

Effects of forest management on California Spotted Owls: implications for reducing wildfire risk in fire-prone forests

DOUGLAS J. TEMPEL,^{1,4} R. J. GUTIÉRREZ,² SHEILA A. WHITMORE,¹ MATTHEW J. REETZ,¹ RICKA E. STOELTING,¹
WILLIAM J. BERIGAN,¹ MARK E. SEAMANS,³ AND M. ZACHARIAH PEERY¹

¹Department of Forest and Wildlife Ecology, 1630 Linden Drive, University of Wisconsin, Madison, Wisconsin 53706 USA

²Department of Fisheries, Wildlife and Conservation Biology, 1980 Folwell Avenue, University of Minnesota, St. Paul, Minnesota 55108 USA

³Division of Migratory Bird Management, 755 Parfet Street, Suite 235, U.S. Fish and Wildlife Service, Lakewood, Colorado 80215 USA

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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⁴ E-mail: dtempel@wisc.edu

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>

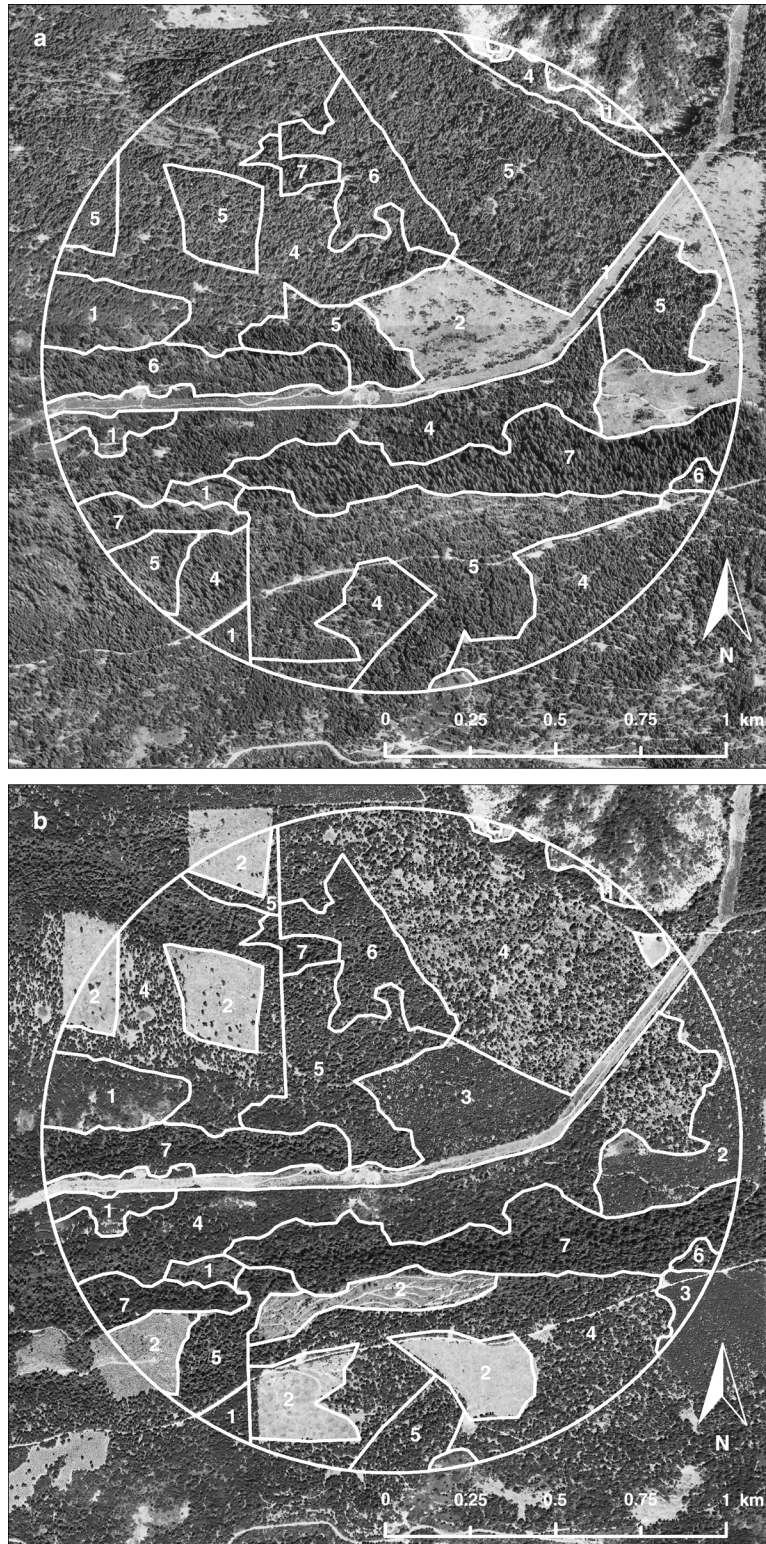


FIG. 1. Example of a vegetation cover map based on aerial photographs taken in 1993 (a) and 2012 (b) for a California Spotted Owl (*Strix occidentalis occidentalis*) territory on our study area in the central Sierra Nevada, California, USA. The territory is delineated by a circular boundary that encompasses 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.

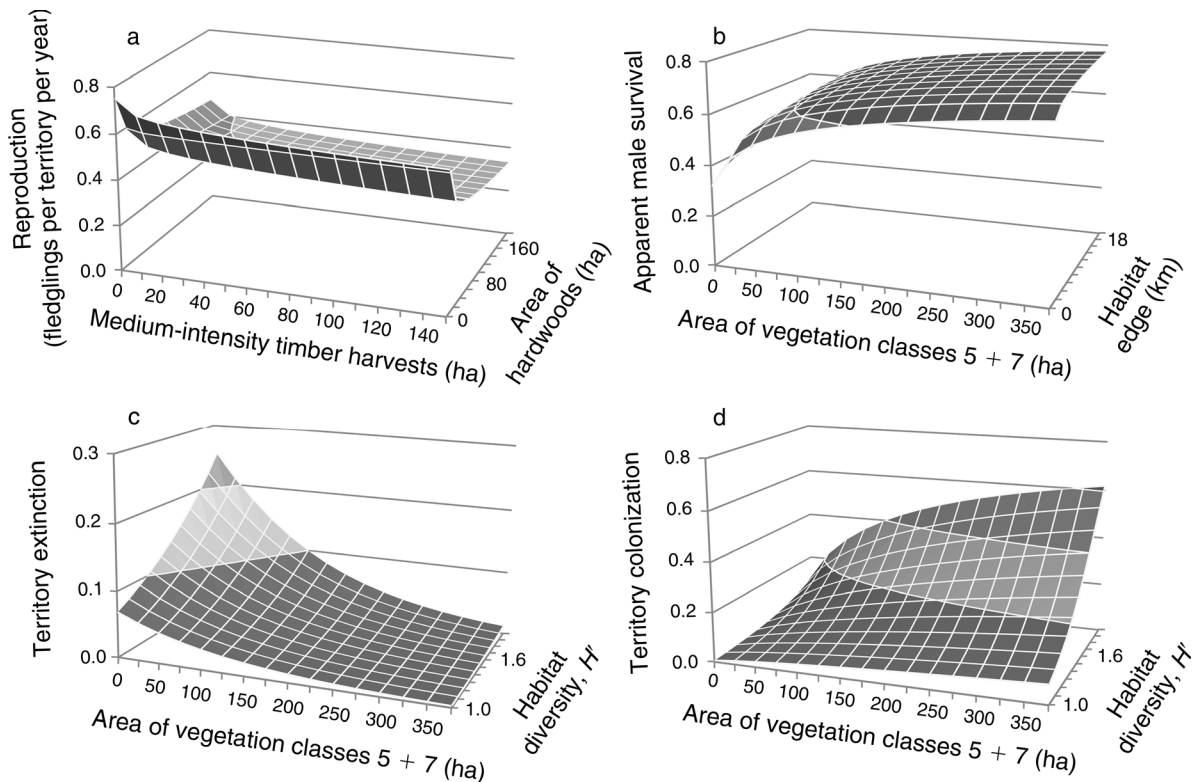


FIG. 2. Vital rates of California Spotted Owls in the central Sierra Nevada, California, 1993–2012, as a function of habitat, timber harvest, and wildfire covariates. We show (a) reproduction for adult females (number of young fledged per territory per year) vs. the total area of medium-intensity timber 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

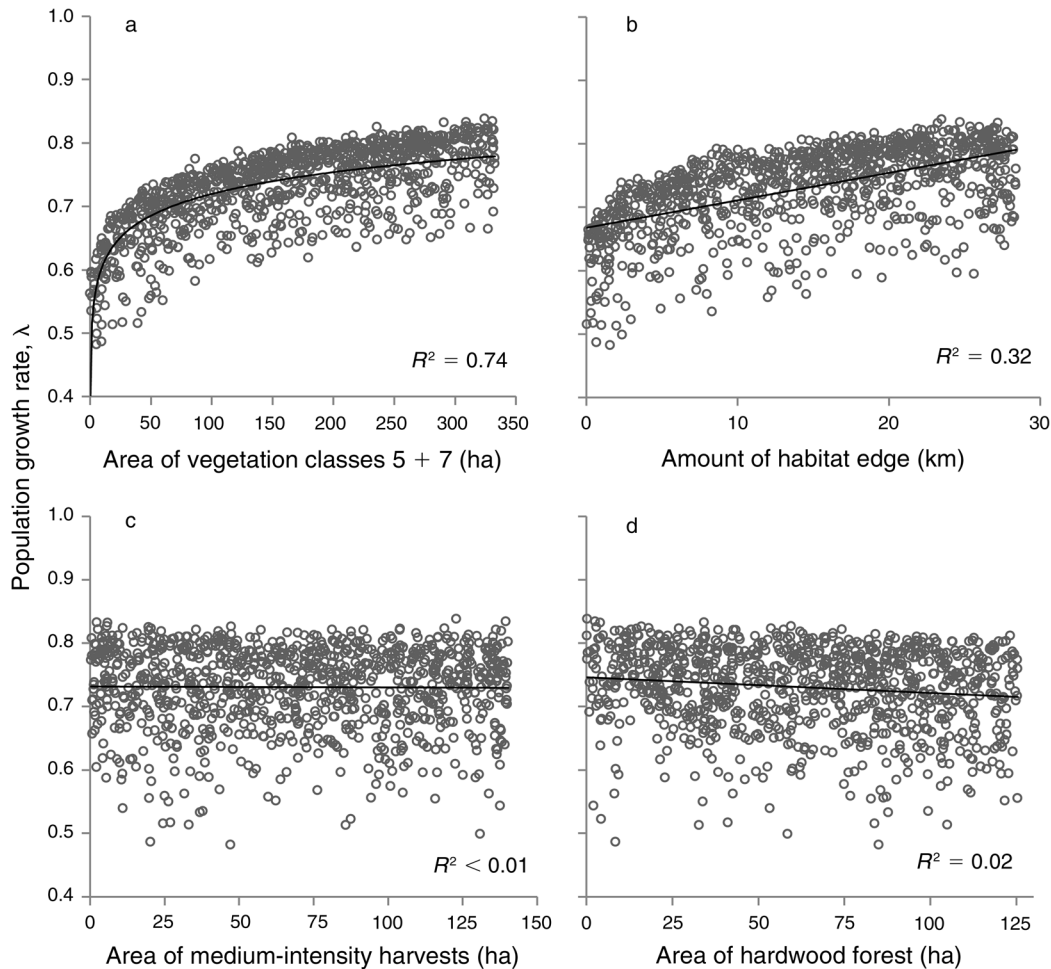


FIG. 3. Results of a life stage simulation analysis that we used to assess the sensitivity of annual population growth rate (λ) of California Spotted Owls to changes in forest vegetation conditions within owl territories. We generated 1000 λ values by randomly drawing (a) area of vegetation classes 5 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

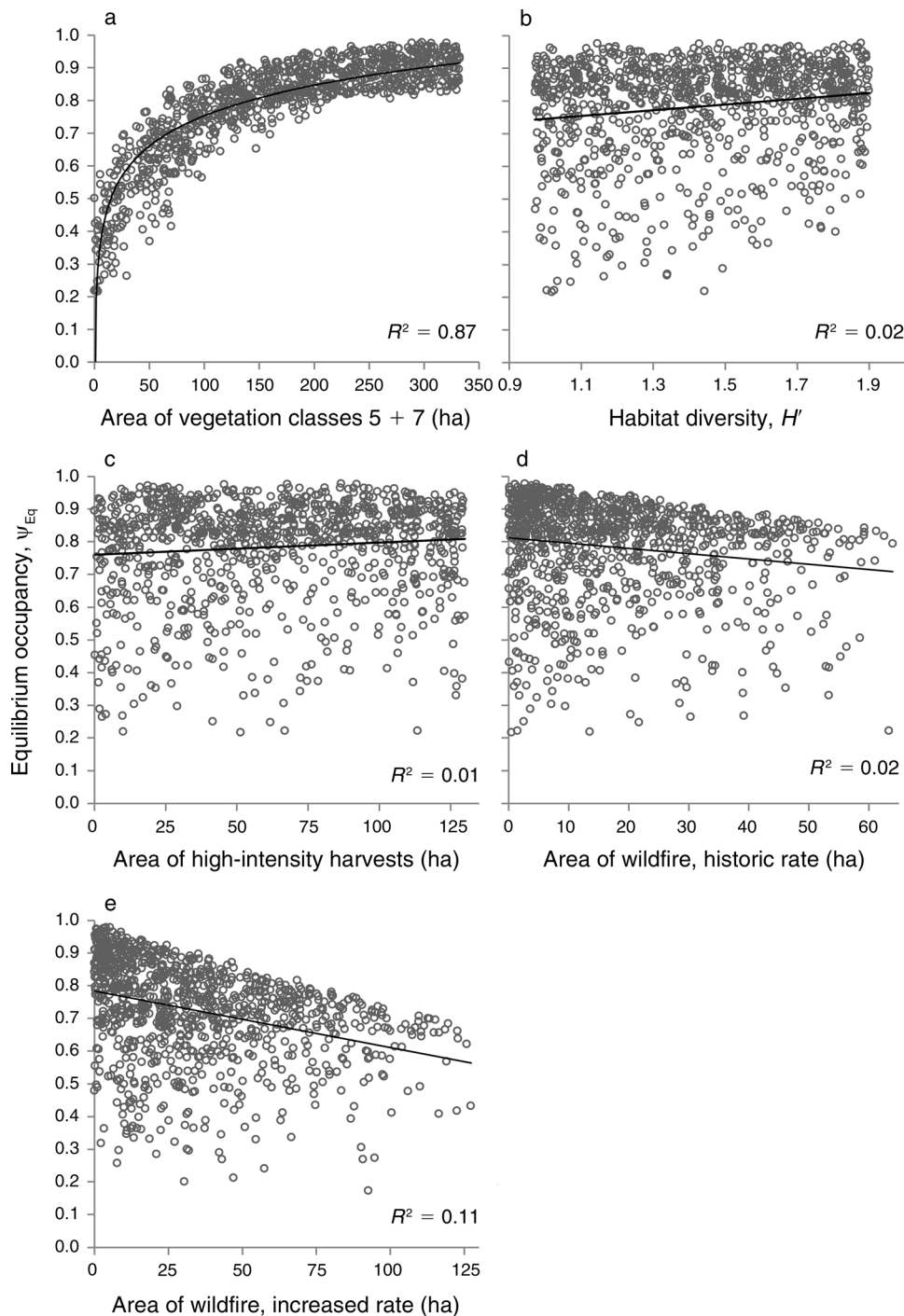


FIG. 4. Assessment of the sensitivity of equilibrium occupancy (ψ_{Eq}) of California Spotted Owl territories to changes in forest vegetation conditions within owl territories. We generated 1000 ψ_{Eq} values by randomly drawing: (a) area of vegetation classes 5 and 7; (b) habitat diversity (Shannon-Wiener 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.

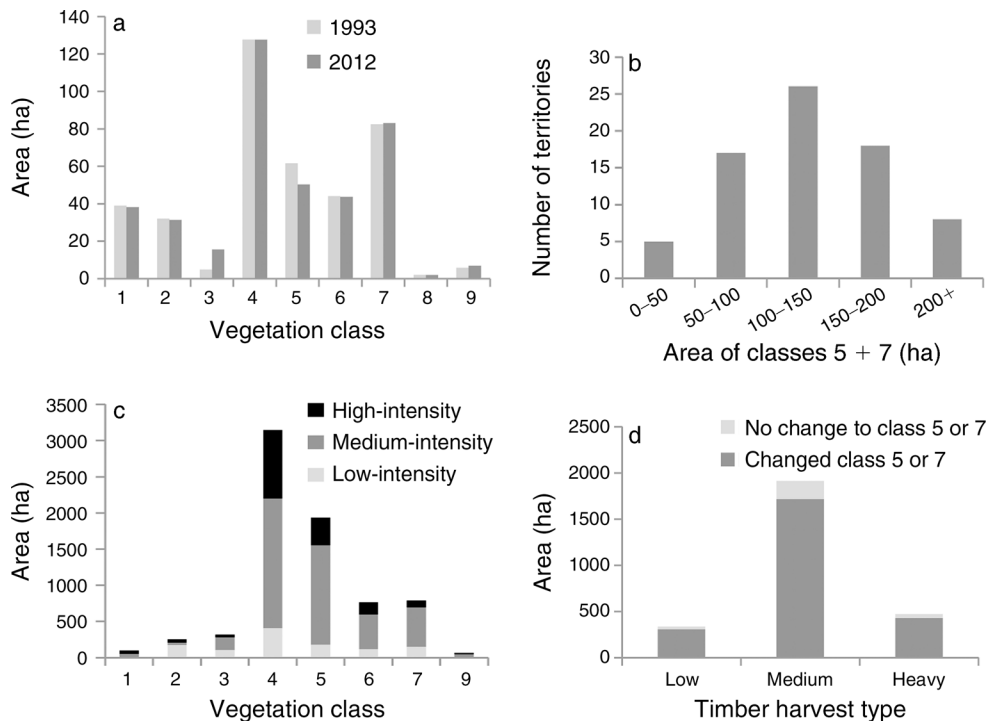


FIG. 5. Vegetation conditions within California Spotted Owl territories on our study area in the central Sierra Nevada, California, as represented by (a) the area of each vegetation class in owl territories on the Density Study Area in 1993 and 2012; (b) the number of owl territories containing different 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

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/13-2192.1.sm>