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RESEARCH ARTICLE

Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management

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ABSTRACT

We assessed the occupancy dynamics of 275 California Spotted Owl (*Strix occidentalis occidentalis*) territories in 4 study areas in the Sierra Nevada, California, USA, from 1993 to 2011. We used Landsat data to develop maps of canopy cover for each study area, which we then used to quantify annual territory-specific habitat covariates. We modeled the relationships between territory extinction and colonization using predictor variables of habitat, disturbance (logging, fire), climate, and elevation. We found that forests with medium (40–69%) and high (≥70%) canopy cover were the most important predictors of territory occupancy in all study areas, and that both canopy cover categories were positively correlated with occupancy. We used analysis of deviance to estimate the amount of variation explained by the habitat covariates (primarily medium and high canopy cover) and found that these covariates explained from 35% to 67% of the variation in occupancy. Climatic covariates were not correlated with occupancy dynamics and explained little of the variation in occupancy. We also conducted a post hoc analysis in which we partitioned canopy cover into 10% classes, because our original partitioning into 3 classes may have lacked sufficient resolution to identify canopy cover levels where occupancy changed abruptly. In this post hoc analysis, occupancy declined sharply when territories contained more area with <40% canopy cover, and the amount of 50–59% and 60–69% canopy cover had a more positive association with occupancy than did 40–49% canopy cover. Our results suggest that some fuels treatments intended to reduce fire risk and improve forest resilience could be located within Spotted Owl territories without adversely impacting territory occupancy if such treatments do not consistently reduce canopy cover below 50%. We suggest that future work quantify components of forest structure (e.g., large tree density, vertical complexity) known to be selected by owls and relate these characteristics to occupancy and fitness metrics.

Keywords: California Spotted Owl, canopy cover, forest management, occupancy, Sierra Nevada, *Strix occidentalis occidentalis*

Meta análisis de la ocupación de territorios de *Strix occidentalis occidentalis* en la Sierra Nevada: asociaciones de hábitat y sus implicaciones para el manejo forestal

RESUMEN

Determinamos la dinámica de ocupación de 275 territorios de *Strix occidentalis occidentalis* en 4 áreas de estudio en la Sierra Nevada, California, entre 1993 y 2011. Usamos datos de Landsat para desarrollar mapas de cobertura del dosel para cada área de estudio, que usamos luego para cuantificar covariables de hábitat anuales específicas de cada territorio. Modelamos la relación entre la extinción y la colonización de los territorios usando variables predictoras de hábitat, disturbio (tala, incendios), clima y elevación. Encontramos que los bosques con cobertura de dosel media (40–69%) y alta (≥70%) fueron los predictores más importantes de la ocupación de los territorios en todas las áreas de estudio, y ambas categorías de cobertura de dosel se correlacionaron positivamente con la ocupación. Usamos análisis de desviación para estimar la cantidad de variación explicada por las covariables del hábitat (principalmente cobertura de dosel media y alta) y encontramos que estas covariables explican entre 35.1% y 67.1% de la variación en la

ocupación. La covariables del clima no se correlacionaron con la dinámica de ocupación y explicaron poco de la variación en ocupación. También hicimos un análisis post-hoc en el que hicimos particiones de la cobertura del dosel en clases de 10% porque nuestra partición original en 3 clases podría no tener suficiente resolución para identificar los niveles de cobertura del dosel en los que la ocupación cambia abruptamente. En este análisis post-hoc, la ocupación disminuyó fuertemente cuando los territorios contenían menos de 40% de cobertura de dosel, y las clases de cobertura entre 50–59% y 60–69% presentaron una asociación más positiva con la ocupación de lo que la tuvo la clase de cobertura entre 40–49%. Nuestros resultados sugieren que algunos tratamientos con la intención de reducir el riesgo de incendios y mejorar la resiliencia de los bosques podrían ser ubicados dentro de los territorios de *S. o. occidentalis* sin afectar seriamente la ocupación de los territorios si tales tratamientos no reducen la cobertura del dosel por debajo del 50%. Sugerimos que trabajos futuros cuantifiquen los componentes de la estructura del bosque (e.g. densidad de árboles grandes, complejidad vertical) que se sabe son seleccionados por los búhos y relacionen estas características con la ocupación y medidas de aptitud.

Palabras clave: cobertura del dosel, manejo forestal, ocupación, Sierra Nevada, *Strix occidentalis occidentalis*

INTRODUCTION

The range of the California Spotted Owl (*Strix occidentalis occidentalis*) extends from the southern Cascade Range, USA, to northern Baja California, Mexico, but most of its population is found in the Sierra Nevada, California, USA (Verner et al. 1992, Gutiérrez et al. 1995). For nesting and roosting, it selectively uses economically valuable, older forests that have been affected by timber harvesting for more than a century (Gutiérrez et al. 1995). Although it is the only Spotted Owl subspecies not protected under the U.S. Endangered Species Act, management guidelines developed to retain important Spotted Owl habitat in Sierra Nevada forests have been in place for >20 yr (Verner et al. 1992, USDA Forest Service 2004), and Spotted Owl habitat remains a central component of forest management in the Sierra Nevada (USDA Forest Service 2016).

Management of Spotted Owl habitat in the Sierra Nevada is complicated by changing fire regimes that are largely the result of decades of fire suppression, which has allowed uncharacteristic accumulation of fuel loads on the landscape (Stephens et al. 2015). Whereas historical fire regimes were typified by relatively frequent fires that burned mainly at low and moderate severity (Skinner and Chang 1996), the relative proportion and patch sizes of high-severity fires have increased within the past 30 yr (Miller et al. 2009, Miller and Safford 2012). High-severity fire is often characterized by ≥75% mortality of overstory trees and can result in habitat loss for species associated with older forests. In fact, large patches of high-severity fire have been shown to negatively affect occupancy of Spotted Owl territories after controlling for postfire timber harvest (Lee et al. 2013, Jones et al. 2016a). In addition, climate change is expected to increase the incidence of extreme fire behavior in California (Westerling and Bryant 2008, Liu et al. 2013).

As a result, forest managers in the Sierra Nevada modify forest vegetation structure (i.e. implement "forest treatments"), primarily by removing surface and ladder fuels (Finney 2001, USDA Forest Service 2004), in attempts to reduce wildfire intensity, size, and rate of spread. Although concern exists that these treatments may adversely impact Spotted Owl habitat in the short term (5–10 yr), it is possible that they may provide long-term benefits by reducing future habitat loss as a result of high-severity fire (Tempel et al. 2015). Thus, reconciling forest restoration and Spotted Owl habitat conservation is important because owl populations in the Sierra Nevada have declined by up to 50% in the past 20 yr (Conner et al. 2013, Tempel et al. 2014a). Furthermore, managers are now considering recommendations to modify forest treatments to emphasize forest heterogeneity at the spatial scales of the forest stand and the landscape (North et al. 2009, North 2012). Under these recommendations, forest treatments would be less uniform and tailored to local conditions (e.g., topography, soil, aspect), resulting in a range of stand conditions (tree density, canopy cover) on the landscape (North et al. 2009). This approach also is believed to increase forest resilience to ecological stressors such as high-severity fire, warming temperatures, or extended drought (e.g., Asner et al. 2016).

To assess the potential effects of forest management on Spotted Owls, we related territory occupancy dynamics to canopy cover using presence–absence data collected from 1993 to 2011 in 4 long-term demographic study areas in the Sierra Nevada. We also evaluated the relationship between annual climatic variables and territory occupancy dynamics because changing climatic conditions could affect occupancy dynamics (Jones et al. 2016b). To quantify forest structure within owl territories, we used Landsat imagery to develop raster-based maps of forest canopy cover for each study area and assigned canopy cover into categories. We hypothesized that high (≥70%), medium (40–69%), and low (<40%) canopy cover would be biologically meaningful for Spotted Owls in different ways, because forests with ≥70% canopy cover are selected by owls for nesting and roosting (Moen and Gutiérrez 1997), whereas forests with 40–69% canopy cover may be used for foraging, and forests with <40% canopy cover are often

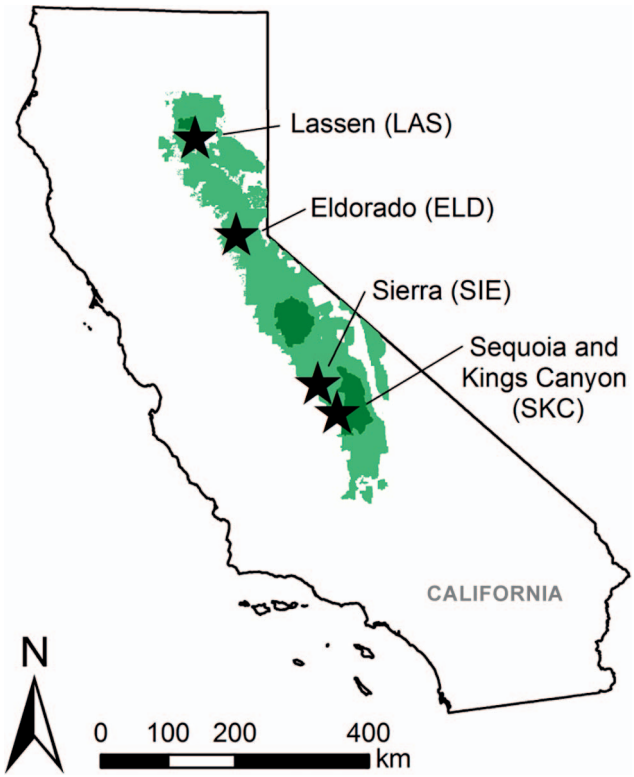

FIGURE 1. Locations of 4 study areas for California Spotted Owls, 1993–2011. Light shading indicates national forests; dark shading indicates national parks.

avoided (Call et al. 1992). We were unable to accurately estimate other important Spotted Owl habitat features (e.g., large trees, snags, vertical structure) with Landsat, and these variables were omitted from our analyses. We also tested whether spatially explicit metrics of forest structure, such as the spatial dispersion of high-canopy-cover forest and heterogeneity in canopy-cover conditions, were related to territory occupancy dynamics.

METHODS

Study Areas

Our long-term demographic study areas were situated on a north–south axis from the southern Cascades to the southern Sierra Nevada, California, USA (Figure 1). The Lassen study area (LAS) was in the southern Cascades, but was managed by the USDA Forest Service as part of the Sierra Nevada province, and the owls here are more likely to be California Spotted Owls than Northern Spotted Owls (*Strix occidentalis caurina*; USDA Forest Service 2004, Barrowclough et al. 2011). The Lassen, Eldorado (ELD), and Sierra (SIE) study areas consisted mainly of public land managed by the Forest Service, but also contained some privately owned land. Most private land within the Lassen study area was not surveyed for owls, but some owl territories on private land adjacent to the Lassen National Forest were included. The Eldorado and Sierra study areas contained 37% and 8% private land, respectively. The Sequoia–Kings Canyon (SKC) study area was entirely within 2 national parks of the same name. Barred Owls (*Strix varia*) were not present in any of the study areas until the last several years of our study, and they were either uncommon (Lassen) or extremely rare (≤3 individuals each in the Eldorado, Sierra, and Sequoia–Kings Canyon sites). Most precipitation in each study area fell as rain or snow during winter and early spring. Summers in all study areas were hot and dry. Additional detailed climatic information is described in Franklin et al. (2004).

The Lassen study area was located in the Lassen National Forest between Mineral and Susanville, California, at 1,200 m to 2,100 m elevation, and encompassed 2,200 km^2. The primary vegetation type in this study area was mixed-conifer forest dominated by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). California black oak (*Quercus kelloggii*) and Pacific dogwood (*Cornus nuttallii*) occurred in the understory, and red fir (*A. magnifica*) was present at higher elevations as pure stands or mixed with white fir.

The Eldorado site was located in the Eldorado and Tahoe national forests east of Georgetown, California, between 300 and 2,500 m elevation, and encompassed 818 km^2. Mixed-conifer forest was the primary vegetation type in this study area, and was dominated by sugar pine, ponderosa pine, white fir, Douglas-fir, and incense cedar. California black oak, canyon live oak (*Q. chrysolepis*), tanoak (*Notholithocarpus densiflorus*), and bigleaf maple (*Acer macrophyllum*) were common understory species. Red fir and lodgepole pine (*Pinus contorta*) occurred at the higher elevations.

The Sierra study site was located in the Sierra National Forest east of Fresno, California, between 300 and 2,900 m elevation, and encompassed 693 km^2. This study area contained 3 major vegetation types. Oak woodland (26% of the study area) dominated by blue oak (*Q. douglasii*), interior live oak (*Q. wislizeni*), canyon live oak, and California foothill pine (*Pinus sabiniana*) occurred at lower elevations. Mixed-conifer forest (61%) dominated by sugar pine, ponderosa pine, white fir, incense cedar, black oak, red fir, and Jeffrey pine (*P. jeffreyi*) occurred at middle elevations. Conifer forest (13%) dominated by red fir, lodgepole pine, and western white pine (*P. monticola*) occurred at higher elevations.

The Sequoia–Kings Canyon study area was located in Sequoia and Kings Canyon national parks northeast of Visalia, California, at elevations ranging from 425 to 3,050 m and encompassed 343 km^2. This study area consisted of 3 major vegetation types. Oak woodlands (24% of the study

area) containing blue oak, interior live oak, canyon live oak, and California foothill pine were present at lower elevations. Mixed-conifer forest (67%) dominated by sugar pine, ponderosa pine, white fir, and incense cedar occurred at middle elevations. Ten giant sequoia (*Sequoiadendron giganteum*) groves (7%) were found within the mixed-conifer zone. Conifer forests dominated by red fir, lodgepole pine, and western white pine occurred at higher elevations.

Spotted Owl Surveys

We conducted Spotted Owl surveys annually across each study area from 1993 to 2011 during the breeding season. All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e. both the areas containing owl territories and all areas not containing owls within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (Lassen) or as individual satellite territories to increase owl sample sizes for demographic analysis (Lassen and Eldorado), and we deleted a portion of the Sequoia–Kings Canyon site in 2006. We accounted for these changes in our analyses. We surveyed all satellite sites used in our occupancy analyses for a minimum of 3 yr; most territories in the core areas were surveyed for $\geq$15 yr. We conducted surveys from April 1 to August 31 in the Lassen and Eldorado study areas and from March 1 to September 30 in the Sierra and Sequoia–Kings Canyon sites. However, no surveys were conducted in the Sequoia–Kings Canyon study site in 2005 because of a temporary suspension of funding.

We imitated Spotted Owl vocalizations at designated survey stations or while walking survey routes through historical owl territories or between survey stations. We determined a responding owl's sex by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If owls were detected during nocturnal surveys, we conducted diurnal surveys to band unmarked owls, resight marked owls, assess reproduction, locate roosting areas, and band fledglings (Franklin et al. 1996). We included both nocturnal and diurnal surveys in our occupancy analyses.

Canopy Cover Map Development

We developed annual, raster-based canopy cover maps at 30 $\times$ 30 m spatial resolution using Landsat 5 Thematic Mapper satellite images from 1990 to 2011 acquired during July or August of each year. In each of these images, we estimated the fractional tree cover (in 1% increments) in a pixel using the Mixed Stratified Spectral Mixture Analysis method (MixSSMA; Koltunov et al. 2014, Koltunov and Ramirez 2015; see Supplemental Material Appendix A for complete details). To test the accuracy of the canopy cover maps, we compared them to 2 independent sets of canopy cover data obtained from airborne LiDAR (Light Detection and Ranging) and by double-blind visual interpretation of multitemporal high-resolution imagery from Google Earth (Google, Mountain View, California, USA) and the National Agriculture Imagery Program (NAIP; USDA Farm Service Agency, Salt Lake City, Utah, USA). The LiDAR data were acquired at a density of $\sim$8–10 points m^{-2} during 2009–2012, but were available only for parts of 2 study areas, Lassen and Sierra. We selected a stratified random sample of 3 $\times$ 3 pixel (90 $\times$ 90 m) polygons with no overlap (550 polygons for the Lassen study site, 376 for Sierra; Supplemental Material Figure S1) and compared the Landsat-derived canopy cover for 2010 with the fraction of LiDAR returns above 3 m. The mean ($\pm$ SD) absolute differences in canopy cover were 8.4 ($\pm$ 8.8) for Lassen and 9.5 ($\pm$ 9.5) for Sierra, and the pseudo r^2 values were 0.83 for Lassen and 0.71 for Sierra (Supplemental Material Figure S2). The test set based on high-resolution imagery was developed for all 4 study areas in 2005 and 2010. We selected 3 $\times$ 3 pixel (90 $\times$ 90 m) polygons with no overlap (195 to 600+ polygons per study area; Supplemental Material Figure S1), and again compared the Landsat-derived canopy cover with the values based on high-resolution imagery. The mean absolute differences in canopy cover ranged between 9.7 and 15.5, and the pseudo r^2 values ranged between 0.33 and 0.80 (Supplemental Material Table S1).

Canopy cover at the pixel scale was grouped into one of 3 classes ($<$40%, 40–69%, $\geq$70%) to minimize the effect of map error on inference. Although our classes were relatively coarse, they were less subject to mapping error than classes with a narrower range of values, and thus more likely to yield robust relationships between canopy cover and territory occupancy. Furthermore, previous Spotted Owl occupancy studies have used similar or identical canopy cover classes to these 3 classes (Blakesley et al. 2005, Seamans and Gutiérrez 2007b, Tempel et al. 2014b). However, forest managers could benefit from finer resolution as to how occupancy is related to canopy cover levels within these classes (e.g., the difference that might be expected if forest treatments reduce canopy cover from 70% to 40% vs. 70% to 60%). Thus, we performed a post hoc analysis using 10% canopy cover classes (see Statistical Analysis—Model selection). It is important, however, to recognize that canopy cover conditions are mapped with lower accuracy in this analysis and that inferences are more likely influenced by map uncertainty. As such, we did not make explicit predictions, for example, of how much forest with 70–80% canopy cover would be needed to achieve a specific target goal of territory occupancy. Rather, we searched for broad patterns across study areas in the directionality of relationships between the area of forest within 10% canopy cover classes and Spotted Owl territory occupancy metrics.

Statistical Analysis

We used the annual survey data to identify Spotted Owl territories and construct occupancy histories for our analyses. We identified owl territories as sites where at least 1 owl was detected during diurnal hours in ≥3 yr, where diurnal hours occurred between dawn and dusk based on civil twilight times (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). For the purpose of quantifying habitat covariates within Spotted Owl territories, we first calculated the geometric center of each territory as the average spatial coordinates of all nest and roost locations in the territory. We then calculated the mean nearest-neighbor distance among territory centers for each study area as the average distance between each territory center and the center of its nearest neighboring territory, and we defined the spatial extent of a "territory" as a circle around each territory center with a radius of half of the mean nearest-neighbor distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius), and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. We did not include nocturnal detections outside a territory circle when compiling occupancy histories to eliminate potential spurious detections of owls from nearby territories or nonterritorial, floater owls. A survey in which no owls were detected needed a total duration of ≥30 min to be included in the occupancy history.

We used a multiple-season, robust-design occupancy model to assess territory occupancy dynamics in each study area separately, in which the statistical model contained parameters for initial occupancy (ψ_1), territory extinction (ε_t), territory colonization (γ_t), and detection probability ($p_{t,j}$; MacKenzie et al. 2003). Our primary sampling periods (t) were breeding seasons (i.e. years), and our secondary sampling periods (j) were bimonthly periods within each breeding season (March 1–15, March 16–31, April 1–15, April 16–30, etc.). Thus, the Lassen and Eldorado study areas had 10 secondary periods each year, and the Sierra and Sequoia–Kings Canyon study areas had 14 secondary periods each year. If multiple surveys were conducted within the same secondary period, we assigned a "0" to the survey history if no owls were detected during any survey and a "1" if at least 1 owl was detected during any survey. When fitting the models for Sequoia–Kings Canyon, we fixed all 2005 detection probabilities and ε and γ from 2004 to 2005 at 0 because no surveys were conducted in 2005. We used program PRESENCE 10.2 (USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA) to fit models and estimate parameters for individual models that contained covariates (Table 1) that we hypothesized would affect detection probability, initial occupancy, territory colonization, and territory extinction.

Model covariates. We hypothesized that within-year detection probability would be higher on survey occasions subsequent to the survey when owl(s) were initially detected at a territory (*initial*) because surveyors might intensify their efforts to relocate detected birds in order to resight or capture them and to assess reproduction (Riddle et al. 2010, Tempel and Gutiérrez 2013). We expected nesting owls (*repro*; value equal to 1 for all surveys in a territory in a given year if reproduction was detected during any survey) to be more easily detected than nonnesting owls because nesting owls defend their territories more aggressively or spend more time near the territory center (MacKenzie et al. 2009, Tempel and Gutiérrez 2013). We also considered linear (*T*), logarithmic (*lnT*), and quadratic (*TT*) time trends for within-year detection probability, and that $p_{t,j}$ could be different during each bimonthly sampling period (*survey*). We hypothesized that among-year detection probability would vary in a linear (*T*), logarithmic (*lnT*), or quadratic (*TT*) time trend, or that $p_{t,j}$ would be different for each year of the study (*year*; Tempel and Gutiérrez 2013).

We used the raster-based canopy cover maps to quantify annual, territory-specific vegetation covariates that could have affected occupancy. We first used ArcMap 10.1 (ESRI, Redlands, California, USA) to calculate the proportion of each owl territory that contained forest (i.e. pixels) with ≥70% canopy cover (*highCC*) and forest with canopy cover between 40% and 69% (*mediumCC*). Previous studies have shown that California Spotted Owls select high-canopy-cover forest for nesting and roosting (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997) and that territory occupancy is positively correlated with the amount of high-canopy-cover forest (Blakesley et al. 2005, Tempel et al. 2014b). Forests with intermediate amounts of canopy cover may function as Spotted Owl nesting or roosting habitat if large, residual trees are present (Moen and Gutiérrez 1997, Hunter and Bond 2001), or might be used by foraging owls (Call et al. 1992).

We then used FRAGSTATS 4.2 (McGarigal et al. 2012) to calculate 3 annual covariates that represented the spatial arrangement or distribution of *highCC* and/or *mediumCC* within a territory. We hypothesized that the density of edge (*edge*) between *highCC* and any vegetation type with <40% canopy cover would be positively correlated with occupancy because these edges could increase the availability of prey such as dusky-footed woodrats (*Neotoma fuscipes*) and other rodents (Sakai and Noon 1997). Similarly, we hypothesized that owls would experience improved foraging conditions if *highCC* was spatially dispersed throughout the territory, rather than being aggregated into large patches. Therefore, we calculated the area-weighted clumpiness index for *highCC* within a territory

TABLE 1. Covariates used to model detection probability ($p_{t,j}$), initial occupancy (ψ_1), territory extinction (ε_t), and territory colonization (γ_t) for California Spotted Owls in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. The predicted effects were: positive correlation between covariate and parameter (+), negative correlation (–), and no specific prediction (x). The covariate was not modeled for a parameter if the predicted effect is blank.

		Predicted effect on parameter			
Covariate	Definition	$p_{t,j}$	ψ_1	ε_t	γ_t
initial	Different *p* in surveys after initial detection of owls.	+			
repro	Reproductive status of owls (0 = not nesting, 1 = nesting).	+			
survey	Different *p* for each survey within a year.	x			
year	Year-specific variation in parameter value.	x		x	x
T	Linear temporal trend.	x			
lnT	Logarithmic temporal trend.	x			
TT	Quadratic temporal trend.	x			
highCC	Proportion of owl territory containing forest with ≥70% canopy cover.	x	+	–	+
mediumCC	Proportion of owl territory containing forest with canopy cover between 40% and 69%.	x	+	–	+
edge	Edge density (m m^{-2}) between *highCC* and any vegetation type with <40% canopy cover.			–	+
clump	Clumpiness index for *highCC*, a measure of its spatial aggregation.			+	–
even	Shannon's evenness index for *highCC*, *mediumCC*, and <40% canopy cover.			–	+
logging	Proportion of owl territory within which canopy cover was reduced by at least 10% in the previous 3 yr from logging (or other causes in SKC [a]).			+	–
fire	Proportion of owl territory within which canopy cover was reduced by at least 10% in the previous 3 yr due to fire.			+	–
Rxfire	Proportion of owl territory affected by prescribed fire in the previous 3 yr.			–	+
Pwinter	Total precipitation (cm) from November to March averaged across all territories in each study area.			+	–
Twinter	Mean of daily minimum temperatures (°C) from November to March averaged across all territories in each study area.			–	+
Pnest	Total precipitation (cm) from April to May averaged across all territories in each study area.			+	–
Tnest	Mean of daily minimum temperatures (°C) from April to May averaged across all territories in each study area.			–	+
Tsummer	Mean of daily maximum temperatures (°C) from July to August averaged across all territories in each study area.			+	–
elev	Average elevation (m) of owl territory.			x	x

[a] SKC = Sequoia–Kings Canyon study area.

(*clump*), which provided an index of fragmentation of *highCC* (McGarigal et al. 2012). Finally, we hypothesized that owls would benefit when *highCC*, *mediumCC*, and any vegetation type with <40% canopy cover were present in equal proportions within a territory because each class may fulfill different requirements of the owl's life history. For example, *highCC* may provide optimal nesting and roosting sites, as well as habitat for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel 1995), which can be an important prey item for Spotted Owls. Conversely, areas containing shrubs and pole-sized timber (<40% canopy cover) may be source habitat for woodrats (Sakai and Noon 1993). Thus, we calculated Shannon's evenness index (*even*) for these 3 classes within each territory.

We also quantified annual habitat disturbance covariates that we attributed either to fire or to timber harvest. First, we used ArcMap 10.1 to identify each pixel on our annual canopy cover maps where canopy cover declined by at least 10% during the previous 3 yr. We then obtained shapefiles from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (http://frap.cdf.ca.gov/) of the perimeters of all California fires, including prescribed burns, that occurred during 1990–2011. We overlaid the fire perimeters on the annual canopy cover maps and attributed >10% canopy cover loss to fire if the pixel was located where a fire had occurred during the previous 3 yr. For pixels located where fire had not occurred during the previous 3 yr, we attributed >10% canopy cover loss to timber harvest (except in the

Sequoia–Kings Canyon study area, where no timber harvest occurred) because no large-scale tree mortality from sources other than fire (e.g., disease, insect outbreaks) occurred in the Lassen, Eldorado, and Sierra study sites. Thus, we calculated annual habitat disturbance covariates for fire (*fire*) or timber harvest (*logging*) within territory circles during the previous 3 yr. We chose a 3-yr timeframe because most logging projects were implemented over a period of 2 to 3 yr and postfire tree mortality often occurred for several years after wildfire. We acknowledge that canopy cover loss from fire and postfire salvage logging were confounded in the *fire* covariate for Lassen, Eldorado, and Sierra, and that the *logging* covariate for Sequoia–Kings Canyon represented canopy cover loss that was the result of disease or insect outbreaks, not timber harvest. Although prescribed fire was essentially nonexistent in the Lassen and Eldorado study areas, prescribed burns were frequently conducted in the Sierra and Sequoia–Kings Canyon study areas. We hypothesized that Spotted Owls may have benefited from managed fires that mimicked historical fires (Roberts et al. 2011). Thus, in the Sierra and Sequoia–Kings Canyon study areas, we included a covariate for the proportion of an owl territory that was affected by prescribed fire in the previous 3 yr (*Rxfire*).

Finally, we calculated annual climate covariates for each study area that may have affected Spotted Owl survival rates and thus indirectly affected occupancy. We hypothesized that cold, wet conditions during winter (November–March) would be energetically stressful for owls and hinder their ability to hunt for prey (Seamans et al. 2002, Seamans and Gutiérrez 2007a). Thus, we predicted that winters with greater precipitation (*Pwinter*) and colder temperatures (*Twinter*) than average would negatively affect occupancy in the following breeding season; for example, that precipitation from November 2003 to March 2004 would affect territory colonization and extinction rates between the 2003 and 2004 breeding seasons. Similarly, we hypothesized that cold, wet conditions during the nesting season (April–May) would be energetically stressful for both female and male owls (Seamans et al. 2002, LaHaye et al. 2004). Once nesting has been initiated, males bring food to incubating females, and after young fledge both males and females hunt for prey to feed their offspring. In this case, we hypothesized that greater precipitation (*Pnest*) and colder temperatures (*Tnest*) would negatively affect occupancy in the following year; for example, that precipitation during April and May 2004 would affect territory colonization and extinction rates between the 2004 and 2005 breeding seasons. We hypothesized that high summer temperatures (July–August; *Tsummer*) would negatively affect owls through heat stress because Spotted Owls appear to be cold-adapted (Weathers et al. 2001). Therefore, we predicted that hot summer temperatures during July and August 2004 would affect territory colonization and extinction rates between the 2004 and 2005 breeding seasons. We extracted all climatic data (1992–2011) from PRISM (PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA) at 4-km spatial resolution using ArcMap 10.1. We first extracted the climate covariate values for each territory (see Jones et al. 2016b), and then calculated annual values for each study area as the average of all territory values. We used annual climatic means rather than territory-specific values because temperature and precipitation were highly correlated with elevation at the territory level ($r > 0.8$; Jones et al. 2016b). We felt that it was more important to treat elevation as a territory-specific covariate given that managers can employ different management practices at different elevations. Despite variation among territories in climatic variables, mean study area values are often correlated with Spotted Owl demographic rates and capture broad-scale variation in weather conditions (e.g., wet vs. dry years). We estimated average elevation at each territory (*elev*; m) using 30-m resolution digital-elevation models in ArcMap 10.1.

Model selection. We used a hierarchical, multistage framework to evaluate our occupancy models because we had many covariates and wished to avoid fitting an excessive number of models, which could result in spurious relationships by chance. We examined correlations between covariates appearing in the same models, and none of these covariates were highly correlated ($r < 0.65$). At each stage, we compared candidate models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002), and then used the best model (i.e. lowest AIC value) from a given stage as the base model for the next stage (see Supplementary Material Tables S2–S5 for all modeling results). The stages in our modeling framework were:

(1) We assessed within-year, survey-specific variation in detection probability using the following covariates: *repro*, *initial*, *survey*, *T*, *lnT*, *TT*, and constant value (i.e. the null model and indicated by '.'). In this stage, we included general year effects for the other model parameters including among-year variation in detection probability: $\psi_1(.)$, $\varepsilon(year)$, $\gamma(year)$, $p(year)$.
(2) We assessed among-year variation in detection probability using the following covariates: *year*, *T*, *lnT*, *TT*, constant, *highCC*, and *mediumCC*. We included *highCC* and *mediumCC* to ensure that any correlation between these habitat covariates and ε or γ was not simply the result of their effect on detection probabilities. We used the best structure for within-year variation in detection probability from stage 1 and included general year effects for the other model parameters: $\psi_1(.)$, $\varepsilon(year)$, $\gamma(year)$.

(3) We examined potential covariate effects on initial occupancy probability at a territory using the following covariates: *highCC*, *mediumCC*, and constant. Furthermore, we considered linear, logarithmic, and quadratic relationships between the habitat covariates (*highCC*, *mediumCC*) and ψ_1. We used the best structure for within-year and among-year variation in *p* from the previous modeling stages and included general year effects for territory extinction and colonization rates: ε(*year*), γ(*year*).

(4) We examined the potential effects of our primary habitat covariates (*highCC*, *mediumCC*) on territory extinction and colonization because we expected these covariates to have the strongest association with occupancy dynamics (e.g., Tempel et al. 2014b). We again considered linear, logarithmic, and quadratic relationships between these covariates and ε and γ because previous Spotted Owl studies have found evidence for nonlinear relationships (Dugger et al. 2005, Forsman et al. 2011, Tempel et al. 2014b). We also included a model with an interaction term between *highCC* and *mediumCC*. We modeled habitat effects on ε and γ separately. When we modeled extinction probability, we included a general year effect for colonization (γ[*year*]). When we modeled colonization probability, we included a general year effect for extinction (ε[*year*]).

(5) We next assessed the potential effects of covariates related to the spatial arrangement of habitat and habitat disturbance from logging or fire: *edge*, *clump*, *even*, *logging*, *fire*, and *Rxfire* (the latter for Sierra and Sequoia–Kings Canyon study areas only). We modeled ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and any covariates from this stage that appeared in the top-ranked model.

(6) Then we assessed 10 models that represented different combinations of our climate covariates (*Pwinter*, *Twinter*, *Pnest*, *Tnest*, and *Tsummer*). We again modeled ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and any covariates from this stage that appeared in the top-ranked model.

(7) Finally, we modeled the potential effects of *elev* on ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and *elev*, as well as a model with interaction terms between climate covariates (if any were still in the model) and *elev*.

Furthermore, we included interactions between *highCC*, *mediumCC*, and other covariates under the hypothesis that territories containing more Spotted Owl habitat would be more resilient to disturbance (Seamans and Gutiérrez 2007b) or adverse climatic conditions (Jones et al. 2016b). We included interactions between *elev* and climate because territories located at higher elevations were expected to have colder temperatures and more precipitation than territories at lower elevations. We did not retain a model if the standard errors for any beta coefficients were inestimable, which frequently occurred for models with interaction terms.

We assessed the importance of covariates in the top-ranked occupancy model for each study area in 2 ways. First, we calculated equilibrium occupancy (ψ_{eq}) from the territory colonization and extinction rates as $\gamma/(\gamma + \varepsilon)$ (MacKenzie et al. 2006). When using this equation, one assumes that γ and ε are stable over time, which was not likely to be true for some of our study areas. Therefore, we did not interpret ψ_{eq} as an expected long-term proportion of occupied territories within each study area, but rather we used ψ_{eq} to assess the relative importance of covariates in the top model by examining how occupancy varied over a range of typical values for these covariates. Second, we used the analysis of deviance (ANODEV) test in Program MARK (White and Burnham 1999) to estimate how much variation in occupancy was explained by the habitat and climate covariates in the top-ranked models. The ANODEV test compares the amount of deviance explained by the covariates in a model with the amount of deviance not explained by these covariates and thus provides an estimate of r^2 for the model (Skalski et al. 1993). The global model for each study area that we used for the ANODEV test consisted of the top-ranked model with additional annual effects for γ and ε, and the constant model consisted of the best structure for detection probability with constant values for γ and ε.

Finally, because *mediumCC* and *highCC* encompassed a relatively large range in canopy cover, we performed a post hoc analysis in which we grouped canopy cover into 10% classes and evaluated whether occupancy changed abruptly between levels of canopy cover. For each study area, we successively replaced any habitat covariates for extinction and colonization in the top-ranked model with a covariate for the proportion of a territory containing 0–9% canopy cover, a covariate for 10–19% canopy cover, etc., up to 90–100% canopy cover. For example, the top-ranked model for Lassen was ψ_1(.), ε(*highCC* + *mediumCC* + *Tsummer*), γ(*highCC* + *Twinter* + *elev*), *p*(*year*, *repro* + *initial*), so we fit the model ψ_1(.), ε(*0–9% canopy cover* + *Tsummer*), γ(*0–9% canopy cover* + *Twinter* + *elev*), *p*(*year*, *repro* + *initial*), then fit the model ψ_1(.), ε(*10–19% canopy cover* + *Tsummer*), γ(*10–19% canopy cover* + *Twinter* + *elev*), *p*(*year*, *repro* + *initial*), etc. We then used the beta coefficients for extinction and colonization from each model to iteratively compute ψ_{eq} for each 10% canopy

TABLE 2. Mean values (SD) for the habitat, climate, and elevation covariates used to assess California Spotted Owl territory occupancy dynamics in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Study site abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, and SKC = Sequoia–Kings Canyon. Covariate definitions are provided in Table 1.

	Study area			
Covariate	LAS	ELD	SIE	SKC
highCC [a]	0.26 (0.12)	0.37 (0.19)	0.24 (0.12)	0.29 (0.18)
mediumCC [a]	0.33 (0.05)	0.24 (0.06)	0.40 (0.08)	0.37 (0.08)
edge (m m^{-2})	43.6 (13.1)	50.6 (16.6)	41.5 (19.4)	26.8 (16.2)
clump [b]	0.33 (0.08)	0.41 (0.15)	0.23 (0.08)	0.33 (0.09)
even [b]	0.94 (0.06)	0.88 (0.14)	0.92 (0.07)	0.90 (0.09)
logging [a]	0.008 (0.020)	0.008 (0.015)	0.010 (0.016)	0.007 (0.024)
fire [a]	0.004 (0.032)	0.006 (0.053)	0.011 (0.055)	0.012 (0.040)
Rxfire [a]	—	—	0.011 (0.055)	0.030 (0.098)
Pwinter (cm)	91.5 (31.1)	118.3 (37.7)	73.4 (27.2)	78.4 (26.7)
Pnest (cm)	18.7 (10.1)	24.5 (12.6)	14.5 (9.4)	14.9 (9.4)
Twinter (°C)	−3.4 (0.7)	0.4 (0.5)	−0.5 (0.6)	−1.7 (0.7)
Tnest (°C)	0.4 (1.1)	3.7 (1.3)	3.1 (1.6)	1.8 (1.4)
Tsummer (°C)	26.9 (1.2)	29.0 (1.1)	28.1 (0.9)	26.8 (0.9)
elev (m)	1732.7 (160.0)	1441.0 (205.3)	1643.5 (562.0)	1783.4 (385.2)

[a] Covariate values are the proportion of an owl territory.
[b] Unitless index.

cover class when the covariate value for the class was equal to 0.25 (i.e. 25% of the territory consisted of vegetation in that 10% canopy cover class).

RESULTS

Survey Results and Environmental Conditions during the Study Period

We identified 90, 74, 66, and 45 owl territories in the Lassen, Eldorado, Sierra, and Sequoia–Kings Canyon study areas, respectively. Eldorado was the only study area in which the mean proportion of *highCC* within owl territories was greater than *mediumCC* (0.37 vs. 0.24), but *highCC* varied more than *mediumCC* in all 4 study areas (Table 2). Logging (tree disease in Sequoia–Kings Canyon) or fire generally affected <1% of any given owl territory annually, regardless of study area (Table 2). Wildfires that occurred from 1990 to 2011 affected a small number of territories in each study area (12 in Lassen, 14 in Eldorado, 3 in Sierra, and 14 in Sequoia–Kings Canyon), although some of these territories were greatly affected by high-severity fire (>50% of the territory). In contrast, prescribed fire was more common than wildfire in the 2 southern study areas, as 20 territories were affected by prescribed burns in Sierra and 22 in Sequoia–Kings Canyon. The Sierra and Sequoia–Kings Canyon study areas were drier than the 2 northern study areas; Eldorado was the wettest and warmest study area (Table 2).

The covariate *highCC* exhibited more spatial variation (spatial CV ranged from 0.47 to 0.61) than *mediumCC* (spatial CV ranged from 0.13 to 0.24). Temporal variation was much lower than spatial variation for both *highCC* (temporal CV ranged from 0.01 to 0.03) and *mediumCC* (temporal CV ranged from 0.02 to 0.05). The variation in climate covariates shown in Table 2 was due solely to temporal variation because we calculated a single value for these covariates within a study area during each year of our study (see Statistical Analysis—Model covariates).

Estimates of Parameters

Within each study area we estimated annual extinction and colonization probabilities and bimonthly detection probabilities using the model $\psi_1(.)$, $\varepsilon(year)$, $\gamma(year)$, and the most parsimonious structure for $p_{j,t}$ within a given study area. Additionally, we derived annual estimates of territory occupancy probability from ψ_1, ε, and γ. Territory occupancy declined over time in the Lassen, Eldorado, and Sierra study areas as the result of declining colonization and increasing extinction rates, but increased over time in the Sequoia–Kings Canyon study site (Figure 2). Initial territory occupancy probabilities were high for all study areas (Lassen = 1.00, Eldorado = 1.00, Sierra = 0.96, Sequoia–Kings Canyon = 0.91), and these rates were not due to a sampling artifact (i.e. pseudo-increase in early years of sampling associated with a learning curve) because all territories within the core study areas were surveyed in 1993. Territory occupancy probabilities in 2011 (Lassen = 0.85, Eldorado = 0.73, Sierra = 0.71, Sequoia–Kings Canyon = 1.00) were lower than at the beginning of the study in all study areas except Sequoia–Kings Canyon. Owl densities (i.e. number of occupied territories) in Lassen, Eldorado, and Sierra appeared to be at or near their maximum values in 1993 and slowly declined over time as some territories became unoccupied and were not

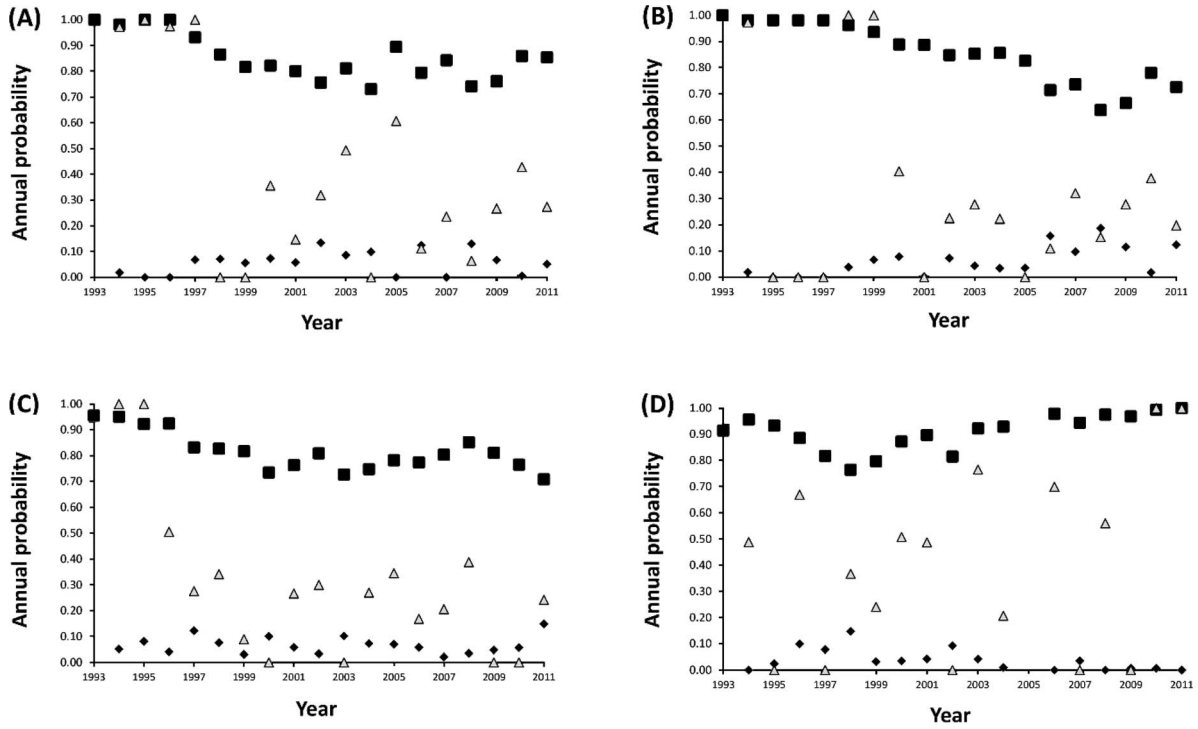

FIGURE 2. Annual estimates of occupancy (■), extinction (◆), and colonization (Δ) probabilities for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011, calculated using the dynamic occupancy model with annual variation in extinction and colonization probabilities and the best detection probability structure for each study area. Annual occupancy estimates were derived from the extinction and colonization estimates. The study areas are: (**A**) Lassen, (**B**) Eldorado, (**C**) Sierra, and (**D**) Sequoia–Kings Canyon. Note that no surveys were conducted in the Sequoia–Kings Canyon site in 2005.

recolonized, a pattern which has previously been reported for Eldorado (Tempel and Gutiérrez 2013). Detection probabilities during bimonthly sampling periods were higher for Eldorado (average = 0.68, range = 0.51–0.91), Sierra (average = 0.70, range = 0.35–0.90), and Sequoia–Kings Canyon (average = 0.71, range = 0.49–0.82) than for Lassen (average = 0.56, range = 0.39–0.70).

Model Selection Results

Detection probability. The reproductive status of birds at a territory, *repro*, was positively correlated with *p* in all 4 study areas (i.e. nesting owls were more likely to be detected than nonnesting owls; Table 3; see also complete model-selection results [stages 1–7] for each study area in Supplemental Material Appendix B). For within-year variation in detection probability, *initial* was positively correlated with *p* in the Lassen and Eldorado study sites; thus, owls were more likely to be detected during surveys subsequent to the initial detection at a territory in a given year (Table 3). For Sierra and Sequoia–Kings Canyon, within-year detection probability followed a quadratic relationship (*TT*), so that *p* increased gradually during the survey season before dropping off sharply in August and September (Table 3). In Lassen, Eldorado, and Sierra, the best model for annual variation in detection probability contained year-specific parameter estimates (*year*). However, the best model for annual variation in *p* in Sequoia–Kings Canyon suggested that *p* was positively correlated with forest conditions (*highCC*, *mediumCC*) within a territory (Table 3).

Occupancy. We have provided the complete model-selection results (stages 1–7) for each study area in Supplemental Material Appendix B. In the Lassen study area, the top-ranked occupancy model was $\psi_1(.)$, ε(*highCC* + *mediumCC* + *Tsummer*), γ(*highCC* + *Twinter* + *elev*). As predicted, territory extinction was negatively correlated with both *highCC* and *mediumCC*, and colonization was positively correlated with *highCC*. With respect to climate covariates, *Tsummer* had a positive relationship with ε, and *Twinter* was positively related to γ (i.e. territories were more likely to be colonized following warmer winters). In addition, colonization was positively related to *elev*. Although the covariates in the top-ranked occupancy model were supported in model selection, the 95% confidence intervals for the beta coefficients overlapped zero for all terms except ε(*highCC*) and γ(*elev*).

In the Eldorado study area, the top-ranked model was $\psi_1(.)$, ε(ln[*highCC*] + ln[*mediumCC*] + *logging* + *edge*),

TABLE 3. Beta coefficients (SE) for covariate effects on model parameters in the top-ranked California Spotted Owl territory occupancy models for 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Covariate definitions are provided in Table 1. Blank cells denote that a covariate did not affect a given parameter, and + indicates that there are separate beta coefficients for each year that we do not list to save space. Bold font indicates that the 95% confidence interval did not overlap zero.

	Beta coefficients		
Covariate	Detection ($p_{t,j}$)	Extinction (ε_t)	Colonization (γ_t)
Lassen:			
year	+		
repro	**1.49 (0.09)**		
initial	**0.85 (0.07)**		
highCC		**−9.94 (2.58)**	2.98 (2.98)
mediumCC		−5.27 (3.74)	
Tsummer		0.26 (0.15)	
Twinter			0.83 (0.45)
elev			**4.78 (2.36)**
Eldorado:			
year	+		
repro	**1.53 (0.12)**		
initial	**1.23 (0.09)**		
ln(*highCC*)		**−6.48 (1.86)**	
ln(*mediumCC*)		−7.07 (5.34)	**8.24 (3.35)**
logging		−42.28 (21.61)	
edge		**4.22 (1.80)**	
Sierra:			
year	+		
repro	**1.42 (0.12)**		
T	**1.81 (0.71)**		
TT	**−3.09 (0.59)**		
highCC		−2.39 (1.56)	0.94 (1.94)
mediumCC		**−5.25 (1.99)**	**9.96 (3.15)**
edge		**3.63 (0.90)**	**−2.61 (1.04)**
Pwinter		0.41 (0.26)	
Sequoia–Kings Canyon:			
repro	**1.29 (0.11)**		
highCC	**0.78 (0.25)**	−16.13 (10.64)	**−33.05 (11.85)**
$(highCC)^2$			**61.06 (21.38)**
mediumCC	**2.26 (0.58)**	−16.09 (8.68)	
*highCC*mediumCC*		44.88 (30.67)	
T	0.66 (0.80)		
TT	**−1.60 (0.68)**		
fire		−40.57 (34.40)	
Rxfire			−8.68 (6.77)
Twinter			0.01 (0.65)
elev			**−2.10 (1.00)**
*elev*Twinter*			**5.26 (2.06)**

γ(ln[*mediumCC*]). Again, territory extinction was negatively related to both *highCC* and *mediumCC*, but colonization was positively correlated only with *mediumCC*. Contrary to our expectations, *logging* was negatively correlated with ε, whereas *edge* was positively related to ε. No climate covariates or *elev* were found in the best model. The 95% confidence intervals for the beta coefficients did not include zero for ε(ln[*highCC*]), ε(*edge*), and γ(ln[*mediumCC*]).

In the Sierra study area, the top-ranked model was ψ_1(.), ε(*highCC* + *mediumCC* + *edge* + *Pwinter*), γ(*highCC* + *mediumCC* + *edge*). Territory extinction was negatively correlated with both *highCC* and *mediumCC*, and territory colonization was positively related to both *highCC* and *mediumCC*. In contrast, *edge* was positively related to extinction and negatively related to colonization, so it had a negative association with territory occupancy. Territory extinction was also positively correlated with *Pwinter* (i.e. territories were more likely to become unoccupied following wetter winters). The 95% confidence intervals for the beta coefficients of ε(*mediumCC*), ε(*edge*), γ(*mediumCC*), and γ(*edge*) did not overlap zero.

In the Sequoia–Kings Canyon study area, the top-ranked model was ψ_1(.), ε(*highCC* + *mediumCC* + *highCC*mediumCC* + *fire*), γ(*highCC* + $[highCC]^2$ + *Rxfire* + *Twinter* + *elev* + *elev*Twinter*); thus, Sequoia–Kings

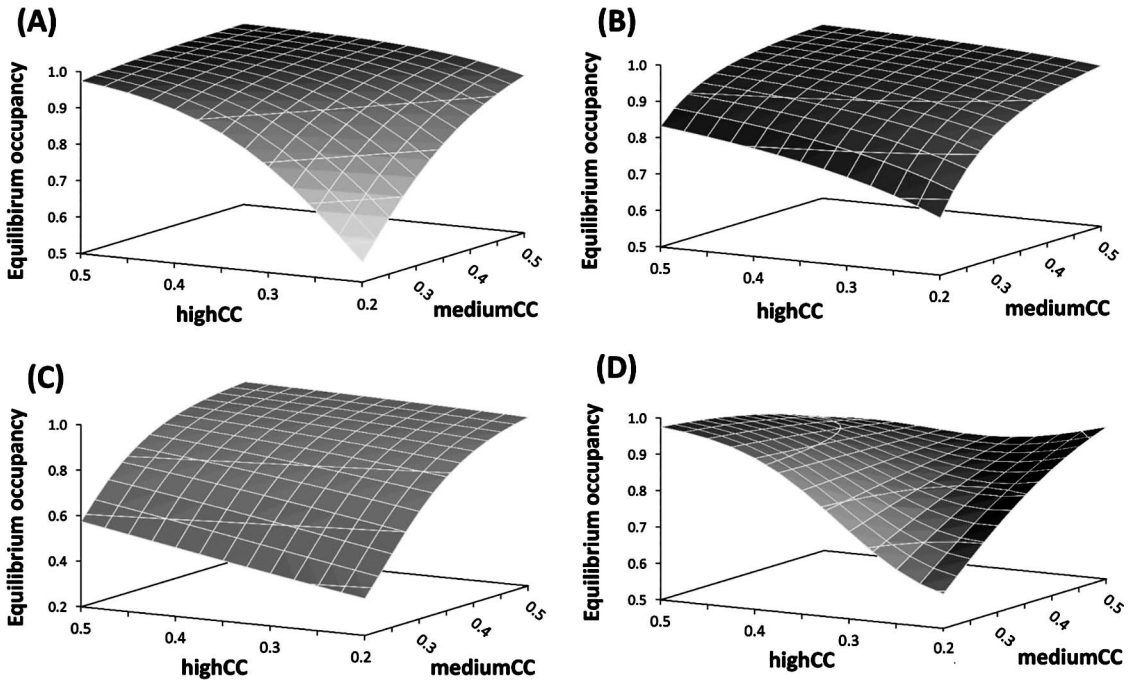

FIGURE 3. Equilibrium occupancy for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Occupancy is plotted against the proportion of owl territories containing forest with ≥70% canopy cover (highCC) and forest with 40–69% canopy cover (mediumCC). We used the beta coefficients from the top-ranked extinction and colonization models in each study area: (**A**) Lassen, (**B**) Eldorado, (**C**) Sierra, and (**D**) Sequoia–Kings Canyon.

Canyon was the only study area for which interaction terms appeared in the best model. The extinction beta coefficients for *highCC* and *mediumCC* were both negative, but their interaction was positive. Furthermore, the colonization coefficient was negative for *highCC* and positive for $(highCC)^2$, so that colonization was lowest at intermediate amounts of *highCC*. Territory extinction was negatively related to *fire*, and colonization was negatively related to *Rxfire*. Although *Twinter* had a weak association with colonization, *elev* had a negative association, and their interaction was positive. This suggested that territories at higher elevations were less likely to be colonized except after warmer winters. All of the 95% confidence intervals for the extinction beta coefficients overlapped zero, but they did not do so for $\gamma(highCC)$, $\gamma([highCC]^2)$, $\gamma(elev)$, and $\gamma(elev^*Twinter)$.

The only covariates that were consistently important for all 4 study areas were *highCC* and *mediumCC*, so we calculated equilibrium occupancy for each study area while varying these 2 covariates from 0.2 to 0.5, which encompassed the typical range of values in the study areas (Table 2). When doing so, we included all covariates and their corresponding beta coefficients that appeared in the top-ranked model for a study area. For covariates other than *highCC* and *mediumCC*, we either used their average value across the study area (all climate covariates, *elev*, and *edge*) or set their value to zero (*logging*, *fire*, *Rxfire*). For all 4 study areas, equilibrium occupancy reached its lowest value when both *highCC* and *mediumCC* were minimized at 0.2 and reached its highest value (or near it in the case of Sequoia–Kings Canyon) when both were maximized at 0.5 (Figure 3). Furthermore, in Eldorado and Sierra, *mediumCC* was more positively correlated with occupancy than *highCC* (Figure 3). The amounts of *highCC* and *mediumCC* within owl territories were clearly important because the analyses of deviance showed that the habitat covariates explained much of the variation in occupancy in all of the study areas—41% in Lassen, 47% in Eldorado, 67% in Sierra, and 35% in Sequoia–Kings Canyon. In contrast, the climate covariates explained much less variation in occupancy—7% in Lassen, 4% in Sierra, and 4% in Sequoia–Kings Canyon (no climate covariates were included in the top-ranked model for Eldorado).

The post hoc analysis in which we categorized canopy cover into 10% classes suggested that thresholds existed at 30% or 40%, depending on the study area; equilibrium occupancy declined sharply when below these thresholds (Figure 4). In addition, we observed that occupancy for the 40–49% canopy cover class was always lower than occupancy for the 50–59% and 60–69% canopy cover classes, and that occupancy was lower for the 90–100% class in 2 study areas (Figure 4).

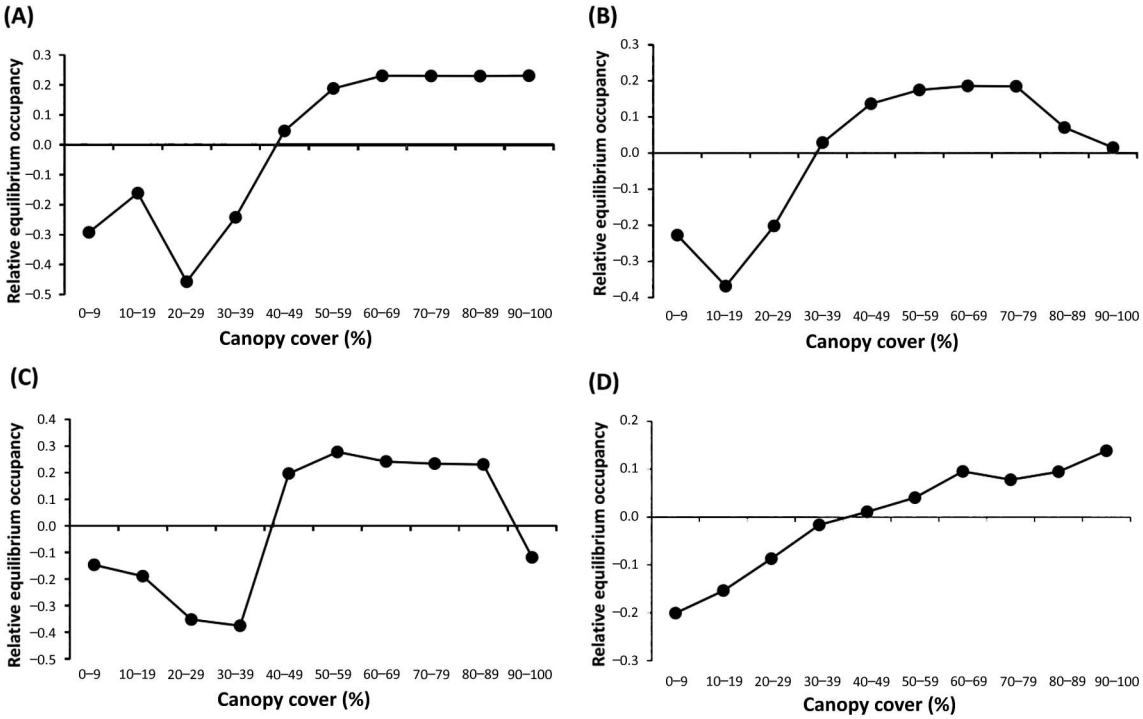

FIGURE 4. Equilibrium occupancy (relative to the mean value) for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Relative occupancy is plotted against the proportion of owl territories containing canopy cover in 10% classes. We used the beta coefficients from the extinction and colonization models to estimate equilibrium occupancy for each canopy cover class, then calculated the "relative" occupancy by subtracting the mean equilibrium occupancy of all 10 canopy cover classes. The study areas are: (**A**) Lassen, (**B**) Eldorado, (**C**) Sierra, and (**D**) Sequoia–Kings Canyon.

DISCUSSION

We modeled the territory occupancy dynamics of California Spotted Owl populations in 4 study areas which were large in spatial extent and spanned the length of the Sierra Nevada. As such, we believe that our results have implications for forest management throughout this region. One of our key findings was the consistently positive association between both medium (40–69%) and high (≥70%) canopy cover forests and territory occupancy metrics (i.e. increased colonization and decreased extinction) and that these vegetation variables explained a high proportion of variance in occupancy. By extension, and as suggested by our post hoc analysis, forests having <40% canopy cover were not Spotted Owl habitat, which supports a long history of such findings from habitat studies of California Spotted Owls (see below). In contrast, we did not consistently find strong support for associations between occupancy and fire, logging, habitat configuration, or climate.

The positive association that we detected between Spotted Owl territory occupancy and the amount of forest with ≥70% canopy cover for each study area is consistent with a previous occupancy–habitat study using Eldorado data only (Tempel et al. 2014b). Notably, the 2 studies used different and independent vegetation data sources (Landsat with verification based on other remote sensing techniques vs. aerial-photo interpretation with ground verification); collectively, they strengthen the inference that high-canopy-cover forests promote territory occupancy by Spotted Owls. Furthermore, other studies have shown that forest with ≥70% canopy cover serves as important nesting and roosting habitat for owls (Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004). In contrast, the positive association between California Spotted Owl occupancy and forest with medium (40–69%) canopy cover is a novel finding.

The proportion of area within owl territories having <40% canopy cover was negatively related to territory occupancy in 3 study areas and nearly so in the fourth (Figure 4), and such forests thus do not appear to constitute suitable Spotted Owl habitat. It has been suggested that much of the Sierra Nevada historically consisted of forests having low tree density with <40% canopy cover (Collins et al. 2015) and, by extension, that such forests were suitable for owls in the past. A possible explanation for this dichotomy is that existing areas of <40% canopy cover that have resulted from forest management or disturbance may not be ecologically equivalent to historical areas of low canopy cover,

particularly if they lack larger trees. However, the negative relationship between occupancy and forests with <40% canopy cover in the Sequoia–Kings Canyon study area, where the vegetation presumably more closely reflected historical conditions under which Spotted Owls evolved (Lydersen and North 2012), suggests that forests with <40% canopy cover may not have constituted suitable Spotted Owl habitat in the Sierra Nevada historically either. Moreover, the relationship with occupancy continued to strengthen as canopy cover increased in Sequoia–Kings Canyon, suggesting that forests with ≥70% canopy cover may have been important to the owls prior to the recent period of fire suppression. However, owl territories in Sequoia–Kings Canyon did not contain appreciably less high-canopy-cover forest than the other study areas (Table 2) and may not have fully reflected "reference conditions" prior to changes associated with fire suppression. Thus, additional work is needed to understand how closely forest characteristics at owl sites in Sequoia–Kings Canyon reflect or do not reflect conditions prior to fire suppression.

We had expected the amount of edge between high-canopy-cover forest and areas with <40% canopy cover to have positive associations with Spotted Owl occupancy via increased prey availability (Franklin et al. 2000), but edge was negatively related to occupancy in 2 of the study areas (Eldorado, Sierra). In addition, our other measures of spatial heterogeneity (evenness, clumpiness) were not supported in the occupancy models for any of the study areas. These spatial metrics may have been relatively unimportant for territory occupancy, although prior research has suggested that habitat heterogeneity and fire history have important effects on Spotted Owl prey abundance and diversity (Roberts et al. 2015). However, we measured habitat heterogeneity at a different spatial scale than Franklin et al. (2000), who mapped forest stands with a minimum size of 2 ha (as opposed to 0.09-ha pixels) and found an edge relationship between old forest and "other" cover types (i.e. not specifically <40% canopy cover as we hypothesized). In addition, habitat configuration may influence Spotted Owl fitness, as demonstrated by Franklin et al. (2000), but not necessarily occupancy, as in our present study. Finally, other aspects of habitat heterogeneity that we did not quantify may have more biological significance for Spotted Owls.

Logging was associated with occupancy in only one study area (Eldorado), where it unexpectedly had a positive association with territory colonization. However, we may have underestimated the amount of logging in the Lassen, Eldorado, and Sierra study areas as evidenced by the low values of our *logging* covariate within these study areas (Table 2). We used the criterion of a 10% reduction in canopy cover to infer logging activity and, therefore, omitted potential logging activities that reduced canopy cover by <10%, which can occur. Furthermore, we examined logging events within a relatively short timeframe, and the cumulative effects of logging activities over decades could still adversely impact Spotted Owl territories. Three of the study areas had a history of timber harvest in the 20th century, which undoubtedly left a historical legacy in terms of the distribution of forest with high canopy cover and large trees within the individual study areas. The Sequoia–Kings Canyon study site did not have this logging history and it had the only study population that did not show a decline in occupancy. This spatial variation in forest conditions among territories was important in these study areas, as evidenced by the strong positive correlation between territory occupancy and forest with medium or high canopy cover.

The relationship between Spotted Owls and fire is complex and likely depends upon the overall severity of the specific fire and the proportion and patch sizes affected by high-severity fire. Some studies have found that fire had no discernible negative impact on Spotted Owl territory occupancy (Roberts et al. 2011, Lee et al. 2012, Lee and Bond 2015). However, other studies of large, contiguous areas affected by high-severity fire have reported negative effects on Spotted Owl territory occupancy after controlling for postfire salvage logging (Lee et al. 2013, Jones et al. 2016a). In our study, fire effects were included in the top-ranked model for only 1 study area (Sequoia–Kings Canyon); few territories were affected by fire in the other 3 study areas, which reduced our statistical power to detect any potential effects. Although Tempel et al. (2014b) reported that fire was negatively related to territory colonization in the Eldorado study area over a similar time period (1993–2012), their model failed to estimate a standard error for the beta coefficient of the fire covariate. We also were unable to estimate a standard error for the fire effect on territory colonization within Eldorado, so we chose to exclude the fire covariate from further modeling stages (see Statistical Analysis—Model selection). In the Sequoia–Kings Canyon study area our results were mixed, in that fire (either wildfire or prescribed fire) that reduced canopy cover by >10% reduced the probability of territory extinction, but the amount of prescribed fire within a territory reduced colonization (Table 3). The mixed results for Sequoia–Kings Canyon suggest that fire may affect owl occupancy in different ways. For example, Southern and Lowe (1968; see also Hirons 1985) suggested that Tawny Owls (*Strix aluco*) could survive poor years because they could mitigate bad years owing to their accumulated experience and intimate knowledge of territories. Under this hypothesis, if fire creates prey habitat by opening canopy and allowing shrubs to grow, it might increase foraging opportunities for established owls that have acquired knowledge of their territory. Alternatively, if fire has negative effects, resident owls might simply shift

foraging areas because they have experience with other potential foraging areas within their territory (i.e. they might mitigate the negative impact). On the other hand, new owls attempting to colonize an area that had experienced some fire (e.g., controlled burns in Sequoia–Kings Canyon in our case) would not have the accumulated territory knowledge (i.e. experience) to avoid areas affected by fire, and thus fire would reduce their incentive to colonize an unoccupied, but available, area.

Our climate covariates were not strongly correlated with Spotted Owl territory occupancy dynamics, but we modeled annual climate covariates to control for potential sources of variation in occupancy dynamics separately from habitat change. Associations between climate and occupancy, however, may be reflected over longer time periods or after time lags (Jones et al. 2016b). For example, if favorable weather conditions result in a year with high reproduction, the effects of these conditions on territory occupancy may not become apparent for several years, until the birds of that cohort have had the opportunity to colonize vacant territories. In addition, bad weather may lead to individual mortality, but no territory extinction will be observed if at least one member of an owl pair survives or if a new individual colonizes the territory before the next breeding season. Thus, occupancy may be relatively insensitive to weather conditions.

Although territory occupancy dynamics were clearly influenced by canopy cover conditions within Spotted Owl territories, we observed declining occupancy rates in 3 study areas as the result of increased extinction and decreased colonization rates in individual territories (Figure 2). These declines occurred despite relatively constant canopy cover conditions over the duration of our study. Additional components of forest structure (e.g., density of large old trees and snags, vertical complexity) undoubtedly make important contributions to owl habitat selection, territory occupancy, and fitness. We did not have the data to accurately quantify these elements at the required large spatial scales over nearly 2 decades or to determine changes in these elements that occurred prior to our study but that could have had lasting effects on owls, but the development of such datasets could significantly advance our understanding of habitat effects on Spotted Owl demography. Interestingly, the one study area (Sequoia–Kings Canyon) in which territory occupancy did not decline was located within a national park, rather than a national forest interspersed with varying amounts of private land. The different occupancy trajectory in Sequoia–Kings Canyon may have been related to different forest management practices, the presence of giant sequoia groves in this study area, a different proportion of oak woodlands, or some combination of these factors (Blakesley et al. 2010).

Management Implications

Recent proposals to revise forest management practices in the Sierra Nevada emphasize increasing forest resilience to fire, climate change, and drought (i.e. the capacity of the forest to return to its predisturbance state while maintaining characteristic ecosystem processes; Allen et al. 2002) by promoting within-stand and landscape heterogeneity (North et al. 2009, North 2012). Fuels and restoration treatments that reduce tree density and canopy cover are considered important tools in this effort (Stephens and Moghaddas 2005, Stephens et al. 2009, Stevens et al. 2014). Thus, a key management consideration involves the degree to which canopy cover can be reduced without causing significant impacts on old-forest species such as Spotted Owls that depend on forests characterized by high canopy cover. When considering the implications of our results, we stress that our study relied on Landsat imagery to quantify canopy cover, whereas forest managers typically use the Forest Vegetation Simulator (FVS; Dixon 2002) to produce canopy cover estimates when planning management activities. Because FVS generally underestimates canopy cover, especially at higher values (Fiala et al. 2006), our canopy cover data should be calibrated against the source data used during planning. We also reiterate that we estimated equilibrium occupancy under the assumption of stable extinction and colonization rates, a condition that was not true for 3 of our study areas (Figure 2), and thus that the values of ψ_{eq} in Figure 3 should not be construed as the expected long-term proportion of occupied territories under different habitat conditions. Nonetheless, we believe that these values can be used to assess the relative importance of the canopy cover covariates on occupancy dynamics, particularly because these covariates exhibited low temporal variation in all study areas.

Collectively, our study suggests that fuels and restoration treatments could be used to reduce canopy cover below 70% in some high-canopy-cover forest within Spotted Owl territories without having a significant impact on expected occupancy rates. Specifically, treatments within a territory comprised of 50% high- and 50% mid-canopy-cover forest (i.e. the peaks in Figures 3A–3C) that convert some high-canopy-cover forest into mid-canopy-cover forest are predicted to incur a relatively modest cost to expected occupancy rates in the 3 national forest study areas (note the modest slope of the declines along the back right edges of the surfaces in Figures 3A–3C). Similarly, treatments within a territory comprised of 50% high-canopy-cover forest and 20% mid-canopy-cover forest that reduce high-canopy-cover forest to 30% of the territory, and where these altered stands also remain at >40% canopy cover, are not predicted to experience major reductions in occupancy. In fact, a slight increase in occupancy would be expected in the Eldorado study area

and a greater increase would be expected in the Sierra study area. However, our study also indicates that territory occupancy rates are likely to be negatively affected if canopy cover is consistently reduced to 40%, as evidenced by the lowest predicted occupancy rates occurring in the bottom right corners of Figures 3A–3D (i.e. where only 20% of a territory is in the high- and mid-canopy-cover classes, and 60% is in the low-canopy-cover class). Moreover, our post hoc analysis, in which we partitioned canopy cover into 10% classes, showed that forest with 50–69% canopy cover was more strongly and positively correlated with occupancy than forest with 40–49% canopy cover. Finally, we caution that forest with 40–69% canopy cover cannot simply be substituted for forest with $\geq$70% canopy cover. The importance of $\geq$70% canopy cover forests as nesting and roosting habitat for California Spotted Owls has been well documented (Bias and Gutiérrez 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004). Indeed, few territories contained $<$20% of high-canopy-cover forest, and as a result our study does not provide a reliable means of assessing the effects of reducing high-canopy-cover forest—and thus nesting and roosting habitat—below this level. In conjunction with declining numbers of large trees (i.e. suitable nest trees) in the Sierra Nevada over the past century (Smith et al. 2005, Lutz et al. 2009), sufficiently large reductions in high-canopy-cover forest are likely to negatively affect owls.

Our study, in conjunction with recent documentation of adverse impacts that large fires have had on California Spotted Owls (Jones et al. 2016a), suggests that maintaining viable Spotted Owl populations in the Sierra Nevada and reducing future wildfire risk using fuels and restoration treatments may be compatible goals, particularly if recent trends in high-severity fire continue or intensify because of climate change (Liu et al. 2013). However, we suggest that forest treatments to reduce fire risk should proceed with caution (be designed to retain some structural heterogeneity and the large trees) because we found declines in territory occupancy during our study, and other studies have reported substantial (up to 50%) declines in Spotted Owl populations in the Sierra Nevada within the past 20 yr (Conner et al. 2013, Tempel et al. 2014b). In addition, Barred Owls have not occurred in our study areas until recently, but evidence from Northern Spotted Owl studies suggest that they could pose an additional and significant threat to Spotted Owl populations in the Sierra Nevada if they continue to invade this region in future years (Yackulic et al. 2014, Dugger et al. 2016). Fuels treatments within Spotted Owl Protected Activity Centers (PACs), which contain $\sim$125 ha of the best habitat around known Spotted Owl nest and roost locations, were largely excluded from treatment during our study, so we lack information on how treatments within PACs could affect territory occupancy. However, given that PACs have been consistently used for nesting and roosting over long time periods (Berigan et al. 2012), future treatments within PACs could negatively affect Spotted Owl territory occupancy because these are centers of owl activity. Furthermore, forest restoration objectives may be achievable without implementing treatments within PACs because PACs occupy a relatively small percentage of the overall landscape in the Sierra Nevada (North et al. 2015). Nevertheless, forest treatments that reduce canopy cover within Spotted Owl territories, if judiciously implemented, could maintain Spotted Owl habitat in the short term so that any long-term benefits as a result of reductions in high-severity fire can be realized.

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CORRECTION

Erratum: Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management

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ABSTRACT

In the first sentence of the fifth paragraph of the Discussion, the authors incorrectly stated the relationship between logging and territory occupancy. The sentence should read instead: "Logging was associated with occupancy in only one study area (Eldorado), where it unexpectedly had a negative association with territory extinction."

Keywords: California Spotted Owl, canopy cover, forest management, occupancy, Sierra Nevada, *Strix occidentalis occidentalis*

Erratum: Meta análisis de la ocupación de territorios de *Strix occidentalis occidentalis* en la Sierra Nevada: asociaciones de hábitat y sus implicaciones para el manejo forestal

RESUMEN

En la primera oración del quinto párrafo de la discusión, los autores indicaron incorrectamente la relación entre la tala y la ocupación del territorio. La frase debe decir en su lugar: "La tala se asoció con la ocupación en sólo un área de estudio (Eldorado), donde inesperadamente tuvo una asociación negativa con la extinción del territorio".

Palabras clave: cobertura del dosel, manejo forestal, ocupación, Sierra Nevada, *Strix occidentalis occidentalis*

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In the first sentence of the fifth paragraph of the Discussion, the authors incorrectly stated the relationship between logging and territory occupancy. The sentence should read instead: "Logging was associated with occupancy in only one study area (Eldorado), where it unexpectedly had a negative association with territory extinction."

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