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

JENNIFER A. BLAKESLEY,[1] Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA
BARRY R. NOON, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA
DAVID R. ANDERSON, Colorado Cooperative Fish and Wildlife Research Unit, 201 Wagar, Colorado State University, Fort Collins, CO 80523, USA

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.

JOURNAL OF WILDLIFE MANAGEMENT 69(4):1554–1564; 2005

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 dominated by large trees (>61-cm diameter at breast height [dbh]) and have moderate to high levels of canopy cover (≥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

---

[1] E-mail jab@cnr.colostate.edu

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 km^2 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 2001*a*), 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 categories 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/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 = 8–11 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 ≥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

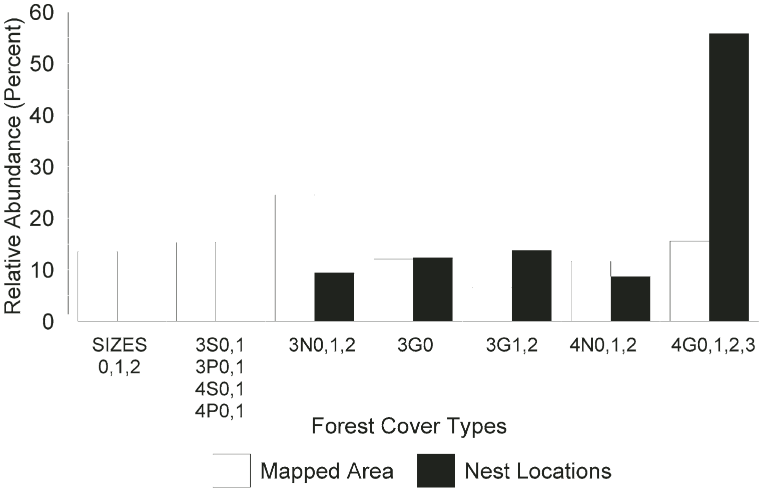

Fig. 1. Relative abundance (percent) of different cover types within circular plots (radius 2.4 km) around 67 California spotted owl site centers in northeastern California, USA, and relative abundance (percent) of nesting attempts (*n* = 138) within cover types. Cover type codes are described in text.

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), $\hat{\beta}$(T) = –0.33, SE ($\hat{\beta}$) = 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 ($\hat{\beta}$[SELCCG] = 0.0044, SE [$\hat{\beta}$] = 0.0019), whereas the amount of nest area dominated by medium-sized trees with canopy cover >70% and the amount of area unforested or dominated by small trees were negatively associated with site occupancy ($\hat{\beta}$[OTHCCG] = –0.0038, SE [$\hat{\beta}$] = 0.0015; $\hat{\beta}$ [NON] = –0.0094, SE [$\hat{\beta}$] = 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, $\hat{\beta}$ [ELEV] = –0.00044, SE [$\hat{\beta}$] = 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 ϕ [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: $\hat{\beta}$ [NESTUSE] = 0.242, SE [$\hat{\beta}$] = 0.141; best model containing SELREM: $\hat{\beta}$ [SELREM] = 0.242, SE [$\hat{\beta}$] = 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 {ϕ (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 + SELCCGREM + OTHCCGREM + NON)	–160.57	7	335.56	1.29	0.10
O (T + Elev + SELCCGREM + OTHCCGREM)	–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: $\hat{\beta}$ = –0.488, SE ($\hat{\beta}$) = 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: $\hat{\beta}$[ELEV] = –0.00078, SE [$\hat{\beta}$] = 0.00035; $\hat{\beta}$[NON] = –0.0080, SE [$\hat{\beta}$] = 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: $\hat{\beta}$[REMNANT 0] = –0.826, SE [$\hat{\beta}$] = 0.247), and higher in size class 3 than size class 4 stands ($\hat{\beta}$[SIZE CLASS 3] = 0.636, SE [$\hat{\beta}$] = 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.

	Site occupancy		Apparent survival		Reproductive output	
Covariate[a]	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
SELCCGREM	0.31	Positive	0.12	Positive	–	–
OTHER	–	–	0.06	Negative	–	–
OTHCCG	0.50	Negative	–	–	–	–
OTHCCGREM	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)	K	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 + SELCCGREM)	Core	–197.03	9	412.63	1.62	0.06
ϕ (Year + SELCCGREM)	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)	K	AIC_c	ΔAIC_c	w_i
R (Year + Elev + NON)	Nest	–114.55	8	245.67	0.00	0.11
R (Year + Elev)		–115.74	7	245.93	0.26	0.09
R (Year + Elev + NESTUSE)	Nest	–115.27	8	247.13	1.46	0.05
R (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.

		Unique nests ($n = 132$)		Nest uses ($n = 174$)[a]	
Code	Definition	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)	K	AIC_c	ΔAIC_c	w_i
S (Remnant + SizeClass)	–64.29	4	112.46	0.00	0.60
S (Remnant + SizeClass + Remnant * SizeClass)	–64.26	5	114.58	2.12	0.21
S (Remnant)	–67.49	3	115.50	3.04	0.07
S (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 interspersion 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.

ACKNOWLEDGMENTS

J. A. Fites-Kaufmann of the U.S. Forest Service completed vegetation mapping and contributed funding to our project. Thanks to the many individuals who collected owl and vegetation data over many years, especially D. W. H. Shaw for supervising the Lassen spotted owl demography study from 1998 to 2003. We thank P. L. Kennedy and W. H. Romme for reviewing previous versions of this manuscript. Major funding was provided by the U.S. Forest Service Region 5 and the Pacific Southwest Research Station. Administrative support was provided by the Colorado Cooperative Fish and Wildlife Research Unit and the Department of Fishery and Wildlife Biology, Colorado State University. C. W. Boal, M. L. Morrison, and 2 anonymous referees helped us improve earlier drafts of this manuscript.

LITERATURE CITED

ANDERSON, D. R., AND K. P. BURNHAM. 2002. Avoiding pitfalls when using information–theoretic methods. Journal of Wildlife Management 66:912–918.

BIAS, M. A., AND R. J. GUTIÉRREZ. 1992. Habitat associations of California spotted owls in the central Sierra Nevada. Journal of Wildlife Management 56:584–595.

BINGHAM, B. B., AND B. R. NOON. 1997. Mitigation of habitat "take:" application to habitat conservation planning. Conservation Biology 11:127–139.

BLAKESLEY, J. A. 2003. Ecology of the California spotted owl: breeding dispersal and associations with forest stand characteristics in northeastern California. Dissertation, Colorado State University, Fort Collins, USA.

———, D. R. ANDERSON, AND B. R. NOON. 2006. Breeding dispersal in the California spotted owl. Condor 108:71–81.

———, B. R. NOON, AND D. W. H. SHAW. 2001. Demography of the California spotted owl in northeastern California. Condor 103:667–677.

BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5:1–437.

———, AND ———. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Second edition. Springer-Verlag, New York, USA.

CALL, D. R., R. J. GUTIÉRREZ, AND J. VERNER. 1992. Foraging habitat and home-range characteristics of California spotted owls in the Sierra Nevada. Condor 94:880–888.

FORSMAN, E. D., R. G. ANTHONY, E. C. MESLOW, AND C. J. ZABEL. 2004. Diets and foraging behavior of northern spotted owls in Oregon. Journal of Raptor Research 38:214–230.

FRANKLIN, A. B., D. R. ANDERSON, E. D. FORSMAN, K. P. BURNHAM, AND F. F. WAGNER. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. Studies in Avian Biology 17:12–20.

———, ———, R. J. GUTIÉRREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

———, R. J. GUTIÉRREZ, J. D. NICHOLS, M. E. SEAMANS, G. C. WHITE, G. S. ZIMMERMAN, J. E. HINES, T. E. MUNTON, W. S. LAHAYE, J. A. BLAKESLEY, G. N. STEGER, B. R. NOON, D. W. H. SHAW, J. J. KEANE, T. L. MCDONALD, AND S. BRITTING. 2004. Population dynamics of the California spotted owl: a meta-analysis. Ornithological Monographs 54.

GOODBURN, S. F. 1991. Territory quality or bird quality? Factors determining breeding success in the magpie *Pica pica*. Ibis 133:85–90.

GUTIÉRREZ, R. J., J. VERNER, K. S. MCKELVEY, B. R. NOON, G. N. STEGER, D. R. CALL, W. S. LAHAYE, B. B. BINGHAM, AND J. S. SENSER. 1992. Habitat relations of the California spotted owl. Pages 79–98 *in* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould Jr., and T. W. Beck, editors. The California spotted owl: a technical assessment of its current status. U.S. Forest Service General Technical Report PSW-133.

HERGER-FEINSTEIN QUINCY LIBRARY GROUP FOREST RECOVERY ACT [HFQLG]. 1998. Title IV of the Department of the Interior and related agencies appropriations act. October 21, 1998. Washington, D.C., USA.

HUNSAKER, C. T., B. B. BOROSKI, AND G. N. STEGER. 2002. Relations between occurrence and productivity of California spotted owls and canopy cover. Pages 687–700 *in* J. M. Scott and P. J. Heglund, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Covelo, California, USA.

LaHaye, W. S., R. J. Gutiérrez, and D. R. Call. 1997. Nest-site selection and reproductive success of California spotted owls. Wilson Bulletin 109:42–51.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Moen, C. A., and R. J. Gutiérrez. 1997. California spotted owl habitat selection in the Central Sierra Nevada. Journal of Wildlife Management 61:1281–1287.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Olson, G. S., E. Glenn, R. G. Anthony, E. D. Forsman, J. A. Reid, P. J. Loschl, and W. J. Ripple. 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. Journal of Wildlife Management 68:1039–1053.

Sakai, H. F., and B. R. Noon. 1993. Dusky-footed woodrat abundance in different-aged forests in northwestern California. Journal of Wildlife Management 57:373–382.

SAS Institute. 2000. SAS/STAT software. Version 8. SAS Institute, Cary, North Carolina, USA.

Sierra Nevada Ecosystem Project. 1996. Status of the Sierra Nevada: assessment summaries and management strategies. Volume 1. Wildland Resources Center Report Number 36, University of California, Davis, USA.

U.S. Forest Service. 1998. Sierra Nevada science review: report of the science review team charged to synthesize new information of rangewide urgency to the National Forests of the Sierra Nevada. U.S. Forest Service, Pacific Southwest Region. Sacramento, California, USA.

———. 2001. Sierra Nevada forest plan amendment final environmental impact statement. Volumes 1–6. U.S. Forest Service, Pacific Southwest Region. Vallejo, California, USA.

———. 2004. Record of decision: Sierra Nevada forest plan amendment final supplemental environmental impact statement. U.S. Forest Service, Pacific Southwest Region, Vallejo, California, USA.

Verner, J., R. J. Gutiérrez, and G. I. Gould Jr. 1992. The California spotted owl: general biology and ecological relations. Pages 55–78 *in* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, editors. The California spotted owl: a technical assessment of its current status. U.S. Forest Service General Technical Report, PSW-133.

Ward, J. P., Jr., R. J. Gutiérrez, and B. R. Noon. 1998. Habitat selection by northern spotted owls: The consequences of prey selection and distribution. Condor 100:79–92.

Waters, J. R., and C. J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. Journal of Wildlife Management 59:858–866.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimates from populations of marked animals. Bird Study 46:120–138.

Zabel, C. J., G. N. Steger, K. S. McKelvey, G. P. Eberlein, B. R. Noon, and J. Verner. 1992. Home-range size and habitat-use patterns of California spotted owls in the Sierra Nevada. Pages 149–163 *in* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, editors. The California spotted owl: a technical assessment of its current status. U.S. Forest Service General Technical Report, PSW–133.

Associate Editor: Boal.