 2016, 2021b; Kramer et al., 2021; McGinn et al., 2025).

While the effect of severe fire on spotted owls is well documented, the impacts of drought-related tree mortality on spotted owls have not been assessed. Increased severity and frequency of drought conditions combined with intensified tree competition for water due to forest densification has induced landscape scale water stress over the last two decades, particularly in the southern Sierra Nevada (Stephens et al., 2018). Prolonged drought can exacerbate bark beetle outbreaks and associated tree mortality (Kolb et al., 2016) and promote fire due to resulting dry fuel (Steel et al., 2022; van Mantgem et al., 2009). While bark-beetle induced tree mortality is a natural disturbance agent in the Sierra Nevada and can create mosaics of age-classes in mature-forests, drought-driven outbreaks can result in mass tree mortality, often affecting large-diameter trees most acutely due to their greater water needs (Steel et al., 2022; Stephenson et al., 2019). Indeed, bark beetle outbreaks have caused more tree mortality than fires in the Southern Sierra Nevada in recent decades (Hicke et al., 2016), highlighting the need for research on the effects of drought-related tree mortality on mature forest species. Further, extensive tree mortality also increases the risk of fire in the Sierra Nevada by increasing fuel loads and fuel continuity, inextricably linking the direct effects of drought to its indirect effects via high severity fire (Cansler et al., 2024; Crockett and Westerling, 2018; Keen, 1929; Stephens et al., 2022).

In response to the rise in disturbance severity, land managers are striving to increase implementation of management to reduce fuels (dead/down debris, shrubs, and small/medium diameter trees) across the Sierra Nevada to promote resilience to severe fire, reduce drought-related tree mortality, and reduce tree densities (North et al., 2022; Stephens et al., 2020). Within dry, frequent-fire forests, such as those in the Sierra Nevada, many studies have shown that reducing surface fuels via mechanical or hand thinning can reduce post-fire tree mortality, lower landscape-scale fire severity, increase post fire seedling regeneration, and increase post-fire heterogeneity (Cansler et al., 2022; Liang et al., 2018; Stephens et al., 2009, 2020; Tempel et al., 2015; Tubbesing et al., 2019). Given spotted owls prefer to forage in areas with denser understory, where larger-bodied prey are abundant (Hobart et al., 2019; Tempel et al., 2015; Ward and Noon, 1998), thinning has the potential to negatively impact spotted owl habitat in the short-term by removing ladder fuels and surface vegetation. Some studies have detected negative effects of fuels management on spotted owl occupancy and nocturnal habitat use, but these were limited in temporal scales, spatial scales, and sample size, and were unable to distinguish among different types of management (Gallagher et al., 2019; Stephens et al., 2014; Tempel et al., 2015). In contrast, some studies have found slight positive or neutral effects of fuels management on spotted owls, though these studies were also limited in sample size (Irwin et al., 2015, 2013; Lee and Irwin, 2005). Along with financial and access-based constraints, concern over the effects of fuels management on spotted owls is restricting the pace and scale at which these practices are implemented (Collins et al., 2010;

Kramer et al., 2021). As such, fuels management implementation in California is insufficient to meet California's restoration goals (Knight et al., 2022). Despite several decades of research, the relative effects of intensifying disturbance and the management necessary to reduce severe disturbance in spotted owl habitat remains uncertain – embodying the dilemma confronting the conservation of mature-forest species in general.

Here, we leveraged a Sierra Nevada-wide passive acoustic monitoring program and a novel dataset of disturbance history within the Sierra Nevada to compare effects of three disturbance types on spotted owls: severe fire, drought-related tree mortality, and fuels management. Because spotted owls use complex mature forest for roosting, nesting, and foraging, we hypothesized that the disturbance type exerting the most substantial influence on prevalence of large-diameter trees, canopy complexity, and understory density will have the greatest effect on spotted owl site occupancy. Thus, we predicted that the proportion of a site that has burned at high severity will have a greater negative impact on occupancy than the proportion of a site that experienced drought-related tree mortality or fuels management, given severe fire's impacts on all three metrics of forest structure. We also predicted that drought-related tree mortality will have a greater negative impact on site occupancy than fuels management as drought-related tree mortality most significantly affects large trees whereas fuels management typically retains large trees. Further, we predicted that more intense management with a greater reduction in canopy cover would have a greater negative impact on site occupancy than less intense management with a lesser reduction in canopy cover. At the population level, given the limited extent of fuels management in the Sierra Nevada, we predicted that severe fire and drought-related tree mortality have negatively impacted the number of occupied sites to a greater extent than fuels management. Finally, we compared the extent of severe fire and drought-related tree mortality and determined their relative effects on the estimated number of occupied sites across the study area. This study is the first to effectively compare the relative effects of the primary agents of forest change in the Sierra Nevada.

2. Methods

2.1. Study area

We conducted ecosystem-scale passive acoustic monitoring across the western slope of the Sierra Nevada, California in 2021 and 2022. The western slope is comprised of woodland and chaparral at low elevations dominated by *Quercus* species, that transitions to mixed-conifer forest at mid elevations, dominated by *Pinus* species, and *Abies* dominated sub-alpine forest at high elevations (Steel et al., 2015). Following over a century of fire suppression, forests of the Sierra Nevada currently have higher stem densities per hectare, higher densities of smaller-sized trees, and a greater proportion of shade-tolerant tree species (Knapp et al., 2013). The Sierra Nevada climate is characterized as Mediterranean, with warm, dry summers and cool, wet winters. Acoustic surveys spanned almost all suitable spotted owl habitat, entailing 28,644 km² across seven national forests (80.5 %), private land (18.1 %), and land owned by other entities (1.4 %; Kelly et al., 2023), with elevation ranging in the study areas from 226 to 3985 m. This area was overlaid with a grid of 4 km² hexagonal sites, the approximate size of spotted owl territories (Fig. 1; Wood et al., 2019). The total sampling grid includes 7161 sites, and we sampled a total of 758 sites and 776 in 2021 and 2022 respectively, with 705 sites sampled in both years.

2.2. Acoustic sampling

We deployed autonomous recording units (ARU; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) in non-contiguous sites to reduce the chance of detecting individual spotted owls in adjacent sites (i.e., reduce “ecological” false detections; Berigan and Jones

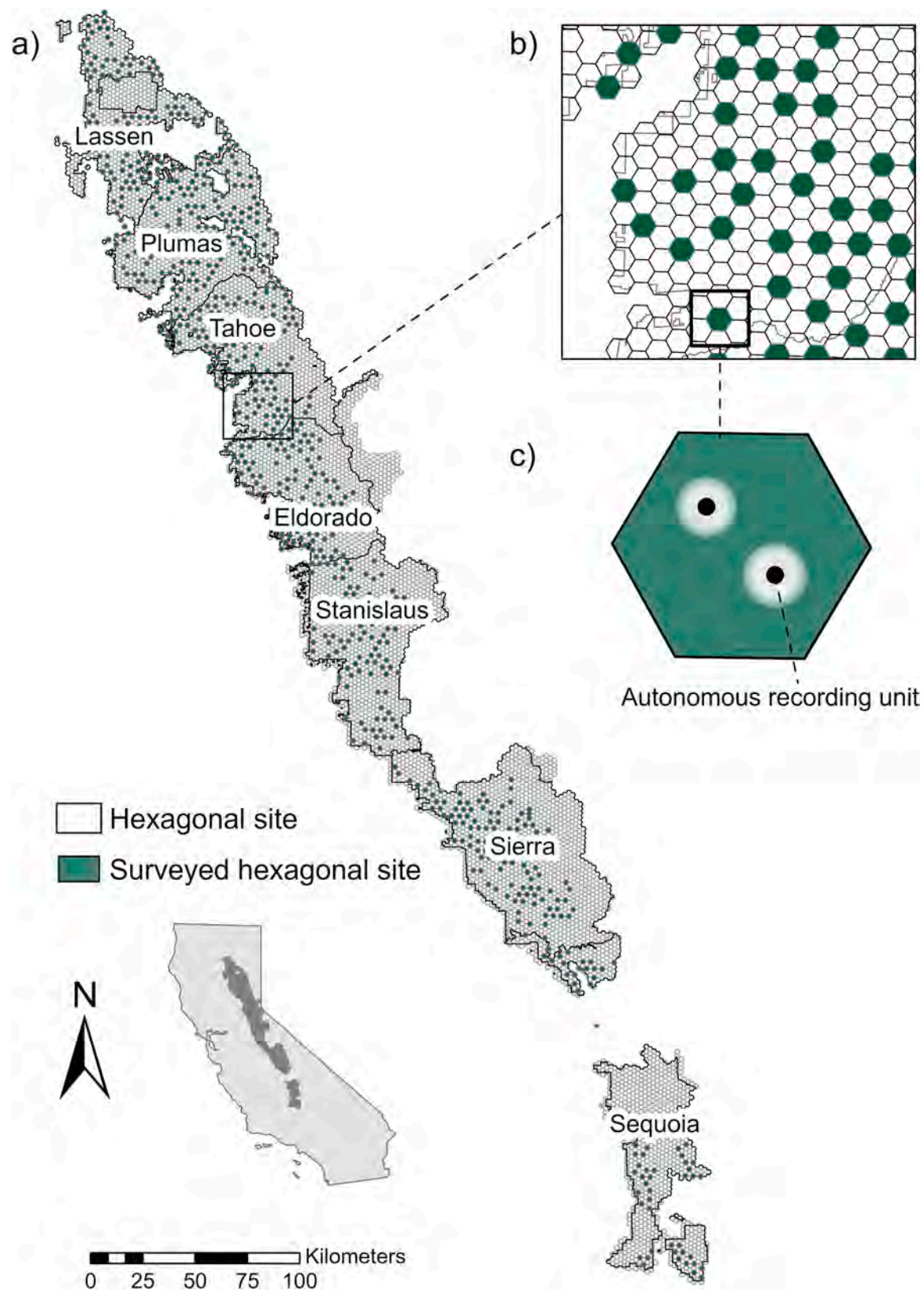


Fig. 1. Location of the a) bioacoustic monitoring study area overlaid with the hexagonal survey grid, b) surveyed sites in green, and c) autonomous recording units across seven national forests in the Sierra Nevada, California.

et al., 2019). Depending on road and trail access, one to four, but generally two ARUs were placed in a site, at least 500 m from each other and 250 m from the hexagonal site border. We attached ARUs to trees around chest height in acoustically advantageous locations within hexagonal sites (e.g. along ridgetops) and programmed the units to record overnight from 18:00–09:00 PDT. We deployed ARUs between early April and mid-July and recorded for five weeks continuously, with the entire deployment period spanning from May 03 – July 19 for 2021 and April 07 – August 08 for 2022. ARUs had a single omni-directional microphone and were programmed to record at a sample rate of 32 kHz with + 33 dB gain and 16-bit resolution.

To identify spotted owl vocalizations, we used audio data from 20:00–6:00 PDT, totaling 10 h per night. Surveyed hexagonal sites were treated as the sampling unit such that detections were pooled across ARUs within sites. We analyzed all audio using BirdNET, a deep convolutional neural network that provides a unitless prediction score for each 3 s interval of audio data that ranges from 0 to 1 representing the algorithm's confidence that a species' vocalization was recorded. We used a customized version of BirdNET which was overfit to the vocalizations of Sierra Nevada species, as well as the recording hardware and settings used in this project (Kahl et al., 2021). Following Kelly et al. (2023), all predictions with a score > 0.989 were verified by manually review in Raven 2.0 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2023). False-positives and audio determined to contain imitated spotted owl vocalizations (as part of playback surveys conducted by other groups) were removed (Berigan et al., 2019; Reid et al., 2021). Thus, we only worked with confirmed true-positive spotted owl detections.

2.3. Disturbance data

We developed a spatially- and temporally-explicit disturbance dataset that differentiates between wildfire, fuels management, and drought/other at 30 m resolution, detailed in Kramer et al. (2025). Briefly, we describe the methods used to develop each disturbance component relevant to this analysis.

We calculated fire severity at a 30-meter resolution following Cova et al. (2023) and Parks et al. (2019), and obtained fire perimeters from the California Department of Forestry and Fire Protection Fire and Resource Assessment Program (CALFIRE FRAP). These fires include wildfire from both non-prescribed human and natural ignitions, but prescribed fire was included in the forest management dataset (see below). We classified a given pixel as high severity when the composite burn index (CBI) was ≥ 2.25 , consistent with severity classification described by Miller et al. (2009) and Miller and Thode (2007).

To characterize patterns in drought or other canopy reducing disturbance and intensity of fuels management, we used the Ecosystem Disturbance and Recovery Tracker (eDaRT) Mortality Magnitude Index (MMI; Koltunov et al., 2020; Slaton et al., 2024). The eDaRT algorithm uses Landsat imagery to estimate the probability that canopy cover changed at 8- or 16-day intervals at 30 m resolution. The MMI product uses eDaRT to estimate the magnitude of these disturbances on an annual time scale, with any given pixel ranging from 0 to 100 representing an estimated 0–100 % loss of canopy cover.

We mapped fuels management activities using a modified version of the USFS Activity Tracking System (FACTS), which contains spatial records of all USFS activities (USDA) and classified intensity using eDaRT MMI. First, from FACTS we filtered for entries with fuels management codes to test our predictions that fuels management impacted spotted owls, accounted for activities lacking completion data, and applied temporal buffers that capture 91 % of change on the landscape due to fuels management activities (Kramer et al., 2025). Importantly, because FACTS data only describe management activities on land managed by the USFS, we were only able to account for management on USFS-managed land. As such, we used a land ownership layer that classed USFS-managed and non-USFS-managed land and included the

proportion of USFS-managed land as an occupancy covariate to account for forest management on non-USFS-managed land, primarily even aged commercial timber harvesting, (see *Occupancy modeling* section). We characterized fuels management pixel intensity as “lighter” (lesser canopy cover reduction) versus “heavier” (greater canopy cover reduction) using pixel-scale eDaRT MMI values. For instance, an MMI score of 25 corresponds to 25 % canopy loss within a pixel, calculated on an annual basis, and summed across the 13-year span for a survey site. We considered several potential MMI thresholds through visual inspections of NAIP imagery and we ultimately selected a threshold of 25 MMI (25 % canopy cover reduction) as it yielded (1) a visible distinction between more and less intensive forest management activities (Figs. 2) and (2) a reasonable number of non-zero values for both lighter and heavier intensity management at the scale of the 4 km² hexagonal survey sites.

We used MMI data to delineate areas of drought or other canopy reducing disturbance when a pixel was not within a fire perimeter or a fuels management area. We visually assessed several MMI thresholds using the National Agriculture Imagery Program (NAIP), beginning with a minimum threshold of 10 (Slaton et al., 2024) and ending at a threshold of 20, where MMI thresholds stricter than 20 did not provide a reasonable sample size of non-zero values. We ultimately used a minimum MMI threshold of 12, equivalent to a 12 % canopy reduction within a pixel, as it visually matched a known gradient in drought (Fettig et al., 2019) and provided a large enough sample size of sites with non-zero values. We refer to these pixels as “drought/other” as they represent areas with high levels of canopy cover loss which could be due to drought or other canopy reducing disturbance types (e.g. insect or disease damage unrelated to drought, blowdown, or landslides). Through visual inspections of areas mapped as drought/other against aerial imagery and knowledge of the disturbance history of the area (Asner et al., 2016; Fettig et al., 2019), we were confident that the majority of this mortality was due to drought associated agents. Although the MMI data covered all land ownerships, we could not differentiate between drought or other and forest management on non-USFS managed land (see below), so as with fuels management, we were only able to estimate drought/other on USFS managed land.

Finally, we compiled annual rasters for each disturbance component across a 13-year span (2008–2020 and 2009–2021). Although a pixel could only be assigned a single disturbance type for any given year, pixels in the 13-year composite could have experienced multiple disturbances. For each sampled 4 km² site, we calculated the proportional area affected by each disturbance type for each 13-year span, with all disturbance types individually ranging from 0 to 1 corresponding to 0–100 % of the site disturbed (Fig. 2).

2.4. Occupancy modeling

We tested whether site-level, survey-level, and annual covariates influenced detection and occupancy probabilities (Mackenzie et al., 2002). To do so, we fit a single model using the package “unmarked” (Fiske, 2011) in Program R (R. Core Team, 2025). We used a single-season stacked occupancy modeling framework and considered the effect of year on both detection and occupancy probabilities (Burnett and Roberts, 2015; Fogg et al., 2014; MacKenzie et al., 2002) given we were more interested in regional patterns in occupancy than extinction and colonization dynamics and our surveys were limited to two years. By “stacking” yearly detection histories we increased our effective sample size, with each site and year combination functioning as an independent site and thus supporting the estimation of a greater number of predictor variables. This method has the potential to underestimate error by pseudo-replicating sites; however, we felt this method was preferable to a multi-season model as we were focused on identifying clear disturbance associations and we included year as a fixed effect on occupancy and detection to account for variation between years.

We divided the continuous summer season of sampling into eighteen

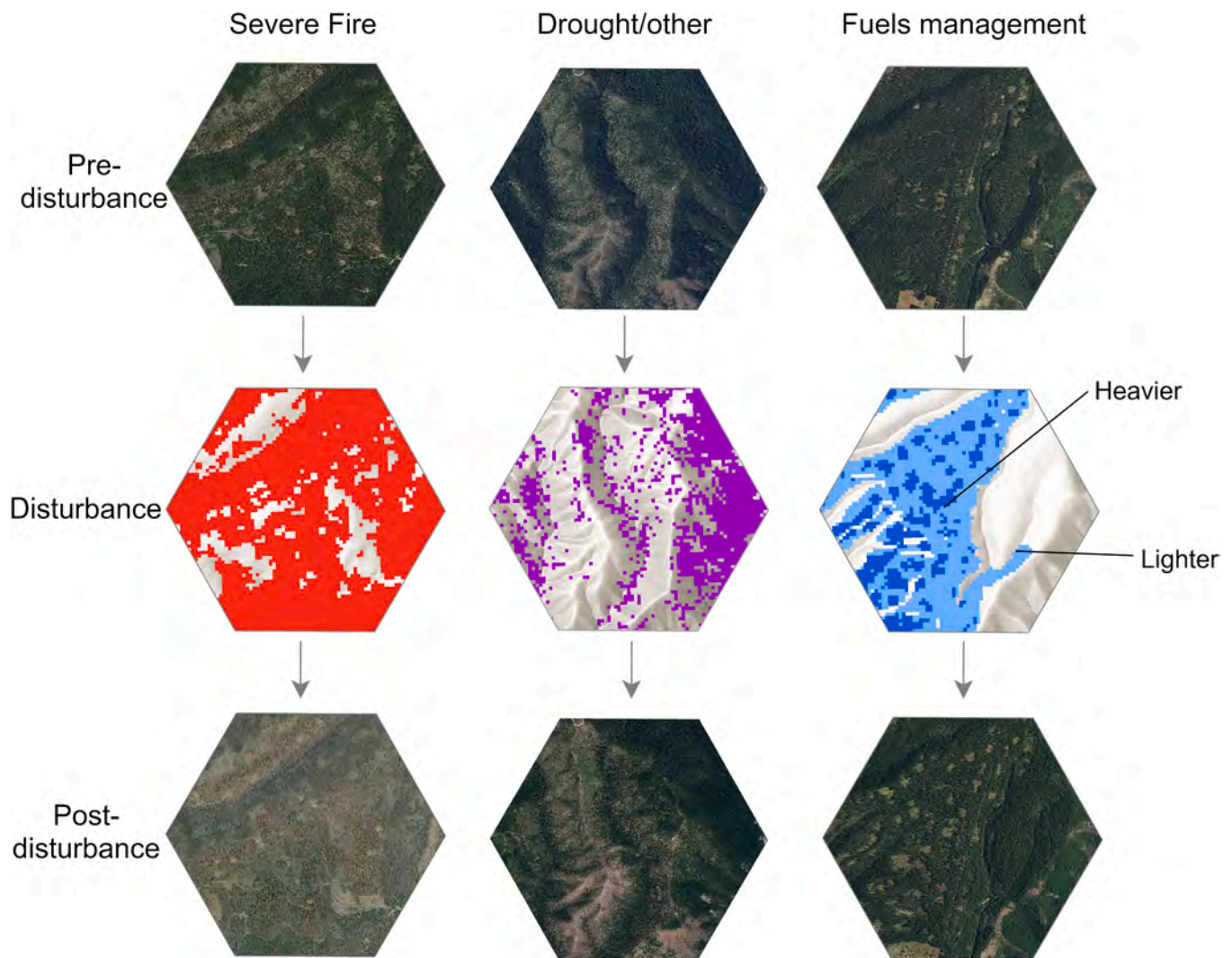


Fig. 2. NAIP imagery of survey sites before and after each disturbance type. Canopy loss attributed to drought/other is difficult to see with the naked eye, highlighting the need for eDaRT and MMI. Highlighted areas indicate the disturbance footprint identified from the [Kramer et al. \(2025\)](#) dataset. Imagery brightness was increased by 10 % to highlight disturbed areas.

week-long secondary sampling periods (j), or visits. Survey effort per visit (up to 80 h of audio per unit) was included as a detection covariate; a visit was considered null if no audio was recorded. For each site, we used a two-night detection criteria where a site (i) was assigned a 1 if there was a confirmed vocalization within that visit, as well as on at least one other different night within a season ([Kelly et al., 2023](#)), or assigned a 0 if these criteria were not met. This method reduced the likelihood of an ecological false-positive and increased the likelihood that the vocalization was from resident owl ([Berigan et al., 2019](#)). Following previous analyses of this acoustic dataset, we used an established global detection model that included survey effort (hours surveyed per visit within a site), secondary sampling period date (mean sampling date of each visit), and categorical year as effects on detection (p) probability ([Winiarski et al., 2024](#); [Winiarski et al., in press](#)). We modeled the probability of site occupancy using the following topographic and landownership variables: the proportion of USFS land, elevation, and latitude (in California Albers projection). Within the Sierra Nevada, bird species distributions vary by latitude and elevation ([Saracco et al., 2011](#); [Siegel et al., 2011](#); [Winiarski et al., 2025](#)). Therefore, to control for the effect of latitude on elevation, we modeled a linear relationship (elevation $\sim$ latitude) and used the residuals to estimate “latitude-corrected elevation”. In addition, we included a quadratic term for secondary sampling period date, to account for potential peaks in calling

activity during the breeding season, and for latitude-corrected elevation to account for peaks in occupancy along elevation gradients. To avoid confounding our disturbance covariates, we did not use any metrics of forest-structure in our model as our disturbance data was more recent than the available forest-structure dataset. We Z standardized all continuous covariates. We modeled the probability of site occupancy using the proportion of a site that experienced severe fire, drought/other, heavier management, and lighter management over the prior 13-years. We drew inferences from a global site occupancy model that included all the aforementioned covariates representing factors potentially affecting detection and occupancy probabilities, assessing the statistical significance of each estimated parameter based on overlap of the 95 % confidence intervals with 0.

2.5. Estimating the number of occupied sites lost or gained to disturbance and management

Using our occupancy model, we estimated the total number of occupied sites lost or gained in association with each disturbance or management type across the entire 7161 site sampling grid for the 2009–2021 period. Our framework was analogous to the “scope for management” approach introduced by [Norris and McCulloch \(2003\)](#) to assess the effects of environmentally-induced changes in survival and

reproductive probabilities on population numbers. To do so, we first estimated predicted occupancy (Ψ) for each site i given the area that was disturbed (or managed for fuels) where D_i represented proportional disturbed area within a site:

$$\text{logit}(\Psi_{i,\text{disturbed}}) = \beta_0 + \beta_1 D_i$$

We then estimated predicted occupancy for each site assuming no disturbance had occurred (i.e., $D_i = 0$):

$$\text{logit}(\Psi_{i,\text{undisturbed}}) = \beta_0$$

Both predictions were made assuming observed values at site i for the topographic and landownership covariates included in the site level occupancy model. Then we estimated the difference in predicted occupancy for each site i between the disturbed and undisturbed scenarios ($\Delta\Psi_i$) as follows:

$$\Delta\Psi_i = \Psi_{i,\text{undisturbed}} - \Psi_{i,\text{disturbed}}$$

By summing the difference between predicted site occupancy of disturbed sites assuming disturbance did versus did not occur, we estimated the expected number of occupied sites lost or gained from each type of disturbance ($\Delta\Psi_{\text{total}}$) as:

$$\Delta\Psi_{\text{total}} = \sum_{i=1}^n \Delta\Psi_i$$

We also estimated the proportional change in occupancy, $\Delta\Psi_{\text{proportional}}$, caused by each disturbance across the 13-year period by dividing $\Delta\Psi_{\text{total}}$ by the sum of predicted occupancy assuming no disturbance had occurred:

$$\Delta\Psi_{\text{proportional}} = \frac{\Delta\Psi_{\text{total}}}{\sum_{i=1}^n \Psi_{i,\text{undisturbed}}}$$

3. Results

3.1. Passive acoustic surveys

In 2021, we deployed 1476 ARUs across 758 four-km²-hexagonal survey sites and in 2022, we deployed 1616 ARUs across 778 hexagonal survey sites, with 705 sites sampled in both years out of the total 7161 hexagonal cells within the grid. In total, 490,823 and 515,692 h were recorded in 2021 and 2022 respectively. Based on the two detection night criteria, naïve occupancy (the proportion of sites with a spotted owl detection) was similar in 2021 (0.293) and 2022 (0.281). When corrected for detection, mean occupancy was estimated as 0.245 and 0.259 for 2021 and 2022 respectively.

3.2. Disturbance mapping

The proportion of area experiencing heavy and light fuels management within hexagonal cells ranged from 0 to 0.495 and 0–0.993, respectively, with means of 0.023 (standard deviation (SD): 0.05) and 0.115 (SD: 0.146), respectively. The proportion of area experiencing drought/other within hexagonal cells ranged from 0 to 0.934, with an average of 0.228 (SD: 0.164), and the proportion area experiencing severe fire within hexagonal cells ranged from 0 to 0.998, with a mean of 0.163 (SD: 0.276).

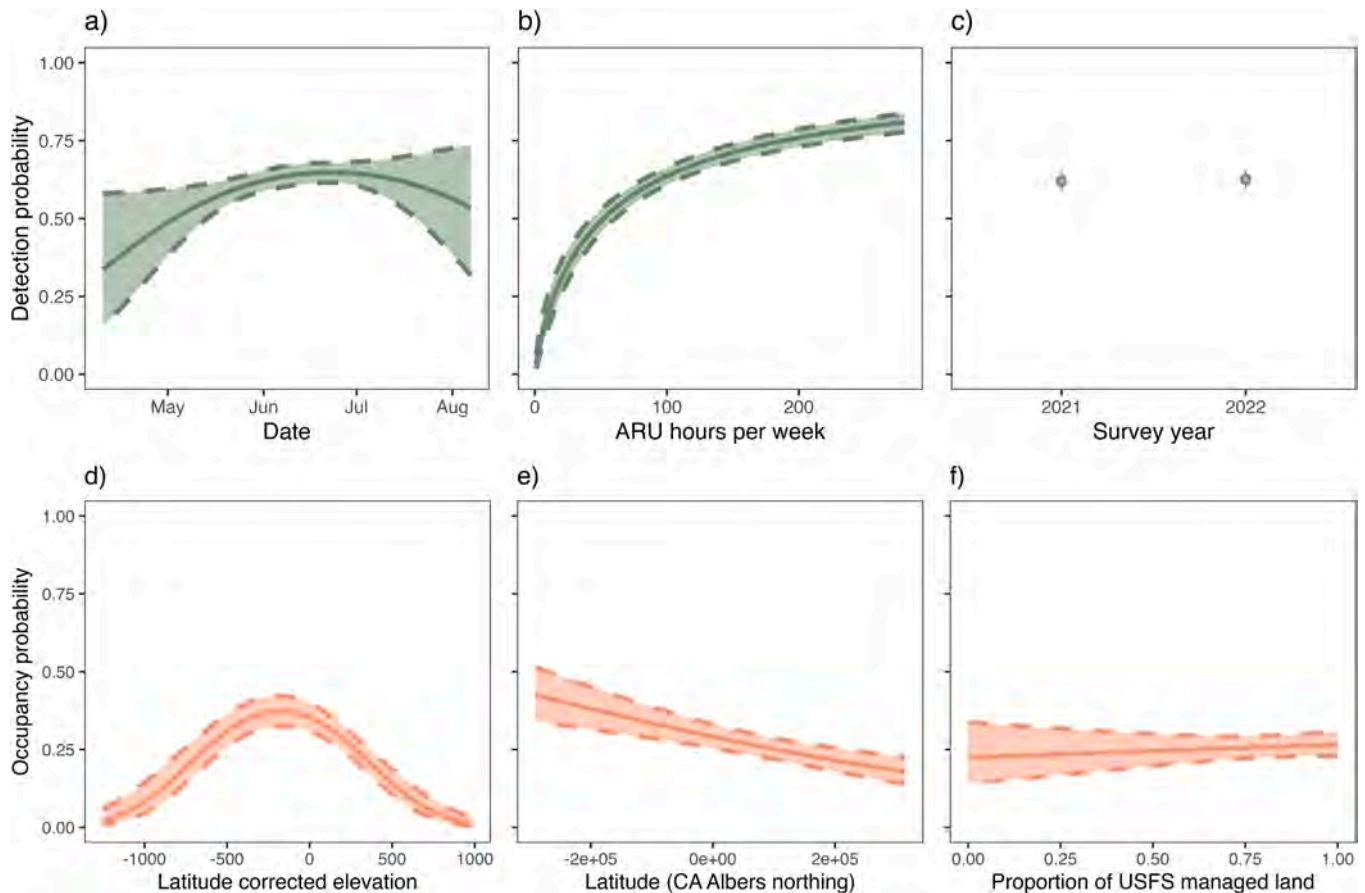


Fig. 3. Detection probabilities for a) mean survey date and b) survey hour per week and c) survey year and occupancy probabilities for d) latitude corrected elevation, e) latitude (CA Albers northing) and f) proportion of USFS land in a survey site where shaded bars represent predicted 95 % confidence intervals.

3.3. Site level occupancy analysis

3.3.1. Detection probability

Mean predicted detection probability across sites was 0.665 (95 % confidence interval (CI) [0.634 – 0.694]) and 0.670 (95 % CI [0.638 – 0.700]) in 2021 and 2022, respectively. The probability of detecting a spotted owl at a given site increased more survey effort (β : 0.571, 95 % CI [0.479 – 0.662]; Fig. 3b). Spotted owls were more likely to be detected in the middle portion of our seasonal survey period as indicated by a positive linear (β : 0.590, 95 % CI [0.014 – 1.166]) and negative quadratic (β : -0.491, 95 % CI [-1.060 – 0.079]) relationship with mean date of the visit, with detection peaking around mid-June (Fig. 3a). Predicted seasonal detection probability of detecting an owl present at a survey site over a typical 5-week sampling period was 0.996 for both 2021 and 2022 (Fig. 3c).

3.3.2. Effects of topography and landownership on occupancy

Spotted owl occupancy peaked at low-to-mid elevation sites, after controlling for latitude (linear β : -0.400, 95 % CI [-0.556 – -0.235],

quadratic β : -0.590, 95 % CI [-0.749 – -0.431]; Fig. 3d) and was highest in the southern Sierra Nevada (β : -0.307, 95 % CI [-0.443 – -0.171]; Fig. 3e). Occupancy did not vary based on the proportional area of USFS landownership (β : 0.052, 95 % CI [-0.096 – 0.201]; Fig. 3f).

3.3.3. Effects of disturbance and management on occupancy

Spotted owls were less likely to occur at sites with more severe fire (β : -0.689, 95 % CI [-0.852 – -0.526] Fig. 4a) and sites where heavier management was implemented (β : -0.203, 95 % CI [-0.355 – -0.052]; Fig. 4c). We did not find support for an effect of lighter management on site occupancy; while the relationship was positive (β : 0.077, 95 % CI [-0.054 – 0.208] Fig. 4d), confidence intervals overlapped 0. In contrast, spotted owls were more likely to occur at sites with more drought/other (β : 0.341, 95 % CI [0.197 – 0.485]; Fig. 4b).

The negative effect of severe fire on spotted owl site occupancy was three times greater than the negative effect of heavier management on site occupancy based on the magnitude of the coefficients. However, this difference was likely attributable to the standardization of covariates where, for example, a 1 standard deviation change resulted in much

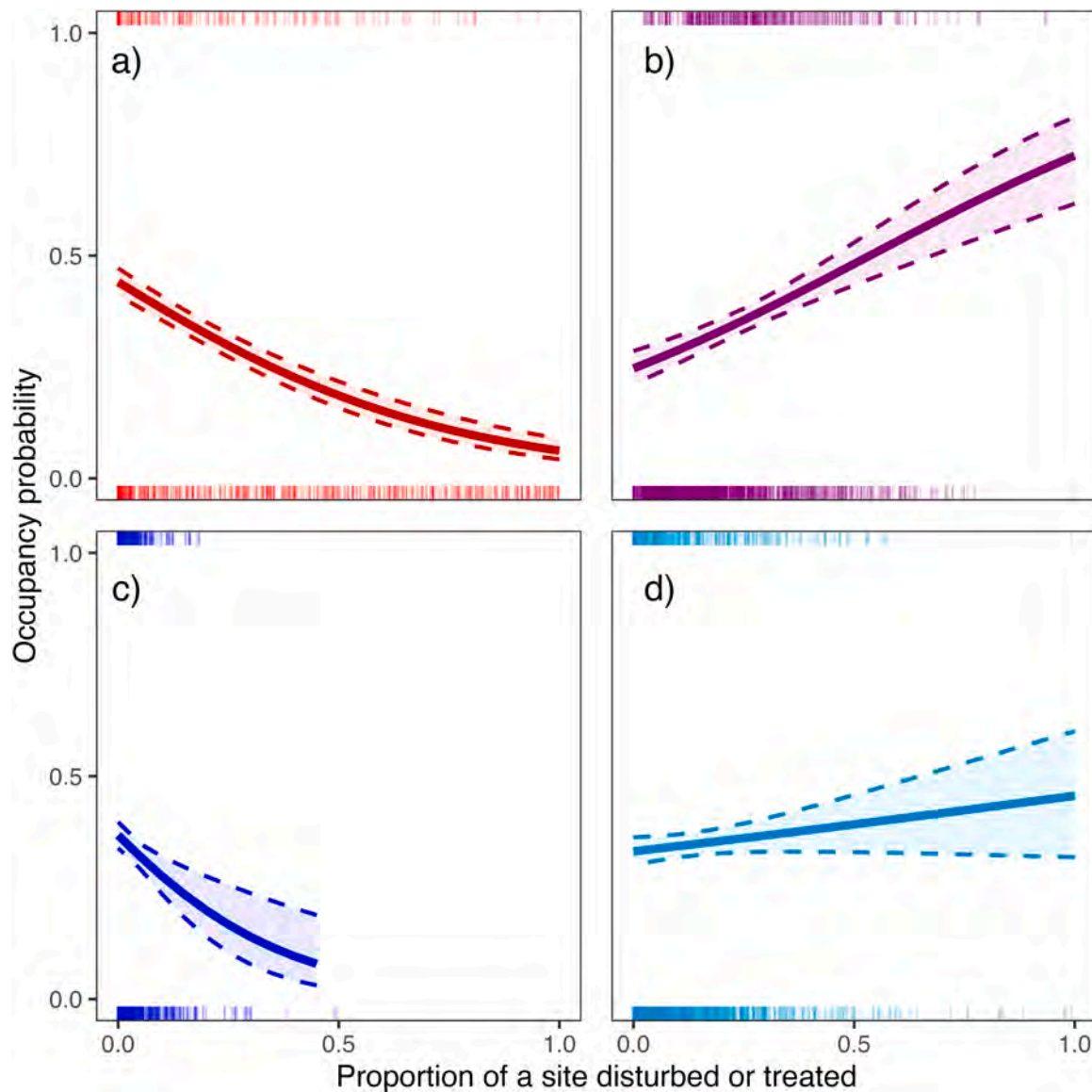


Fig. 4. Occupancy probability as a function of the proportion of a site that was a) severely burned, b) experienced drought/other, or c) heavier and d) lighter fuels management. Estimates end at sampled disturbance maximum. Shaded area indicates 95 % predicted confidence intervals. Rug ticks along the top indicate sites where spotted owls were detected, while ticks along the bottom indicate proportion of disturbance in sites where spotted owls were not detected.

smaller magnitude of change in the proportion of a site experiencing heavier treatment than it would in the magnitude of change in the proportion of a site experiencing severe fire. When all other variables were held constant at their mean values within the dataset, the maximum proportion of a site severely burned (0.998) led to a 0.379 decline in occupancy, from 0.441 to 0.063, while the maximum value of heavier management (0.495) led to a similar 0.302 decline in occupancy, from 0.368 to 0.066.

3.4. Total sites lost or gained to disturbance

When total gains/losses were averaged across all sites and then compared to estimated mean occupancy, severe fire led to a proportional decline ($\Delta \Psi_{\text{proportional}}$) in occupancy per site of 27.6 % (mean change ($\Delta \Psi$) of -0.063 from 0.291 to 0.228 per site) while heavier management only led to a proportional decline in occupancy of 3.5 % (mean change of -0.008 from 0.236 to 0.228 per site). Drought/other led to a proportional increase in occupancy of 24.1 % (mean change of 0.055 from 0.173 to 0.228 per site) and lighter management led to a proportional increase in occupancy of 2.2 % (mean change of 0.005 from 0.233 to 0.228 per site).

Severe fire had the greatest influence on the estimated number of sites occupied by spotted owls ($\Delta \Psi_{\text{total}}$), with an estimated loss of 482 occupied sites out of 7161 total sites (Table 1). By contrast, heavier management resulted in an estimated loss of only 65 occupied sites – more than 7 times fewer than the decline incurred by severe fire. This difference was in part attributable to the fact that heavier treatments were only implemented over only 2.3 % of the study area, whereas severe fire occurred over 16.3 % of the study area, over the past 13 years. Drought/other led to an estimated gain of 440 occupied sites and lighter management led to an estimated gain of 39 occupied sites (Table 1; Fig. 5). In Fig. 6, we provide map-based examples of lower occupancy in severely burned and heavy fuels management areas, and higher occupancy in areas with lighter fuels management and drought/other.

4. Discussion

4.1. Summary of results

Concern over the effects of fuels management on mature-forest associated species continues to impede efforts to promote forest resilience in the face of increasingly large and severe wildfires and drought-

Table 1

Population-level results describing changes in occupancy from four different disturbance types. Mean change in occupancy probability caused by each disturbance or management type is equal to [average occupancy probability with disturbance] minus [average occupancy probability without disturbance]. Proportional change in occupancy is equal to the average change in occupancy caused by each disturbance divided by average occupancy. The total number of occupied sites lost or gained to each disturbance is the difference in occupancy between occupancy with and without each disturbance summed across all sites, rounded to the nearest whole number.

	Severe fire	Drought/other	Heavier management	Lighter management
Average true occupancy – average predicted occupancy had each disturbance not occurred	0.228 – 0.291	0.228 – 0.173	0.228 – 0.236	0.228 – 0.223
Mean change in occupancy ($\Delta \Psi$)	-0.063	0.055	-0.008	0.005
Proportional change in occupancy ($\Delta \Psi_{\text{proportional}}$)	-0.276	0.241	-0.035	0.022
Number of occupied sites gained or lost ($\Delta \Psi_{\text{total}}$)	-482	440	-65	39

related tree mortality. Leveraging a large-scale passive acoustic monitoring program and a novel synthetic dataset mapping spatial and temporal patterns in forest disturbance and management, this study is the first to simultaneously assess the effects of implemented fuels management on a mature-forest associated species and compare these effects to the impact of severe fire and drought at a regional scale. Our results supported our hypothesis that recent high-severity wildfire has negatively impacted spotted owls more than fuels management. When summed across the study area, over the prior 13 years, severe fire led to a loss of 482 occupied sites, while heavier management led to loss of only 65 occupied sites and lighter management resulted in a gain of 39 occupied sites, out of the total 7161 sites. Further, despite suggestions of drought-related tree mortality as a threat to spotted owl conservation (Jones et al., 2021b), this study is the first to demonstrate that spotted owls are actually more likely to occur at sites with a greater proportion of drought/other, and adds to the growing body of literature on the effects of shifting disturbance regimes in western forests on old-forest associated species.

4.2. Corroborating the negative effects of severe fire on spotted owls

As predicted, spotted owls were less likely to occur at sites with a greater proportion of forest that burned severely within the past 13 years – consistent with the large body of research on the relationship between spotted owls and fire. While spotted owls in the Sierra Nevada and other seasonally dry forests appear adapted to a frequent-fire regime consisting of mostly lower severity fire with relatively small patches of higher severity fire, many recent studies have demonstrated that spotted owls are ill adapted to increasingly severe, large, homogenous fire. For example, Jones et al. (2016) found a seven-fold increase in extinction probability at severely burned survey owl territories following the 2014 King Fire, with follow-up studies revealing persistent negative effects on nesting habitat and low territory recolonization up to two decades post severe fire (Jones et al., 2021b; McGinn et al., 2025). Moreover, large and homogenous severe wildfire eliminates spotted owl foraging habitat as foraging spotted owls typically avoid large patches of severely burned area and select for heterogenous areas burned at lower or mixed severity (Eyes et al., 2017; Jones et al., 2020; Kramer et al., 2021). Stable spotted owl populations in national parks characterized by partially restored fire regimes (Conner et al., 2013; Kramer et al., 2021) compared to declining populations in areas that have experienced large severe fires (Jones et al., 2021b; Winiarski et al., in press) indicate that territory-scale effects of wildfire dynamics have landscape and even regional scale population level effects; consistent with our finding that severe fire had the largest population level effect relative to fuels management and drought/other.

Thus, our study further dispels an incorrect narrative that spotted owls are insensitive to large severe fires. In the most comprehensive analysis at the time, Lee (2018) found that severe fire did not reduce spotted owl occupancy, vital rates, or nocturnal habitat selection – with potential analytical and methodology issues and inferences debated by Jones et al. (2020) and Lee (2020). However, all 9 studies published since Lee (2018), including this one, have documented significant adverse effects of severe fire on some measure of spotted owl population or foraging ecology (Brunk et al., 2025a; Jones et al., 2021b, 2020; Kramer et al., 2021; McGinn et al., 2025; McGinn et al., 2023; Schofield et al., 2020; Tempel et al., 2022; Winiarski et al., in press) including a recent large-scale meta-analysis involving 1514 northern and California spotted owl territories and 171 GPS tagged owls (McGinn et al. in review). By contrast no published papers have found large severe wildfire to be benign to spotted owls since the publication of Lee (2018). Some have suggested that declines in spotted owl populations can be attributed to post-fire salvage logging, but the amount of salvage logging is generally relatively small, particularly on public lands, with no or weaker effects than severe fire (Jones et al., 2021b, 2016; McGinn et al., 2025). Thus, the debate is settled – large severe fires pose a major threat

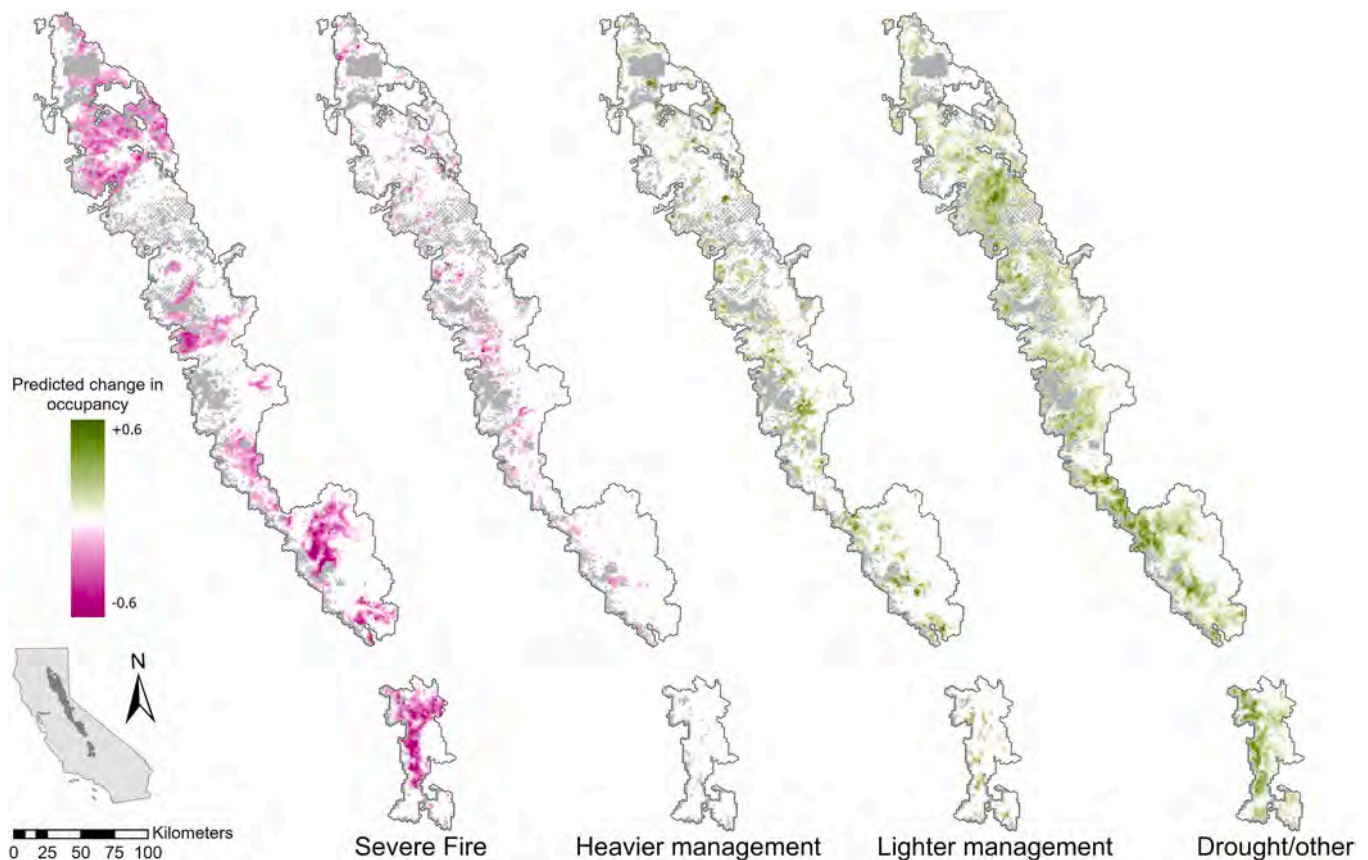


Fig. 5. Changes in occupancy caused by a) severe fire, b) heavier fuels management, c) lighter fuels management, and d) drought/other across the Sierra Nevada. Negative changes in occupancy are shown in pink, and positive changes are shown in green. Non-USFS land is shown in gray.

to spotted owls and forest restoration efforts may be needed to curb this threat (see also below).

4.3. Benefits of drought/other to spotted owls

While the adverse effects of severe fire on spotted owls are clear, the potential impacts of drought-related tree mortality on spotted owls have been uncertain. Drought and associated tree mortality are natural processes shaping seasonally dry forests, where under normal conditions, drought-related tree mortality can create a mosaic of seral stages and promote forest resiliency (Asner et al., 2016; Stephens et al., 2018). However intensifying drought events have led to mass tree mortality, leading to uncertainty in how mature-forest species will respond and how to manage drought-affected forests (Fettig et al., 2019). Contrary to our prediction, spotted owls were more likely to occur at survey sites with a greater proportion of drought/other. Given that our acoustically based detections were obtained from both crepuscular and nocturnal periods, when owls may be in roost or nest areas or quite far from them, we suspect that owls may be selecting for areas with greater proportions of drought/other as a result of improved foraging conditions. Specifically, following historical densification and homogenization of Sierra Nevada forests, drought-related tree mortality of some conifer trees may create more gaps and openings in the forest, and thus more fine-scale forest heterogeneity that may benefit larger-bodied prey such as dusky-footed woodrats (*Neotoma fuscipes*; Kuntze et al., 2023). Indeed, spotted owls have higher prey capture success, consume more woodrats, and deliver more prey biomass to nests in territories with more heterogeneous forest conditions (Hobart et al., 2019; Wilkinson et al., 2023; Zulla et al., 2022). In contrast with high severity fire, drought-related tree mortality kills but does not eliminate trees, resulting in high remaining biomass. Dusky-footed woodrats are more likely to occur at

sites with higher understory cover and dead and down debris (Kuntze et al., 2025), which may be enhanced by drought-related tree mortality. Moreover, hardwoods such as oaks (*Quercus* spp.), which provide masting food resources for prey, are more resilient to drought, but are also often overtopped by dense conifers. These species may increase in vigor as the canopy thins as a result of drought-related tree mortality, potentially also promoting foraging opportunities for owl prey species like the dusky-footed woodrat.

Despite the putative benefits of drought/other to nocturnally foraging spotted owls, drought could compromise other life-history activities and potentially lead to population declines over the long-term via compounded interactions with other disturbance effects. As a cold-adapted species, spotted owls typically spend warmer daytime hours roosting in mature forest stands characterized by cooler microclimates (Barrows, 1981). Drought-related tree mortality is typically biased towards larger trees in the Sierra Nevada (Steel et al., 2022; Stephenson et al., 2019), which reduces canopy cover and complexity, inevitably leading to warmer microclimates. McGinn et al. (2023) found that roosting spotted owls were regularly exposed to temperatures above their thermoneutral zone during heatwaves, with potentially adverse effects on populations. Thus, the potential immediate benefits of drought-related tree mortality to foraging success may be outweighed by long-term negative physiological effects, when considered in the currency of fitness. Drought-related tree mortality could also negatively impact spotted owls given dead woody biomass can amplify fire severity and post-fire tree mortality (Cansler et al., 2024; Crockett and West-erling, 2018; Stephens et al., 2022). As such, drought-affected forests may precipitate another trade-off where spotted owls benefit from increased foraging opportunities but experience greater loss of nesting and foraging habitat from drought-fueled severe fires. Clearly, more research is needed to understand the multi-faceted ways in which

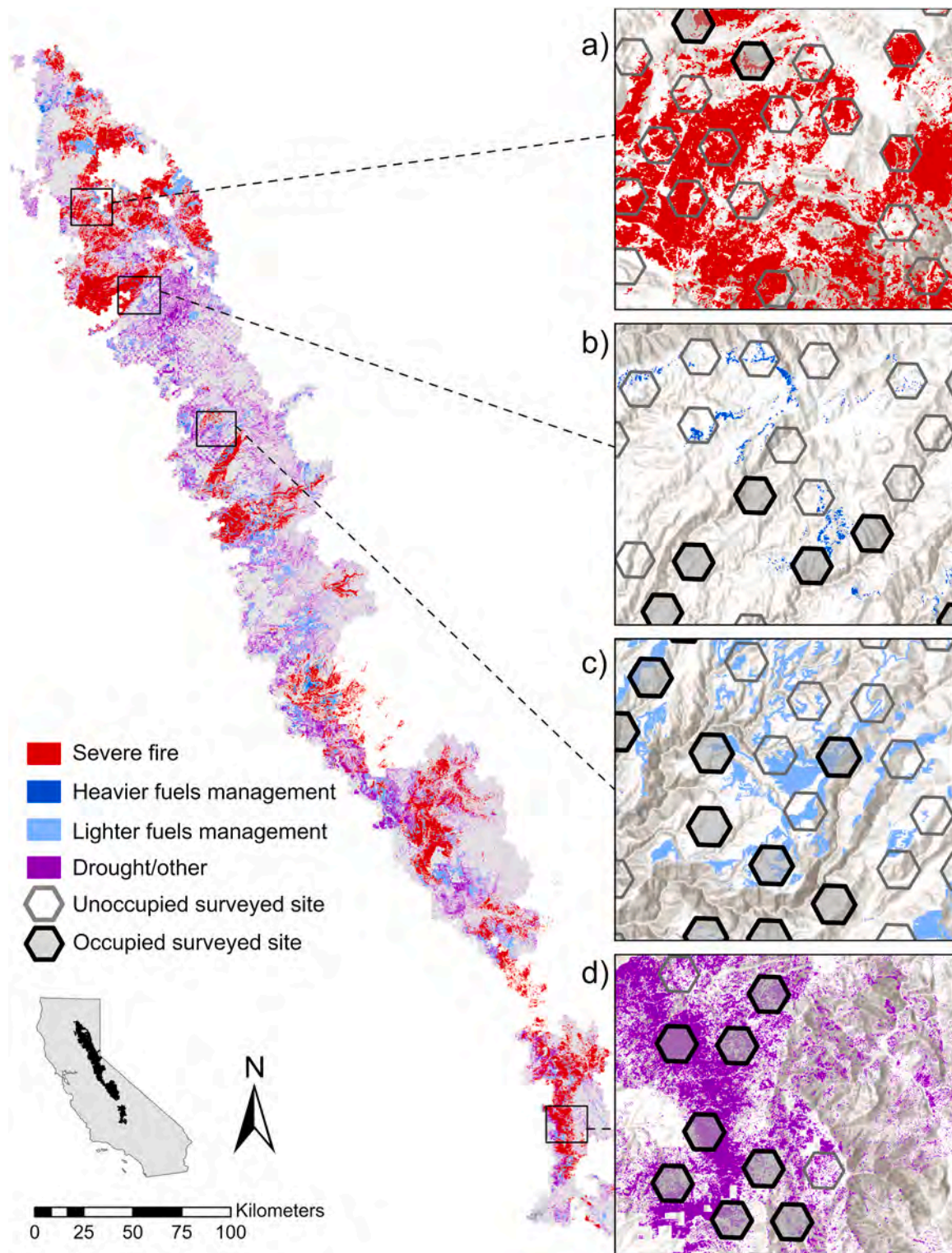


Fig. 6. a) High severity fire, b) heavier fuels management, c) lighter fuels management, and d) drought/other mapped across the monitoring grid with surveyed hexes in bold outline and color of hexes indicating occupancy status. Each zoomed in map contains only the relevant disturbance type.

drought affects spotted owls, biodiversity broadly, and, ultimately, drought-prone and drought-affected forests.

4.4. Fuels management effects depend on treatment intensity

Concern over the potential effects of fuels management on spotted owls has constrained efforts to promote resilient forests (Peery et al.,

2017). Some previous studies have detected short-term negative effects of fuels management on spotted owl habitat (Tempel et al., 2015), nocturnal habitat use (Gallagher et al., 2019), occupancy (Seamans and Gutiérrez, 2007; Stephens et al., 2014; Tempel et al., 2022), and demographic rates (Tempel et al., 2014), while others found neutral or positive effects of fuels management on spotted owl space use (Irwin et al., 2015, 2013; Lee and Irwin, 2005). Yet inferences from these

studies were limited by small sample sizes of territories with fuels management or ability to distinguish fuels management from other forest management activities or natural disturbances. Assessments of fuels management effects on spotted owls have also been challenged by limitations with the quality of available fuels management data, including inconsistencies, errors, and missing information in the FACTS database (Knight et al., 2022). However, the creation of the fuels management and forest disturbance dataset by Kramer et al. (2025) combined with bioregional-scale acoustic monitoring allowed us to conduct the first comprehensive assessment on the effects of different intensities of fuels management on spotted owls – or any mature-forest associated species.

We found diverging effects of fuels management based on fuels management intensity, where spotted owls were less likely to occur at sites with greater proportional area of heavier fuels management (>25 % canopy cover reduction) but insensitive to the proportional area of lighter fuels management at a survey site (<25 % canopy cover reduction). Moreover, when summed across the population, heavier fuels management led to an estimated loss of 65 occupied sites, while lighter management led to an estimated gain of 39 occupied sites, with a net estimated loss from fuels management of 26 occupied sites. Thus, our results were consistent with predictions that recent fuels management has negatively affected spotted owl occupancy, depending on intensity, but that the negative effect was small relative to severe fire. However, the maximum value of heavier fuels management reduced occupancy by a similar amount as the maximum value of severe fire, suggesting that implementation of heavier fuels management at the scale of recent severe fire may produce comparable declines in occupancy.

While heavier fuels management implemented at broader scales may cause similar near-immediate declines in spotted owl occupancy as severe fire, fire and forest modeling analyses suggest heavier fuels management may provide longer term benefits to spotted owls by curbing severe fire activity (Ager et al., 2007; Jones et al. 2024; Jones et al., 2021a; McGinn et al., 2025; Tempel et al., 2014). Importantly, McGinn et al. (2025) found that heavier fuels management provides net benefits to spotted owl occupancy within megafire footprints by reducing the adverse effects of severe fire compared to sites that were untreated. Further, fuels management activities in the Sierra Nevada are estimated to last around 20 years before fuel loads return to pre-management levels (Agee and Skinner, 2005; Stephens et al., 2012). In contrast, large, continuous patches of severe fire can prompt failed conifer regeneration, leading to type conversion, and effectively converting forested land to non-forested land (Collins et al., 2011; Dove et al., 2020). As such, negative effects of fuels management will likely be short term until vegetation regrows (Tempel et al., 2015), compared to potential long-term type conversion of essential spotted owl habitat attributed to uncharacteristic severe fire.

These diverging effects of management based on intensity suggest that managers can strategically combine management of heavier intensity and lighter intensity management to both balance negative occupancy influences while reducing risks to occupancy loss from severe fire (see *Management Implications* below). Given that spotted owls nest and roost in areas with large trees, high canopy cover, and understory density, management that significantly reduces canopy cover (i.e., “heavy management”) will reduce occupancy, potentially by reducing nesting habitat quality, increasing predation risk, or producing unfavorable microclimates – as is potentially the case with drought/other. Conversely, management that creates greater structural heterogeneity may improve spotted owl habitat quality via enhanced prey populations, as described above. Our categorization of management is delineated only on the degree of canopy cover reduction as quantified with MMI, leaving the effects of altering specific elements of forest structure, such as ladder fuels or canopy base height, less clear.

Further research could assess space usage, including foraging, nesting, and roosting, in response to fuels management activity leveraging the new fuels management dataset developed by Kramer et al. (2025)

and assessing spotted owl responses to specific management activities. In addition, while spotted owls function as an effective indicator species for mature, closed forests, effects of fuels management on indicator species of other habitat preferences, such as the olive-sided flycatcher (*Contopus cooperi*) which are associated with mature, open forests, will be important to support broader avian communities (Brunk et al., 2025b). Nevertheless, our results demonstrate that the effects of fuels management vary by intensity, with lighter management having negligible effects on spotted owl occupancy compared to measurable negative effects of heavier management on spotted owl occupancy. However, the effects of fuels management were ultimately eclipsed by the negative effects of severe fire at both the site and population level.

5. Management implications

While reducing fuel loads and severe fire risk in the Sierra Nevada and conserving spotted owl habitat have long been perceived as conflicting objectives (Peery et al., 2017), our findings – in conjunction with previous work – suggests that resilience-oriented management could benefit spotted owl conservation. Specifically, fuels management activities that reduce canopy cover by < 25 % are unlikely to adversely impact spotted owl occupancy or populations, even when implemented broadly across home ranges and landscapes. Moreover, prior work indicates that forest structural components targeted in fuels management, such as increasing canopy base height, reducing ladder fuels, and reducing canopy bulk density can promote spotted owl foraging habitat (Wright et al., 2023). However, lighter intensity fuels management activities may not yield desired reductions in severe fire behavior if implemented exclusively (McGinn et al., 2025), whereas heavier intensity management that reduces canopy cover by > 25 % is more likely to curb severe fire (McGinn et al., 2025) but potentially reduce spotted owl occupancy. Nevertheless, our results, in conjunction with numerous previous studies, indicate that wildfire has had a greater impact on spotted owls than fuels management (Barry et al., 2025; Jones et al., 2021a; McGinn et al., 2025; Wright et al., 2023) and that fuels management, that reduces canopy cover by < 25 % are unlikely to negatively affect spotted owl populations (Ager et al., 2007; Jones et al., 2021a; McGinn et al., 2025; Tempel et al., 2015). Heavier fuels management activities, which can have negative effects on spotted owl populations, may need to be implemented judiciously to avoid detrimental effects, for example outside of high quality nesting habitat or within areas unsuitable for supporting denser forest conditions (ridge-tops, south-facing slopes), in combination with lighter management activities, could promote spotted owl viability as the climate rapidly warms. Risks to spotted owls can be mitigated by targeting small- and medium-diameter trees while retaining large-diameter trees used for nesting (Jones et al., 2021a), roosting (McGinn et al., 2023), and foraging activities (Wright et al., 2023; Zulla et al., 2022, 2023).

While we have found evidence of synergies between fuels management and spotted owl conservation, the management of drought-prone and drought-affected forests and their impact on spotted owls are less certain and likely more complex. Managers often target drought-prone forests for reductions in tree densities to lower competition and water stress, and ultimately increase resistance to direct drought mortality and bark beetle-associated mortality (Bernal et al., 2023; Restaino et al., 2019; Vernon et al., 2018). While drought/other increased site occupancy for spotted owls, presumably by enhancing foraging conditions and/or as they may be the only remaining forested conditions in the vicinity of large-severe fires, further reductions in tree densities could negate these benefits in the future while reducing the secondary risk of loss of severe fire. Drought-related tree mortality likely reduces the quality and availability of nesting habitat, increases the likelihood and intensity of subsequent wildfires (Cansler et al., 2024; Stephens et al., 2018), and potentially exacerbates the adverse effects of severe fire on spotted owls. As such, we do not suggest a “hands-off” management approach that may promote drought-related tree mortality with the

intention of promoting spotted owl habitat. Moreover, fuels management within areas already affected by extensive drought/other may be needed to reduce the risk of severe wildfires in the future, despite potential impacts to what may be high quality spotted owl foraging habitat. Clearly, more research is needed to understand the trade-offs associated with managing drought-prone and drought-affected forests in the context of changing fire regimes and mature-forest conservation.

6. Conclusions

Shifting disturbance regimes are altering mature forests and in turn, mature-forest associated species, prompting novel management dilemmas. Our work demonstrates that severe fire has led to greater declines in occupancy than lighter fuels management or heavier fuels management. Additionally, our work, in conjunction with other recent studies, suggests strategic implementation of management at varying intensities may benefit spotted owl populations. There appears to be synergy in the conservation of mature-forest species and forest restoration, and intentional fuel management can promote success for both objectives. Further research could evaluate direct effects of distinct management activities, explore the nuanced effects of drought and other canopy reducing disturbance, and expand management and disturbance analyses to avian communities within the Sierra Nevada.

CRedit authorship contribution statement

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The data that has been used is confidential.

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