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Authors: Eyes, Stephanie A., Roberts, Susan L., and Johnson, Matthew D.

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*RESEARCH ARTICLE*

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

**Stephanie A. Eyes,[1,2a]* Susan L. Roberts,[2#] and Matthew D. Johnson[1#]**

[1] Department of Wildlife, Humboldt State University, Arcata, California, USA
[2] U.S. Geological Survey, Yosemite Field Station, Oakhurst, California, USA
[a] Current address: National Park Service, Yosemite National Park, El Portal, California, USA
[#] These authors contributed equally to the paper.
* Corresponding author: stephanie_eyes@nps.gov

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**ABSTRACT**

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

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

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

**RESUMEN**

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

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

## INTRODUCTION

In the multilayered, structurally complex, and large tree–dominated forests (hereafter, 'old forests') occupied by the California Spotted Owl (*Strix occidentalis occidentalis*), fire is critical for maintaining forest structure and function (Collins et al. 2011). Currently, California Spotted Owl populations are declining due to habitat loss and fragmentation (Tempel et al. 2014). The role of stand-replacing fires is complex and research has produced

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

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

Diversity in vegetation and fuels composition and structure, weather, and topography results in a mosaic of postfire forest patches burned at varying fire severities, including interspersed areas untouched or measurably unchanged by fire (Miller and Urban 1999, Collins et al. 2007). This postfire spatial habitat complexity can increase a foraging owl's access to different types of habitat and number of habitat edges, including high and low contrast edges (Miller and Urban 1999, Franklin et al. 2000, Collins et al. 2007). Research examining how different edge types affect owl foraging habitat quality is limited, but some studies have revealed that Northern Spotted Owls (*S. o. caurina*) avoid high contrast edges (sharply defined edge between 2 different habitat patches, e.g., a patch burned at low fire severity adjacent to a patch burned at high severity) and prefer low contrast edges (blended edges between different habitat types, e.g., a habitat patch unchanged postfire adjacent to patch burned at low fire severity), depending on the spatial scale used to examine habitat selection (Glenn et al. 2004, Clark 2007, Comfort et al. 2016). Therefore, by creating a patchwork of stands of different ages, fire may enhance foraging opportunities for Spotted Owls by increasing the number or amount of edges present in the landscape (Franklin et al. 2000). However, others have argued that patch edges fragment habitat, decrease owl survival (Blakesley et al. 2005), and increase owl home range size (Schilling et al. 2013), although differences in primary prey species may contribute to these differences.

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

## METHODS

### Study Area

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

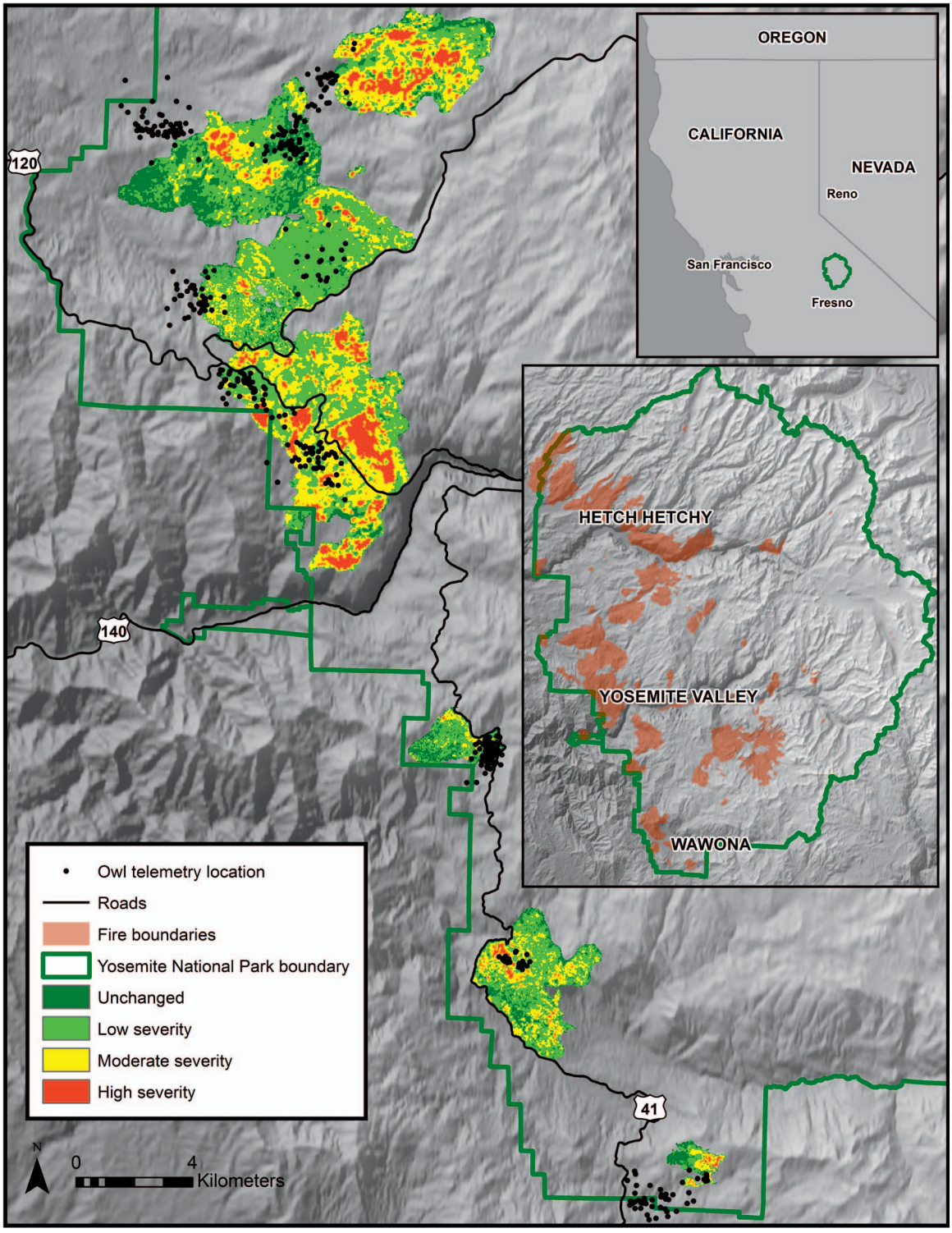


**FIGURE 1.** Study area used to examine California Spotted Owl foraging habitat use patterns within California, USA, and Yosemite National Park, 2010–2012. Inset map of Yosemite National Park shows all fires that have burned in Yosemite since 1997. Large map shows fire severity patterns for specific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

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

### Field Methods

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

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

### Home Range Analysis

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

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

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

### Habitat Selection Analysis

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

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

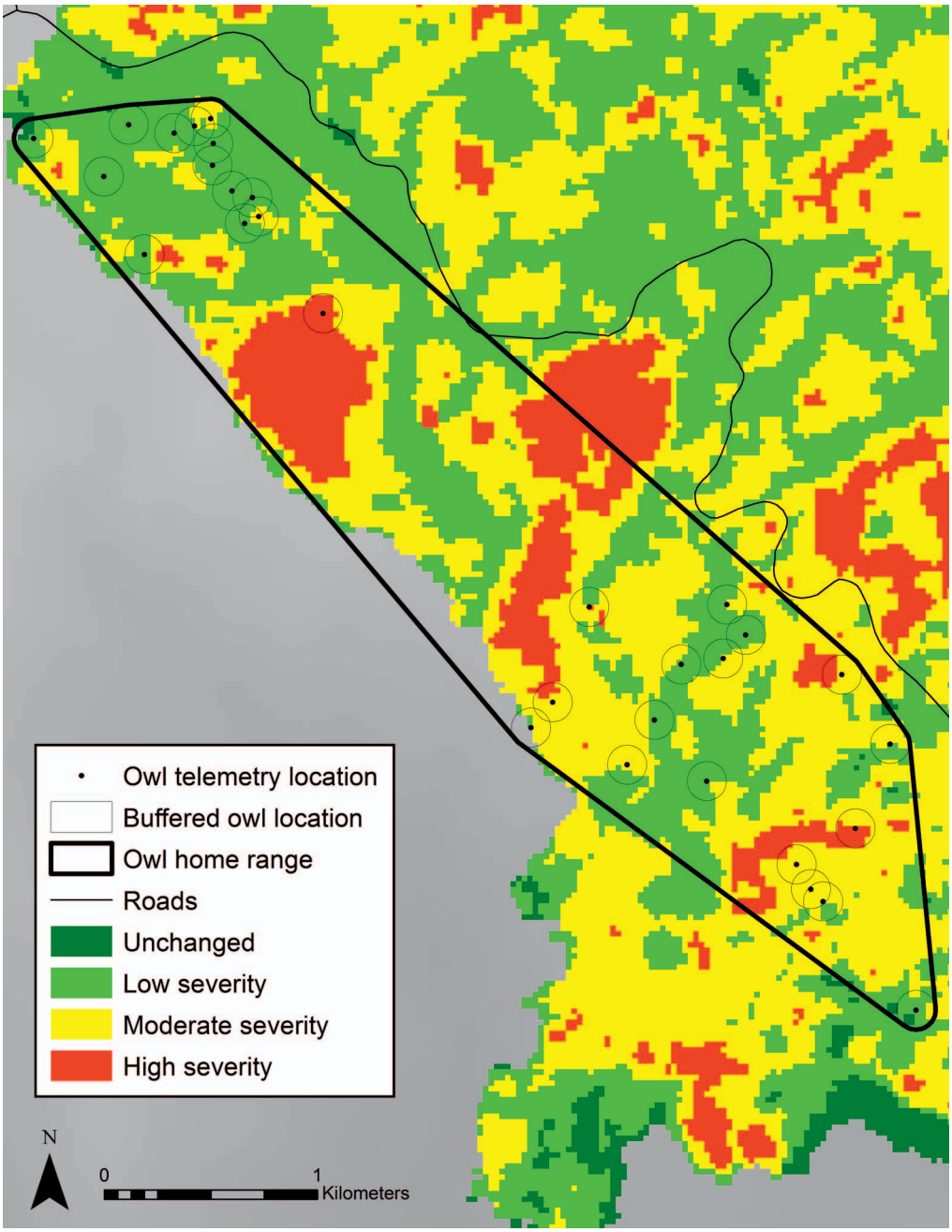


**FIGURE 2.** An example of one California Spotted Owl home range showing fire severity patterns within a home range in Yosemite National Park, California, USA, 2012. Black dots represent owl telemetry locations and circles show the buffered owl location with a 92-m radius to represent telemetry error.

### Habitat Variables

We calculated all predictor variables using ArcGIS and GME and used fire severity maps generated by Yosemite fire specialists to describe the extent and boundaries of fires in each owl's home range. To quantify fire severity, we used the relative differenced Normalized Burn Ratio (RdNBR), which measures the amount of spectral (reflectance) change in vegetation after fire (Miller and Thode 2007). Miller and Thode (2007) created relative thresholds to classify all RdNBR values into 4 fire severity patch types: no detectable change (hereafter, unchanged); low; moderate; and high. Following van Wagtendonk and Lutz (2007), we reclassified these types with integer values of 2, 3, 4, and 5, respectively, to aid in the calculation of a total fire severity index (FSI) for each buffered owl location. Reclassification with integer values allowed every

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

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

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

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

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

## Model Development and Selection

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

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

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

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

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

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

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

[a] Unburned = area untouched by fire outside the fire perimeter; Unchanged = no detected change in vegetation, relative differenced Normalized Burn Ratio (RdNBR) threshold <42; Low = surface fuels consumed with little change to overstory structure, RdNBR threshold ≥42 and <220; Moderate = understory vegetation, midstory shrubs, and small trees consumed and ~0.5% canopy trees killed, RdNBR threshold ≥220 and <566; High = nearly all mature plants killed (~75% of canopy trees), RdNBR threshold ≥566.
** Unburned mean and range of patch sizes were not calculated because unburned areas consisted of large, contiguous patches of forest.

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

## RESULTS

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

### Home Range Analysis

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

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

### Habitat Selection Analysis

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

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

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

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

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

[b] $\text{AIC}_c = 2148.00$.

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

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

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

Two models were within 2 $\Delta\text{AIC}_c$ units of the top model and together all 3 carried 63% of the Akaike weight (Table 2). Because no model had a substantial amount of weight (i.e. >0.75), we model-averaged all models in the set and report odds ratios from this averaged model (Table 3). Confidence intervals for the odds ratio estimates did not overlap 1 for distance to roost predictors, low contrast edge, and no edge, while those for fire severity index, slope, and elevation included or slightly overlapped 1 (Table 3). However, in estimates from the top model only, the 95% confidence interval for the odds ratio for FSI did not overlap 1 (Table 3).

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

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

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

[a] 95% CI does not overlap 1.

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

## DISCUSSION

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

Our study joins several others that have documented that distance to the roost or nest is important for foraging habitat selection by Spotted Owls (Glenn et al. 2004, Irwin et al. 2007, 2012, Wiens 2012, Bond et al. 2016). Spotted Owls have high site fidelity to nest sites and tend to roost near the eventual nest site, which is typically used for many years (Forsman et al. 1984). Furthermore, Spotted Owls are central-place foragers and often remain near the nest site in the nonbreeding season, so nest and roost locations may play a significant role in owl foraging habitat selection throughout the year (Forsman et al. 1984, Carey and Peeler 1995). Rosenberg and McKelvey (1999) argued that not including distance to the nest or roost in habitat selection models might bias selection for habitat characteristics near the central place, perhaps resulting in a false suggestion that it is the habitat type that the owls are selecting rather than merely its adjacency to the nest. In our study, support was strongest for a nonlinear effect of distance to the roost, with a slight flattening at intermediate distances from the

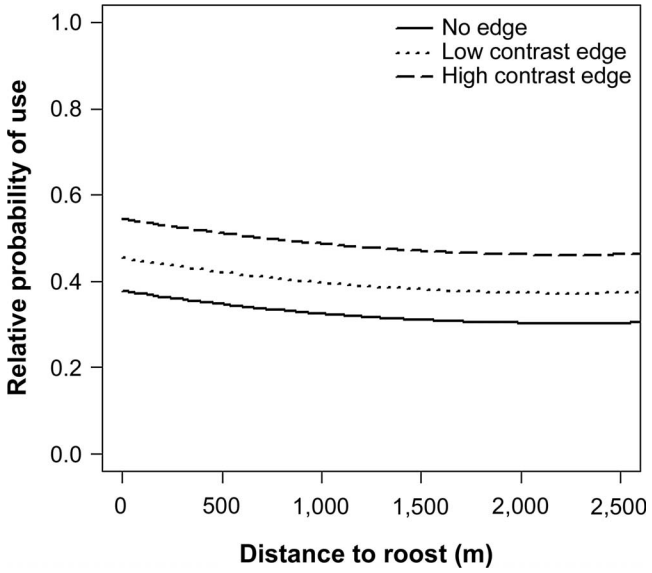


**FIGURE 3.** Modeled relative probability of California Spotted Owl habitat use as a function of distance to roost and edge type in Yosemite National Park, California, USA, 2010–2012.

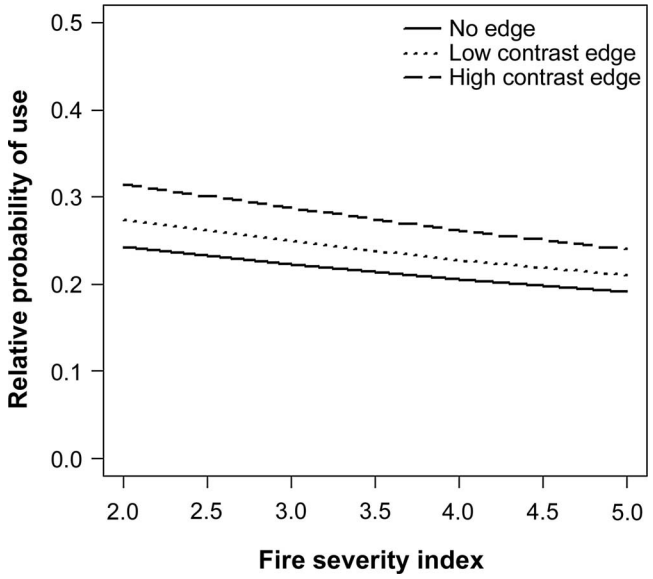


**FIGURE 4.** Modeled relative probability of California Spotted Owl habitat use as a function of fire severity index and edge type in Yosemite National Park, California, USA, 2010–2012.

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

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

Our analyses showed that California Spotted Owls in our study area also had a weak negative relationship with FSI (Figure 4). This negative relationship with FSI suggests that, while owls in Yosemite frequently used edges created by high severity fire, they may have avoided the interiors of large patches burned at high fire severity, a result similar to that from research on California Spotted Owls in megafires (Jones et al. 2016) and Northern Spotted Owls (Comfort et al. 2016). Therefore, perhaps small proportions of patches burned at high fire severity embedded in a larger matrix of areas burned at low and moderate fire severities may be beneficial for owl foraging habitat by creating high contrast edges.

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

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

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

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

Although we discovered that distance to roost, patch edge metrics, and fire severity patterns explained California Spotted Owl foraging habitat selection, we recommend that our top models be interpreted with caution, since it is likely that there are other factors that affect Spotted Owl foraging that we did not measure, such as prey availability. The tests that we used to evaluate our models assume that we measured all of the effects that may influence Spotted Owl foraging, which this study never intended to do; therefore, the low variability explained by the 'best' model is not unexpected. Incorporating owl ID as a random effect did not explain any of the variance in the model, meaning that the probability of use was not influenced by individual owls, a result also seen in 2 other studies (Gillies et al. 2006, Williams 2008). Future research investigating microscale habitat characteristics associated with foraging locations or prey abundance and movement could help to shed more light on owl habitat use patterns. Our low model evaluation values indicate that other variables that we did not measure may be more important to patterns of Spotted Owl foraging habitat selection.

## Conclusion

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

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**Ethics statement:** This field research was approved by Humboldt State University's Institutional Animal Care and Use Committee (IACUC protocols 10/11.W.67-E and 11/12.W.89-A).

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

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