THE EFFECTS OF FIRE SEVERITY ON CALIFORNIA SPOTTED OWL HABITAT USE PATTERNS

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ABSTRACT

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Fire is a dynamic ecosystem process in mixed-conifer forests of the Sierra Nevada, however there is limited scientific information addressing wildlife habitat use in burned landscapes. Recent studies suggest stand-replacing wildfires may be a major source of habitat loss for spotted owls (*Strix occidentalis*). While fire promotes heterogeneous forest patches, high severity fire may create large canopy gaps that can fragment closed-canopy habitat preferred by spotted owls. Large areas of high severity fire may eliminate protective cover or perch sites for spotted owls, while unburned or low to moderate severity fire containing intact forest canopy may provide protective cover or high prey availability. I used radio telemetry to determine whether foraging California spotted owls in Yosemite National Park showed selection for particular types of fire severity. My results suggest that spotted owls exhibited habitat selection for lower fire severities, edge sites, and locations near the roost within their home range. Although owls selected high contrast edges with greater relative probabilities than low contrast edges, I did not detect a statistical difference in these edge types. Protecting the remaining forests from stand-replacing fires via mechanical thinning or prescribed fire is a priority for management agencies, and my results suggest that fires of low to moderate severity can create habitat conditions suitable for California spotted owls.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The California spotted owl (*Strix occidentalis occidentalis*), one of three subspecies, occurs in forested habitats of the western slopes of the Sierra Nevada, in the Coast Ranges from Monterey to Santa Barbara County, and in the mountainous regions of southern California and Baja California (Verner et al. 1992). Because several populations are declining (Blakesley et al. 2010, Conner et al. 2013, Tempel and Gutiérrez 2013), the California Department of Fish and Wildlife and USDA Forest Service consider it a Species of Special Concern (Troyer and Blackwell 2004, Davis and Gould 2008). While spotted owl populations are declining due to habitat loss and fragmentation as well as competition from barred owls (*Strix varia;* Tempel et al. *In press*, Gutiérrez et al. 2006); recent research suggests that stand-replacing fires may pose a new threat to spotted owl habitat loss (Roloff et al. 2005, Ager et al. 2007, Spies et al. 2010).

The California spotted owl occupies late-successional forests with high canopy cover and large trees (Gutiérrez et al. 1992, Blakesley et al. 2005, Roberts et al. 2011); land also economically valuable for timber harvesting, emphasizing a need to investigate habitat use patterns for this species. Habitat use patterns describe how individuals distribute themselves across habitat types (Jones 2001). For spotted owl conservation, it is important to understand habitat use patterns and characteristics necessary to meet different life history needs for nesting, roosting, and foraging. Nest sites have high structural complexity and basal area of large conifers and hardwoods and have more broken-top trees and snags (Bias and Gutierrez 1992, LaHaye et al. 1997). Roost sites tend to have high tree density and canopy cover, low densities of small trees and shrubs (Zabel et al. 1992, Chatfield 2005) and more residual old-growth trees (>100 cm diameter at breast height or dbh) creating a multi-layered forest canopy (Moen and Gutiérrez 1997). Foraging sites are moderately dense forest stands close to nests and small streams with trees greater than 15 cm dbh, large hardwoods (Call et al. 1992, Irwin et al. 2007, Williams et al. 2011), higher woody debris and increased snag presence (Bias and Gutierrez 1992, Gutiérrez et al. 1992). Foraging habitats contain more variable characteristics due to the distribution and habitat needs of primary owl prey which include: woodrats (*Neotoma* spp.), northern flying squirrels (*Glaucomys sabrinus*), and white-footed mice (*Peromyscus* spp.; Call et al. 1992, Irwin et al. 2012). Dusky-footed woodrats (*N. fuscipes*) reside in forested and shrub habitats with a mix of overstory trees and large logs and stumps (Innes et al. 2007) while less is known about bushy tailed woodrats (*N. cinerea*), but in Oregon and Washington they occupy areas at intermediate to high elevations near streams and rocky slopes (Carey et al. 1999). Northern flying squirrels primarily use closed-canopy mixed-conifer and red fir (*Abies magnifica*) forests and need large trees and snags for nesting (Meyer et al. 2007*b*, Smith 2007, Pyare et al. 2010). Similar to the spotted owl, overstory canopy cover is also important to flying squirrels as Lehmkuhl et al. (2006) found the densities of northern flying squirrels significantly declined when tree canopy cover dropped below 55 percent. As habitat generalists, *Peromyscus spp*. occur in a variety of forest types and seral stages (Grinnell and Storer 1924, Jameson 1951).

Throughout the range of the California spotted owl, fire played a critical role in maintaining forest structure and function in these late-successional forests (Scholl and Taylor 2010, Collins et al. 2011). Given the essential role of fire in forests associated with spotted owls, and because the spatial extent and behavior of fire is changing with a warming climate (Brown et al. 2004, Westerling et al. 2006, van Mantgem et al. 2013) and decades of fire suppression (Collins et al. 2011), it is critical to gain a better understanding of the effects of fire on California spotted owl use of these declining habitats.

Fire severity patterns influence important characteristics of owl habitat such as canopy closure, forest structure and composition, and persistence of large trees (Collins et al. 2011, Roberts et al. 2011). Fire severity, a measure of the amount of change that occurred in forests due to fire (Agee 1993, van Wagtendonk 2006), is a continuum, but frequently classified into four broad categories: 1) no detected change (unchanged); 2) low severity; 3) moderate severity; and 4) high severity (Miller and Thode 2007). Low severity fires consume surface fuels (e.g., litter, downed logs, and low vegetation), with little change to overstory structure; few canopy trees are killed by low severity fires and most of the mature plants survive (Kaufmann et al. 2007). In moderate severity fires, understory vegetation, midstory shrubs and small trees are generally consumed and approximately half of the canopy trees are killed (Keeley 2009). High severity fires result in the most drastic vegetation changes with effects varying from significant decreased canopy closure to stand-replacing fires where nearly all of the mature plants are killed (Miller and Thode 2007).

A variety of factors influence patterns of fire behavior and fireline intensity (rate of energy released as the fire burns) across the forest landscape. Diversity in living vegetation structure, fuels, local weather, and topography result in a mosaic of patches of varying burn severities, including interspersed areas untouched or unchanged by fire (Miller and Urban 1999, Collins et al. 2007). Through direct and/or indirect tree mortality, fire can potentially create large gaps in the canopy and fragment the landscape. Large patches of stand-replacing fire may cause vegetation type changes (e.g., shrub cover only where there previously was forest) that persist through time and eliminate protective cover, nest trees, and perch sites for spotted owls, thereby negatively impacting habitat quality (Ager et al. 2007, Stephens et al. 2013). In contrast, a landscape composed of a matrix of unchanged and low to moderate severity burned habitat with an intact forest canopy may provide increased prey abundance and protective cover for owls, thus improving habitat (Roberts et al. 2011).

Variation in fire severity creates different types of vegetation patches, thereby increasing the spatial complexity, access to different types of habitat, and number of habitat edges, including high and low contrast edges (Turner et al. 1994, Collins et al. 2007). High severity forest patches may have abrupt transitions in vegetation structure and composition compared with patches burned at other severities creating high contrast edges; whereas there appears to be a gradual transition in forest types between areas burned at lower severities creating low contrast edges (Figure 1). Research examining how different edge types affect owl foraging habitat quality is limited, but some studies reveal that northern spotted owls (*S. o. caurina*) avoided high contrast edges and preferred low contrast edges (Glenn et al. 2004, Clark 2007, Comfort 2013). These habitat patch edges may provide important foraging habitat due to increased prey availability, suitable perch sites, and open flying space (Franklin et al. 2000). Furthermore, the amount of edge had a weak positive effect on northern spotted owl survival in southern Oregon (Schilling et al. 2013). Therefore, by creating a patchwork of stands of different ages, fire may enhance foraging opportunities for the spotted owl by increasing the number or amount of edge present in the landscape (Ribe et al. 1998, Folliard et al. 2000, Franklin et al. 2000). However, others argue patch edges fragment the habitat, decrease owl survival (Blakesley et al. 2005), and increase owl home range size (Schilling et al. 2013).

Given the important role of fire throughout the range of all spotted owl subspecies, several studies have examined the effects of fire on owl demographics. The results of these studies have been variable and at times contradictory, highlighting the need for additional research directed towards resolving these inconsistencies. Fire decreased site occupancy and survival in Mexican (*S. o. lucida*; Jenness et al. 2004) and northern spotted owls (Bevis et al. 1997, Gaines et al. 1997, Clark 2007). However, these studies examined only short-term effects of fire (1-5 yrs), failed to closely examine fire severity, and most failed to account for confounding effects of post-fire salvage logging. Furthermore, extinction probabilities increased with increasing area of high severity fire, salvage logging, and early seral forests (Clark et al. 2013) and colonization probabilities for California spotted owls decreased with high severity fire (Tempel et al. *In press*). Whereas Lee et al. (2012) concluded that fires with up to 32 percent high severity fire had no effect on extinction or colonization probabilities for California spotted owls in burned forests of the Sierra Nevada. Other studies also revealed that fire had little short-term effect on survival, site fidelity, mate fidelity, and reproductive success in all three subspecies (Willey 1998, Bond et al. 2002). Some studies demonstrated that fires of low to moderate severity retained habitat characteristics required by spotted owls. For example, site occupancy did not decline after the occurrence of low to moderate severity fires in California and Mexican spotted owls (Sheppard and Farnsworth 1997, Roberts et al. 2011).

Very little information exists on the complex relationship between fire severity and California spotted owl foraging habitat use in the Sierra Nevada. Bond et al. (2009) claimed California spotted owls foraged in all fire severity patches, but high severity patches were used more than expected, suggesting that these patches may provide important foraging habitat. However, their conclusions involved a number of limitations: 1) a limited number of replicates (*n* = 4 territories); 2) their results were confounded by examining forests with a history of significant logging and fire suppression; and 3) their study area comprised of only a single fire and that fire was not representative of the natural range of variation for any of the fire severity metrics (e.g., patch size, frequency) in the Sierra Nevada (Meyer *In review*). Thus, illustrating the need to examine how fire severity affects patterns of owl habitat use without these significant limitations.

I studied the effects of fire on California spotted owl habitat use patterns in Yosemite National Park, California. I examined owl response to a range of fire severities and edge types. I used radio telemetry to examine patterns in space use relative to fire severity. I hypothesized that fire severity was important to owl habitat use because of changes in forest structure and canopy cover (Shaffer and Laudenslayer 2006, Beaty and Taylor 2007). I also hypothesized that abiotic factors, such as slope, aspect, and distance to streams and roosts would influence owl foraging habitat use (Clark 2007, Irwin et al. 2012). Specifically, based on hypothesized relationships and previous work on spotted owl habitat use, I predicted that spotted owls would: 1) avoid forest patches burned at high severity (large canopy gaps); 2) avoid high contrast edges between different forest patches while preferring low contrast edges; 3) forage most often in forest patches that are unburned or burned at low severity (closed or partially-closed canopy); 4) forage closer to streams and roosts; and 5) forage in areas with less steep slopes and northern aspects. By providing insight into owl use of fire severity patterns, this study may help inform future fuels reduction efforts in similarly managed public lands (i.e., National Parks).

Figure 1. Conceptual diagram of edge types in a burned forest landscape. From left to right, figure represents the transition between a high severity burned forest with a high contrast edge to a moderate severity, low severity and unchanged forest with a low contrast edge.

STUDY AREA

Yosemite National Park (hereafter, “Yosemite”) spans 302,688 hectares (ha) in the central Sierra Nevada of California. I surveyed for 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*). Annual temperatures and precipitation for Yosemite Valley range from -3°C to 32°C and 0.8 cm to 15.7 cm, respectively, with mostly snow falling at higher elevations of the Park (U.S. National Park Service *n.d.*). A Mediterranean climate of cool, wet winters and warm, dry summers characterizes Yosemite’s climate.

Lower montane forests of Yosemite are fire-prone forests that typically experienced frequent low to moderate severity fires prior to the arrival of Europeans in North America (Skinner and Chang 1996, van Wagtendonk 2007). Beginning in 1970, Yosemite allowed fires to burn under controlled conditions and implemented a prescribed burning program (van Wagtendonk 2007). In Yosemite, researchers mapped all fires that occurred since 1930 and they are available for use with geographic information system (GIS) software; however, I focused only on fires that burned in the past 15 years (van Wagtendonk et al. 2002; Figure 2).

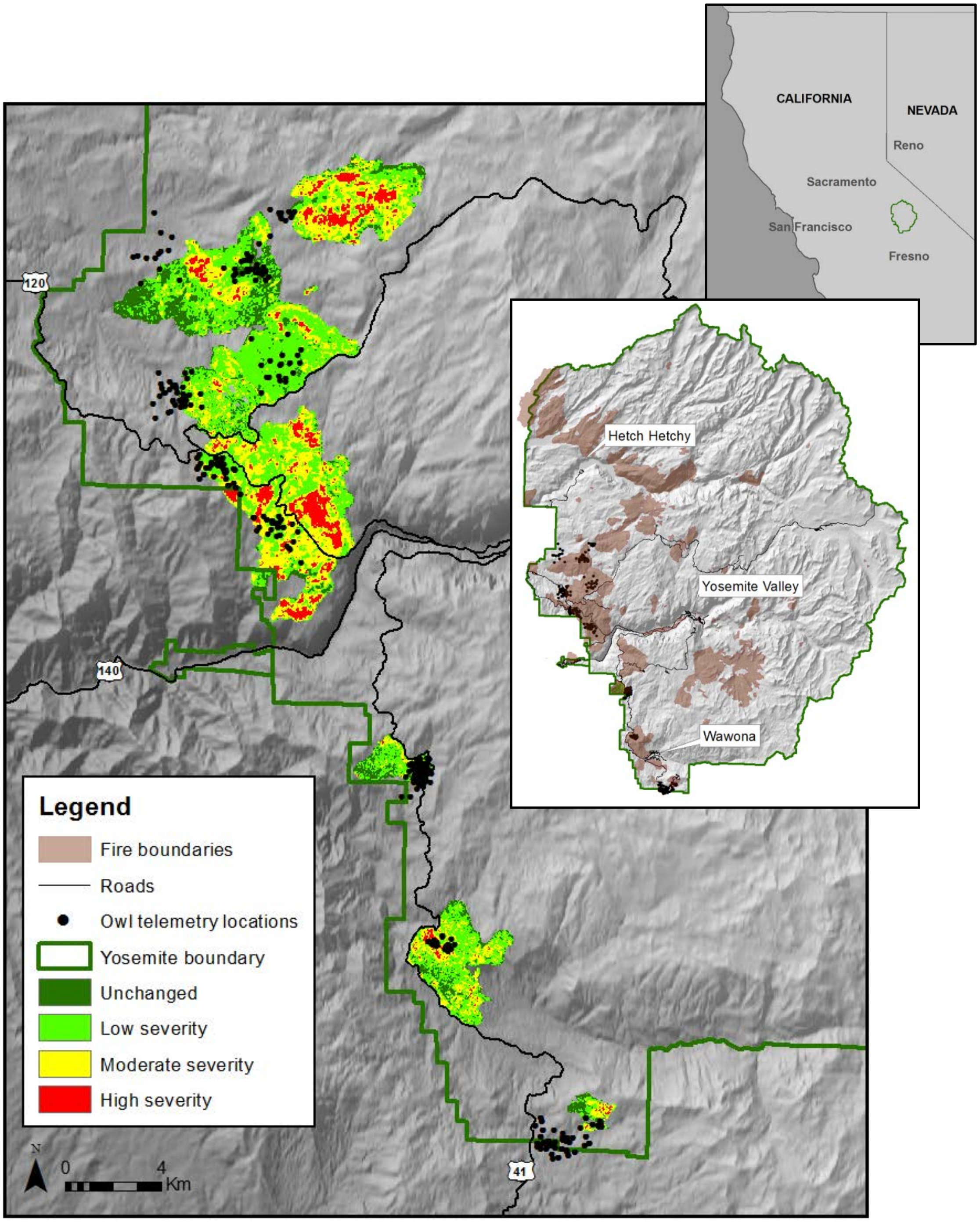

Figure 2. Study area within California and Yosemite National Park. Inset map of Yosemite National Park shows California spotted owl locations in relation to all fires that have burned in Yosemite since 1997. Large map shows fire severity patterns for specific fires near owl locations.

METHODS

Field Methods

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).

I located owls following established protocols (Forsman 1983) at previously known nest or roost sites (Roberts et al. 2011). I selected ten sites based on the occurrence of a recent (1-15 yrs) wildfire or prescribed fire, presence of a known owl pair, and field crew accessibility. I only chose sites less than three kilometers (km) from a road or trailhead and sites had to be within a three hour drive of each other so I could monitor all sites each night. I considered fires that burned within one km of known spotted owl activity centers when selecting owl territories.

During the breeding seasons, I captured owls using methods previously described by Forsman (1983) and Bull and Henjum (1990). I attached a backpack-mounted radio transmitter (AVM Instrument Company, Ltd., Colfax, CA, USA) to the captured owl with Kevlar ribbon (3/16”wide, Bally Ribbon Mills, Bally, PA, USA) following established procedures (Guetterman et al. 1991). Glenn et al. (2004) showed that spotted owl mates do not forage independently, so each year a radio-tagged owl in this study was from a unique territory. After attaching radio transmitters, I located and observed owl behavior on three separate occasions during daylight hours to assess condition of owls. I recaptured owls at the end of each breeding season to remove radio transmitters since our period of observation was only during the breeding season and the transmitter batteries only lasted for six months.

I performed nocturnal telemetry surveys to collect foraging locations. I used Communication Specialists receivers (model R-1000; Communications Specialist, Inc., Orange, CA, USA) and three element yagi antennas to track all radio-tagged owls. I obtained owl foraging locations using triangulation from established monitoring stations (Guetterman et al. 1991). I established telemetry monitoring stations at each site along roads or trails ≥170 m apart and georeferenced each station using a hand-held GPS (Garmin etrex, Garmin, Olathe, KS, USA). I marked each station with reflective markers and used compass bearings from these stations to estimate owl locations. For every survey, I took compass bearings from all stations and recorded signal strength for each bearing (Guetterman et al. 1991). I plotted all signal bearings on 1:24,000 scale topographic maps and three or more bearings would intersect to form a polygon representing the owl’s location. Because I surveyed all stations each night, most surveys resulted in multiple polygons and I used signal strength to objectively select the most accurate bearing set and polygon. Thus, ensuring the selected owl location polygons were composed of bearings with the highest signal strengths.

I monitored owls throughout their nocturnal foraging period from 30 minutes after sundown to 30 minutes before sunrise, with only one foraging location collected per owl each night. To ensure I sampled each owl at different times throughout the sampling period, I randomly assigned telemetry survey start times to each owl. If I detected an owl during the telemetry survey from unsolicited auditory vocalizations, I recorded the sex, location, approximate distance, and azimuth to the owl from the known location (i.e. telemetry station). If I visually observed a radio-tagged owl during the telemetry survey, I recorded the location using a GPS. In these situations, I used the auditory and visual detections as the owl's foraging location rather than the radio telemetry triangulated estimate.

After selecting the best bearings from each survey, I used Program LOAS (Location of A Signal) software version 4.0b (Ecological Software Solutions, Urnäsch, Switzerland) to generate owl point locations from the bearings recorded at the telemetry stations, and only used polygons ≤5 ha. Locations greater than 5 ha were often a result of poor signal strength, however only 4 percent of locations resulted in polygons larger than 5 ha. I used the arithmetic mean estimator in LOAS to select point locations as the center of all polygons.

I assessed the accuracy of my telemetry locations by following the same procedures I would for the nocturnal surveys (i.e., used the same stations) and triangulating to owls at known locations; the owls were stationary at diurnal roosts as located and observed by another observer. This other observer determined the owl's actual location by following the strongest signal until they visually located the owl. I also placed transmitters at locations unknown to observers similar to other telemetry studies (Glenn et al. 2004, Wiens 2012). The naïve observer then performed triangulations to determine the location of the hidden transmitter. Using distance calculations, I compared locations estimated by triangulations to actual locations to calculate radio telemetry bias and determined mean and median values for telemetry error. I used the median error distance (92 m, $\bar{x}$ = 150 m, n = 18) to avoid the influence of outliers and created a telemetry error circle around each foraging location.

Home Range Analysis

I plotted owl locations in ArcGIS 10.0 and created a buffered owl location using the median error distance (92 m) as my radius (Figure 3). From these telemetry locations, I calculated a home range for each owl with ArcMap 10.0 and Geospatial Modeling Environment (GME) using 100 percent Minimum Convex Polygons (MCP) including a 92 m error buffer. I then calculated home range sizes by summing the area contained within the MCP. Home range sizes between males and females did not significantly differ (see Results); therefore I pooled them for the analyses. In order to conform to a normal distribution, I log-transformed the home range sizes and used the geometric mean which provides a better measure of the middle of a data set than the arithmetic mean (Sheskin 2004).

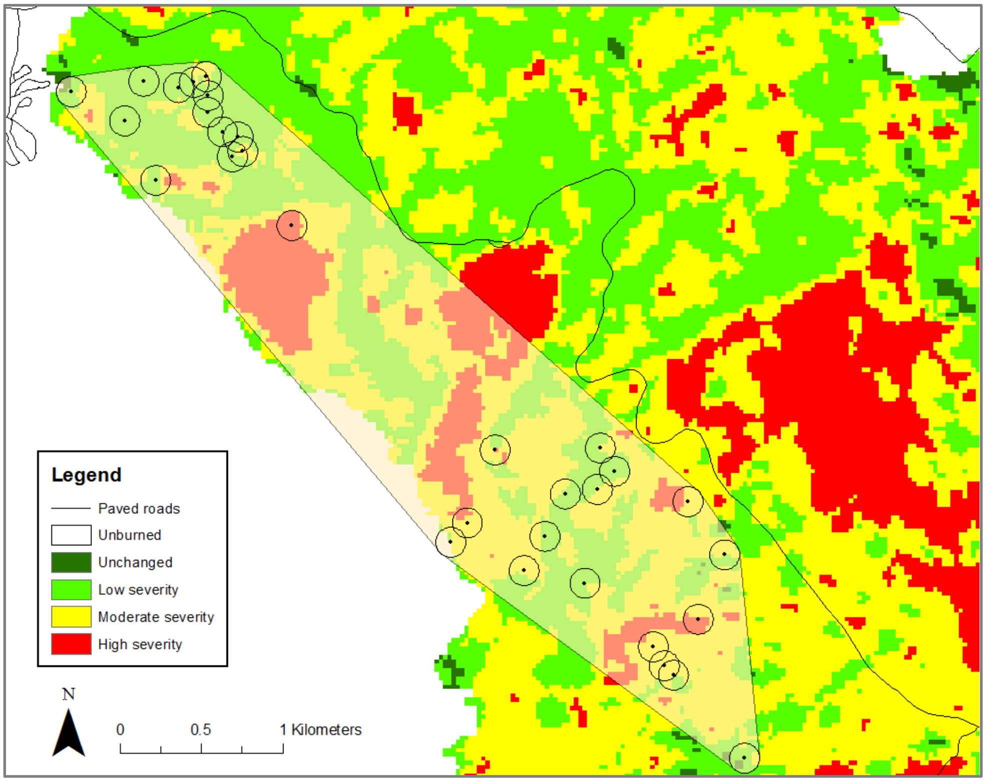

Figure 3. An example of one California spotted owl home range showing fire severity patterns within a home range. Black dots are owl telemetry locations and circles are the buffered owl location with a 92 m radius to represent telemetry error.

Habitat Selection Analysis

To investigate foraging habitat selection, I compared used habitat locations to available habitat locations using logistic regression to estimate a resource selection function (RSF; Manly et al. 2002). My response variable was owl use and I assigned used locations a value of one and available locations a value of zero. I compared used resources (owl telemetry locations) to available resources within the owl's home range, examining resource selection at the home range scale, or third order selection (Johnson 1980). I defined available habitat within the MCP, rather than within a fixed kernel home range estimate because MCPs may more accurately represent available area than fixed kernel methods (Gillies et al. 2006, Kauhala and Auttila 2009, Milakovic et al. 2012, Comfort 2013). Depending on the particular habitat variable, I used the point center location or the entire telemetry circle in calculations (see below).

I randomly generated three times as many available locations within each owl's home range in ArcGIS 10.0 to minimize rates of contamination and overlap (Johnson et al. 2006, Williams et al. 2011). Contamination is defined as 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 on the same location as a used location. I also buffered available locations with a 92 m radius to account for the same spatial error as the used locations. I calculated the same habitat variables for both used and available locations. I examined resource selection for all owl locations pooled because I did not expect owl foraging behavior to differ between sites, and thus did not treat owl identity as a random effect (Gillies et al. 2006, Clark 2007, Williams 2008). Furthermore, all owls had relatively similar numbers of locations, so I did not expect individual owls to influence the results.

Habitat Variables

I calculated all predictor variables using ArcGIS 10.0 and GeoSpatial Modeling Environment (Table 1). I used the fire severity maps generated by the National Park Service to describe the extent and boundaries of fires in each owl's home range. I used the Relative differenced Normalized Burn Ratio (RdNBR) to quantify fire severity. RdNBR measures the amount of change in the vegetation after fire (Miller and Thode 2007). Miller and Thode (2007) created relative thresholds to classify all RdNBR values into four fire severity patch types: unchanged/unburned; low; moderate; and high. I reclassified continuous values for fire severity into these categories following values outlined in van Wagtendonk and Lutz (2007). I reclassified these types with integer values 2, 3, 4, and 5, respectively, to aid in the calculation of a total fire severity index (FSI) for each buffered owl location. Reclassification of integer values allowed for every combination of fire severity patch composition within each buffered owl location to have its own unique value.

I overlaid the used and available locations to determine fire severity composition (Figure 2). I calculated proportional area of each fire severity patch within the buffered owl location using ArcGIS 10.0 and GME and then multiplied the area of each patch type by its corresponding RdNBR integer value. I calculated total fire severity index for each foraging location by summing all these values (Roberts et al. 2008). For example, a patch comprised of 75 percent low severity fire (3) and 25 percent unchanged (2) had an FSI value of 2.75 (0.75 × 3 + 0.25 × 2). Therefore, 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. Smaller FSI values indicate forest burned at lower severities, while higher values indicate forest burned at higher severities. I did not calculate distance to fire severity patches because many buffered owl locations contained multiple fire severity types. Given telemetry error, the owl could have been located anywhere within the buffered owl location, thus affecting the distance measurements. However, FSI incorporates area or amount of fire severity patch within each buffered owl location.

Other fire covariates included edge metrics related to fire severity. I defined used and available locations as no edge, low contrast edge, or high contrast edge. I classified all used and available locations as an edge if they contained more than one fire severity category. I classified edge locations that contained patches of high severity fire as high contrast edges and edge locations without high severity fire as low contrast edges (Clark 2007).

Abiotic covariates included horizontal distance to roost (m), horizontal distance to stream (m), slope (°), elevation (m), and aspect (8 cardinal directions) as a categorical variable. I generated all abiotic covariates in ArcGIS 10.0 using a 10-meter Digital Elevation Model (DEM) for the study area to generate slope and aspect layers. I classified aspect into eight categories: north, northeast, east, southeast, south, southwest, west, and northwest aspects. I used the point location, or center of buffered owl location to calculate these metrics.

I checked all predictor variables for normality by assessing normal quantile-quantile plots and used the appropriate transformation if normality assumptions were violated. However, logistic regression does not require that predictor or response variables be normally distributed (Johnson 1998). I calculated correlation matrices in R to determine correlation between covariates. All correlation coefficients between variables were < 0.2 so all variables were included in subsequent models.

Model Development and Selection

I developed *a priori* models incorporating three sets of covariates: abiotic; fire; and edge. I translated verbal hypotheses into models to determine the effects of covariates on spotted owl habitat use. I developed candidate models based on previous spotted owl research or information relevant to managers. I used an information theoretic approach based on Akaike's Information Criterion (AIC) to evaluate several plausible models using R (Anderson 2008). I used corrected AIC ("AIC_c") to account for small sample sizes and ranked models using AIC_c weights to identify support for models in the candidate set. AIC_c weights penalize for excessive numbers of variables in a model. I considered the model with the lowest AIC_c value and the largest AIC_c weight as the best model (Anderson 2008). The difference between the AIC_c value of the top model and all other model AIC_c values is the ΔAIC_c and can be used to rank models. I considered models with $\Delta AIC_c < 2$ from the best model as plausible models because of increased parsimony, striking a balance between log likelihood values and number of parameters (Anderson 2008). However, I examined model weights to determine best fitting models.

I conducted model selection in stages to limit the number of models in the final candidate set. I first tested for an effect of year and then selected the best topography models which included slope, aspect, and elevation. I then determined the best models that included distance to stream and roost. Once I determined the best models with abiotic covariates, I incorporated FSI, edge, and edge type predictor variables.

Because I collected data over several years, I treated year as a categorical blocking variable to account for variability across years. Therefore, I first determined if year was an important predictor to explain habitat selection. I included year as a null model and compared each other predictor to the null model with year. In each case the individual predictor variable alone explained more than year, indicating that predictors other than year better explain the response of owl use, according to AIC_c. I also included an interaction with year for all predictors to examine if the effect of a predictor differed across years. I found this model to have less evidence than the individual predictor model and, therefore, did not include year in subsequent analyses.

I examined abiotic factors associated with topography of a site including elevation, slope, and aspect. I hypothesized that topographical characteristics would be important because of differing forest structure associated with these characteristics. Aspect and slope can influence canopy cover, important for owl prey (Roberts et al. 2008). Furthermore, topography can affect fire severity and frequency with higher canopy cover and cooler climates for northern aspects while southwestern aspects are more open and hotter (Lydersen and North 2012). I incorporated elevation in models because it is important in fire patterns (McKelvey and Busse 1996) and tree species change with elevation affecting prey abundance (Copetto et al. 2006). I incorporated quadratic forms for slope and elevation to determine if animals were selecting intermediate elevations or slopes (Milakovic et al. 2012). I did not use interactions between topographic variables because it is not biologically significant to interact elevation, slope, and aspect without proper transformations (Stage 1976, Stage and Salas 2007). After ranking all possible additive topography models I selected all models within 2 ΔAIC_c from the top model for use in subsequent analyses with other predictor variables (Schoolmaster et al. 2013).

I included abiotic covariates such as distance to roost and perennial stream because they were found to be important in previous studies (Glenn et al. 2004, Clark 2007, Irwin et al. 2007, 2012, Williams et al. 2011). I hypothesized that distance to roost was important because spotted owls are “central-place foragers” and have high site fidelity for roost locations (Carey and Peeler 1995). I hypothesized that distance to perennial stream affected owl foraging because riparian areas are important for prey (Meyer et al. 2007*a*) and foraging (Glenn et al. 2004, Irwin et al. 2007). Because the relationship with distance may be nonlinear, I incorporated all distance covariates as a quadratic term. I used AIC_c to determine whether the quadratic form or linear form of these two abiotic factors best represented the data and only considered these models in the final candidate set of models.

I hypothesized that fire severity was important to owl habitat use because of corresponding changes in forest structure (Shaffer and Laudenslayer 2006, Beaty and Taylor 2007) and included the fire severity index in models. Small values of FSI indicated that the forest burned at lower severities and had greater canopy cover, a factor important for flying squirrels, primary prey for spotted owls (Meyer et al. 2007*a*, *b*). In contrast, larger values of FSI indicated that the forest burned at higher severity which may be important for creating open flying space for foraging.

I hypothesized that edge was important for spotted owl foraging because it was found to affect life history traits (Tempel et al. *In press*, Franklin et al. 2000), so logistic regression models included a binary predictor variable indicating whether a location was edge or non-edge. To identify selection of high and low contrast edges, I also included edge type as a predictor variable in models. I did not include these two predictor variables in the same models because I wanted to independently distinguish between the importance to foraging habitat selection of edge versus non-edge and high versus low contrast edge.

I translated the above hypotheses into a final candidate model set in various combinations with the best models from abiotic predictor variable model sets. I related models to plausible biological responses between owls and their habitat and I combined all variables because I hypothesized that multiple factors may best explain owl habitat selection.

I created a 95 percent confidence set of models by including models whose weights summed to 0.95. I evaluated logistic regression coefficients from the top models by calculating 95 percent confidence intervals to determine strength of estimates. I used selection ratios, or odds ratios, to examine the change in the relative probability of selection for every one unit change in the covariate (Manly et al. 2002). To avoid using the logit scale, I calculated odds ratios by exponentiation of the beta coefficients. I did not model average the 95 percent confidence set to obtain estimates of coefficients because my purpose for modeling habitat selection was primarily to reveal influential variables, rather than to obtain a model to predict future owl habitat use (Elith and Leathwick 2009, Bean 2012).

Table 1. Abbreviations and definitions of predictor variables used in candidate models for California spotted owl foraging habitat selection.

Variable	Definition	Abbreviation
Distance to stream	Distance (m) from center of buffered owl location for used and available points to nearest stream.	DistStream
Distance to roost	Distance (m) from center of buffered owl location for used and available points to roost.	DistRoost
Elevation	Elevation (m) at center of buffered owl location for used and available points.	Elev
Slope	Slope (degrees) at center of buffered owl location for used and available points.	Slope
Aspect	Cardinal direction for aspect at center of buffered owl location for used and available points i.e. N, NE, E, SE, S, SW, W, NW.	Aspect
Fire severity index	Index value for fire severity proportions within buffered owl location for used and available points; Values range from 2 (low) to 5 (high).	FSI
Edge	Two values of edge: edge and no edge. Edge sites contained patches of multiple fire severity types and no edge sites contained 100% of the same fire severity type.	Edge
Edge type	Three 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.	EdgeType: HCEdge; LCEdge; NoEdge

Model Evaluation

Although AIC ranks the candidate models, I used model evaluation (or validation) to determine the quality of models in a candidate set (Barry and Elith 2006). Because use-availability studies lack mutually exclusive categories, i.e. used resource units drawn from available units, Receiver Operating Characteristic (ROC) and Area Under Curve (AUC) techniques may not be the most appropriate evaluation method (Wiens et al. 2008). Therefore, I evaluated models following procedures outlined in Boyce et al. (2002) and Johnson et al. (2006). Using the top model from the final candidate set, I calculated the predicted probabilities for each used and available observation and then divided the dataset into 20 equally sized bins. For each bin, I calculated the mean predicted probability and the proportion of used observations within each bin. I calculated Pearson's correlation coefficients to determine if there was a linear relationship between the mean predicted probability and the proportion of used observations in a bin. A good model should have a correlation close to one while a poor model should have a correlation close to zero. I used linear regression to determine if the slope of the regression line was significantly different from zero or one, if the intercept was close to zero, and calculated the R^2 value (Johnson et al. 2006).

Furthermore, I also calculated the deviance R^2, which compares model deviance to null deviance. A perfect model has a deviance R^2 equal to one, while a poor model has deviance R^2 equal to zero. However, Hosmer et al. (2013) recommend caution in interpreting deviance R^2 values for logistic regression, as low R^2 values are common in logistic regression models.

RESULTS

Field Methods

Across 90 field days over the three years, I captured 13 owls (8 females and 5 males) from eight unique territories within Yosemite. I collected 480 owl foraging locations (used points) over approximately 300 field days and generated 1431 random (available) points for a total of 1431+480 observations for the logistic regression analysis.

Home Range Analysis

Average male and female home range size was 302 ha and 451 ha, respectively, and ranged from 65 ha to 2900 ha (Figure 4). Overall mean home range size for males and females combined was 391 ha. There was no statistically significant difference in home range size between males and females (F = 0.469, df = 1 and 13, P = 0.50). Although one female home range was 2900 ha, log transformation removed the influence of this outlier. Mean home range size also did not differ between years using MCP estimates (F = 0.167, df = 1 and 13, P = 0.690).

I examined fire severity patterns within owl home ranges and, collectively, fires within the vicinity of owl home ranges burned nearly 75 percent of most owl home ranges; however, two owl home ranges contained less than 5 percent burned area within their home range. Overall, average area that was unburned or unchanged in all owl home ranges was 53 percent, while 25 percent, 16 percent, and 4 percent were burned at low, moderate, and high severities, respectively. High severity patches used multiple times by owls ranged in size from 0.1 ha to 36.0 ha ($\bar{x}$ = 6.5 ±10.5).

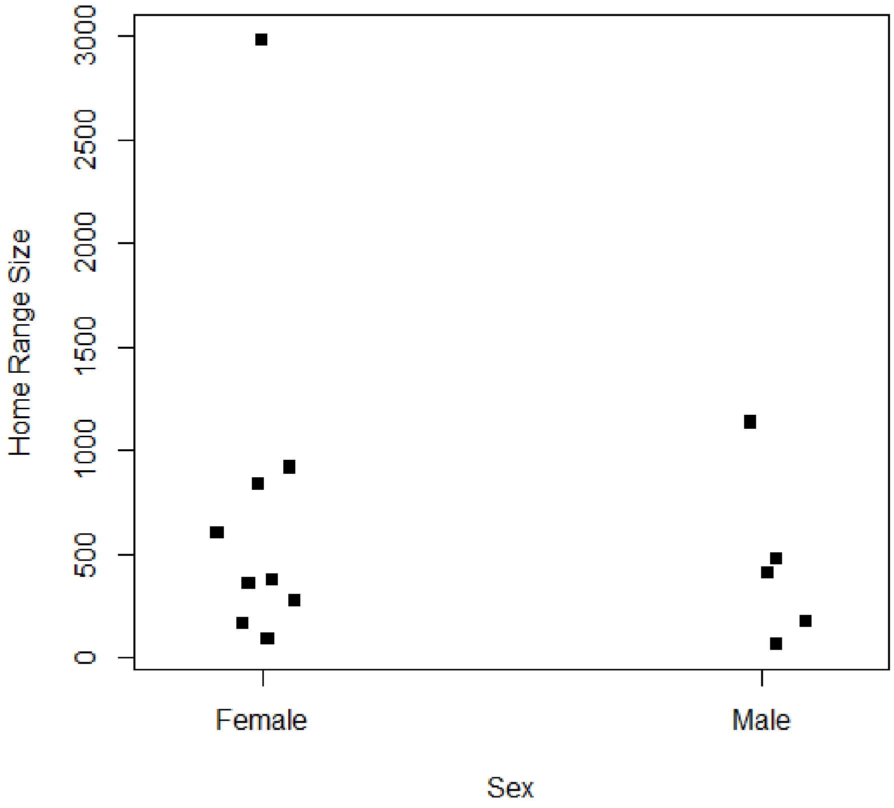

Figure 4. Range of home range sizes for male and female California spotted owls in Yosemite National Park.

Habitat Selection Analysis

Analysis of topographic variables indicated that slope and elevation were the most important factors to consider in the final candidate model set (Table 2). The addition of the slope^2 term did not increase the log-likelihood from the model with only slope, thus I considered it a pretending variable (Anderson 2008) and did not include in subsequent analysis. However, I placed more emphasis on including slope in models with other predictor variables since it was strongly significant and confidence intervals did not overlap zero. Models including aspect had poor support so I removed it from subsequent analyses.

I determined that the quadratic form of distance to roost was the most important factor to include in the final candidate model set after examining distance to stream and roost variables (Table 3). The quadratic form of distance to roost had the lowest AIC_c value and no other models were within two ΔAIC_c of the top model indicating a non-linear effect for distance to roost (see below). Furthermore, all other models had less support than the null model. Therefore, I incorporated only this non-linear effect in the final candidate set of models.

After selecting the best models from the abiotic variable candidate model sets, the models with the strongest support included: distance to roost, distance to roost^2, fire severity index, edge type (high contrast, low contrast and no edge), slope, elevation, and edge (edge and no edge). Average distance to roost was 1310 (±1518) m. Average fire severity index was 2.79 (±0.82). Average values for slope and elevation were 12.1 (±5.9) degrees and 1692 (±161) m, respectively. Four models were within two ΔAIC_c units from the top model and contained 57 percent of model weight; therefore I restricted model interpretations to those four models (Table 4). All models within the 95 percent model set had substantially higher support than the null model which had less than 1 percent of model weight.

The top model ($\Delta AIC_c = 0$, $w_i = 0.20$) contained edge type, distance to roost, distance to roost^2, and FSI. The best model resource selection function was estimated as:

$$\mathrm{w(x) = exp(0.178 - 0.189(LCEdge) - 0.502(NoEdge)}$$

$$\mathrm{-0.000299(DistRoost) + 0.0000000662(DistRoost^2) - 0.256(FSI)}$$

In addition, 95 percent confidence intervals for odds parameter estimates did not overlap one for fire severity index, and the no edge category of edge type (Table 6). The odds of non-use increased by 1.29 for each one unit increase in FSI (odds ratio = 0.774, 95 percent CI = 0.614-0.934). Relative probability of use was highest for high contrast edge, followed by low contrast edge, and then non-edge sites (Figure 5). The odds of owl use in the high contrast edge type was 1.20 times greater than in the low contrast edge type and almost twice that in the no edge type. However, confidence intervals for all three categories of edge type overlapped each other. Relative probability of use was also influenced by distance to roost since it was an important predictor in top models and confidence intervals did not overlap zero (Table 4 and 5). Furthermore, the non-linear form of distance to roost performed better than the linear form (Table 3). The odds of use were highest closer to the roost and were lowest at ca. 2250 m away from the roost

(Figure 6). Therefore, the importance of proximity to roost increased with decreasing distance to the roost and the odds of use were not equal for all values of distance to roost.

The second best model ($\Delta AIC_c = 0.68$, $w_i = 0.14$) contained distance to roost, distance to roost^2, fire severity index, edge type, slope, and elevation. The odds of non-use increased by 1.27 for each one unit increase in FSI (odds ratio = 0.787, 95 percent CI = 0.620- 0.955). Similar to the top model, the odds of use were greatest in the high contrast edge type and almost twice that in the low contrast edge type (Table 6). However, confidence intervals overlapped zero for all edge categories except the no edge category (Table 5). Owls selected areas with less steep slopes, however confidence intervals slightly overlapped zero (Table 5). The odds of use increased by 1.014 for every one degree decrease in slope (Table 6). Owls appeared to select areas at higher elevations, however the effect was weak since the estimate was close to zero and confidence intervals overlapped zero (Table 5).

The third best model ($\Delta AIC_c = 0.95$, $w_i = 0.13$) contained distance to roost, distance to roost^2, and slope. The odds of use decreased with increasing distance to roost and areas with steeper slopes (Table 6). However, confidence intervals for the slope parameter slightly overlapped zero (Table 5).

The fourth best model ($\Delta AIC_c = 1.59$, $w_i = 0.09$) contained distance to roost, distance to roost^2, FSI, and edge. Owls were more likely to use edge sites than non-edge sites and the odds of owl use of edges was almost twice that in the no edge type (Figure 7). Although confidence intervals for odds ratios on the edge parameters did not overlap one, confidence intervals for logit parameters slightly overlapped zero (Table 5 and 6).

The odds of non-use increased by 1.14 for each one unit increase in FSI (odds ratio = 0.87, 95 percent CI = 0.74-0.93). Distance to roost was also important in predicting owl habitat use and probability of use increased with proximity to roost, similar to other models.

Model Evaluation

For the top model, the linear regression testing the nature of the relationship between the mean predicted probabilities to the proportion of used observations in each bin yielded a Pearson correlation coefficient of 0.623. The slope of the regression line was significantly different from zero ($F = 11.436$, df = 1 and 18, $P = 0.003$) and contained one within the 95 percent confidence interval (95 percent CI = 0.331-1.415). The intercept value was close to zero ($\beta_0 = 0.032$), and the R^2 value for the linear regression was 0.388. The deviance R^2 for the top model was 0.016.

Table 2. AIC$_c$ results examining topographical characteristics that influence California spotted owl habitat use in Yosemite National Park, CA.

Model	K[a]	Log$_e$ ($\mathcal{L}$)[b]	AIC$_c$[c]	ΔAIC$_c$[d]	W$_i$[e]
Slope	2	-1075.11	2154.23	0.00	0.28
Elev+Slope	3	-1074.13	2154.27	0.04	0.28
Slope+Slope^2	3	-1075.04	2156.10	1.87	0.11
Null	1	-1077.09	2156.18	1.95	0.11
Elev+Slope+Slope^2	4	-1074.10	2156.23	2.00	0.10
Elev	2	-1076.11	2156.23	2.00	0.10
Slope+Aspect	9	-1072.25	2162.60	8.37	0.00
Elev+Slope+Aspect	10	-1071.29	2162.70	8.47	0.00
Aspect	8	-1074.15	2164.38	10.15	0.00
Slope+Slope^2+Aspect	10	-1072.14	2164.40	10.18	0.00
Elev+Aspect	9	-1073.17	2164.44	10.21	0.00
Elev+Slope+Slope^2+Aspect	11	-1071.24	2164.62	10.39	0.00

Models in bold selected for use in subsequent analyses.

[a] Number of parameters

[b] Log$_e$ (likelihood)

[c] Akaike's Information Criterion corrected for small sample size.

[d] Difference between model AIC$_c$ and top model AIC$_c$

[e] AIC$_c$ weight

Table 3. AIC$_c$ results examining linear and quadratic forms of distance to stream and distance to roost abiotic variables for California spotted owl habitat use in Yosemite National Park, CA.

Model[a]	K[b]	Log$_e$ ($\mathcal{L}$)[c]	AIC$_c$[d]	ΔAIC$_c$[e]	W$_i$[f]
Roost+Roost^2	3	-1071.26	2148.54	0	0.93
Null	1	-1077.09	2156.18	7.64	0.02
Stream+Stream^2	3	-1075.13	2156.28	7.74	0.02
Stream	2	-1076.16	2156.32	7.78	0.02
Roost	2	-1076.73	2157.47	8.93	0.01

Models in bold selected for use in subsequent analyses.

[a] Roost = Distance to Roost, Stream = Distance to Stream

[b] Number of parameters

[c] Log$_e$ (likelihood)

[d] Akaike's Information Criterion corrected for small sample size.

[e] Difference between model AIC$_c$ and top model AIC$_c$

[f] AIC$_c$ weight

Table 4. Models within the 95% confidence set that best explained California spotted owl habitat use in Yosemite National Park.

Model[a]	K[b]	$\text{Log}_e (\mathcal{L})$[c]	AIC_c[d]	ΔAIC_c[e]	W_i[f]
DistRoost+DistRoost^2+FSI+EdgeType	6	-1066.97	2145.99	0.00	0.20
Slope+Elev+DistRoost+DistRoost^2+FSI+EdgeType	8	-1065.30	2146.67	0.68	0.14
Slope+DistRoost+DistRoost^2	4	-1069.46	2146.93	0.95	0.13
DistRoost+DistRoost^2+FSI+Edge	5	-1068.77	2147.58	1.59	0.09
Slope+Elev+DistRoost+DistRoost^2	5	-1069.13	2148.30	2.31	0.06
DistRoost+DistRoost^2	3	-1071.26	2148.54	2.55	0.06
Slope+Elev+DistRoost+DistRoost^2+Edge	6	-1068.28	2148.60	2.61	0.05
DistRoost+DistRoost^2+Edge	4	-1070.29	2148.60	2.61	0.05
Slope+Elev+DistRoost+DistRoost^2+FSI+Edge	7	-1067.44	2148.94	2.95	0.05
Slope+Elev+DistRoost+DistRoost^2+EdgeType	7	-1067.94	2149.93	3.95	0.03
Elev+DistRoost+DistRoost^2	4	-1070.98	2149.98	3.99	0.03
DistRoost+DistRoost^2+FSI	4	-1071.05	2150.12	4.13	0.03
Slope+Elev+DistRoost+DistRoost^2+FSI	6	-1069.08	2150.20	4.21	0.02

Models in bold within $2\Delta\text{AIC}_c$ from top model.

[a] DistRoost = distance to roost, DistRoost^2 = quadratic term for distance to roost, DistStream = distance to stream, FSI = fire severity index, Elev = elevation

[b] Number of parameters

[c] Log_e (likelihood)

[d] Akaike's Information Criterion corrected for small sample size.

[e] Difference between model AIC_c and top model AIC_c

[f] AIC_c weight

Table 5. Coefficients, standard errors and 95% confidence intervals from top four logistic regression models of California spotted owl habitat use patterns in Yosemite National Park, CA.

	DistRoost+DistRoost^2+FSI+EdgeType				Slope+Elev+DistRoost+DistRoost^2+FSI+EdgeType			
Covariate^a	Coefficient	SE	95% LCI	95% UCI	Coefficient	SE	95% LCI	95% UCI
HCEdge	0.178	0.436	-0.694	1.050	-0.296	0.714	-1.725	1.132
LCEdge	-0.189	0.300	-0.788	0.411	-0.704	0.674	-2.053	0.644
NoEdge	-0.502	0.246	**-0.993**	**-0.011**	-0.972	0.638	-2.248	0.304
Edge	--	--	--	--	--	--	--	--
Roost	-2.990x10^{-4}	1.150x10^{-4}	**-5.290x10^{-4}**	**-6.905x10^{-5}**	-2.696x10^{-4}	1.183x10^{-4}	**-5.062x10^{-4}**	**-3.298x10^{-5}**
Roost^2	6.621x10^{-8}	2.014x10^{-8}	**2.593x10^{-8}**	**1.065x10^{-7}**	6.150x10^{-8}	2.062x10^{-8}	**2.026x10^{-8}**	**1.027x10^{-7}**
FSI	-0.256	0.103	**-0.463**	**-0.049**	-0.239	0.106	**-0.452**	**-0.026**
Slope	--	--	--	--	-0.014	0.009	-0.033	0.004
Elevation	--	--	--	--	3.57x10^{-4}	3.62x10^{-4}	-3.68x10^{-4}	1.08x10^{-3}
Intercept	--	--	--	--	--	--	--	--
	Slope+DistRoost+DistRoost^2				DistRoost+DistRoost^2+FSI+Edge			
Covariate^a	Coefficient	SE	95% LCI	95% UCI	Coefficient	SE	95% LCI	95% UCI
HCEdge	--	--	--	--	--	--	--	--
LCEdge	--	--	--	--	--	--	--	--
NoEdge	--	--	--	--	-0.771	0.197	**-1.165**	**-0.378**
Edge	--	--	--	--	-0.481	0.250	-0.981	0.019
Roost	-3.054x10^{-4}	1.130x10^{-4}	**-5.314x10^{-4}**	**-7.944x10^{-5}**	-2.785x10^{-4}	1.145x10^{-4}	-5.075x10^{-4}	-4.951x10^{-5}
Roost^2	6.426x10^{-8}	1.984x10^{-8}	**2.458x10^{-8}**	**1.039x10^{-7}**	6.150x10^{-8}	1.997x10^{-8}	2.156x10^{-8}	1.014x10^{-7}
FSI	--	--	--	--	-0.134	0.078	-0.290	0.022
Slope	-0.017	0.009	-0.035	0.001	--	--	--	--
Elevation	--	--	--	--	--	--	--	--
Intercept	-0.723	0.142	**-1.007**	**-0.440**	--	--	--	--

Bold values indicate 95% CI that did not overlap 0.

[a] HCEdge = high contrast edge, LCEdge = low contrast edge.

Table 6. Odds, standard errors and 95% confidence intervals from top four logistic regression models of California spotted owl habitat use patterns in Yosemite National Park, CA.

	DistRoost+DistRoost^2+FSI+EdgeType				Slope+Elev+DistRoost+DistRoost^2+FSI+EdgeType			
Covariate[a]	Odds	SE	95% LCI	95% UCI	Odds	SE	95% LCI	95% UCI
HCEdge	1.195	0.521	0.153	2.237	0.744	0.531	-0.319	1.806
LCEdge	0.828	0.248	0.331	1.325	0.494	0.333	-0.173	1.161
NoEdge	0.605	0.149	**0.308**	**0.903**	0.378	0.241	**-0.104**	**0.861**
Edge	--	--	--	--	--	--	--	--
Roost	9.997 x10^{-1}	1.150 x10^{-4}	9.995 x10^{-1}	9.999 x10^{-1}	9.997 x10^{-1}	1.183 x10^{-4}	9.995 x10^{-1}	1.000
Roost^2	1.000	2.014 x10^{-8}	1.000	1.000	1.000	2.062 x10^{-8}	1.000	1.000
FSI	0.774	0.080	**0.614**	**0.934**	0.787	0.084	**0.620**	**0.955**
Slope	--	--	--	--	0.986	0.009	0.967	1.004
Elevation	--	--	--	--	1.000	3.63x10^{-4}	0.999	1.001
Intercept	--	--	--	--	--	--	--	--

	Slope+DistRoost+DistRoost^2				DistRoost+DistRoost^2+FSI+Edge			
Covariate[a]	Odds	SE	95% LCI	95% UCI	Odds	SE	95% LCI	95% UCI
HCEdge	--	--	--	--	--	--	--	--
LCEdge	--	--	--	--	--	--	--	--
NoEdge	--	--	--	--	0.462	0.091	**0.280**	**0.644**
Edge	--	--	--	--	0.618	0.154	**0.309**	**0.927**
Roost	9.997 x10^{-1}	1.130 x10^{-4}	1.130 x10^{-4}	9.995 x10^{-1}	9.997 x10^{-1}	1.145 x10^{-4}	9.995 x10^{-1}	1.000
Roost^2	1.000	1.984 x10^{-8}	1.000	1.000	1.000	1.997 x10^{-8}	1.000	1.000
FSI	--	--	--	--	0.874	0.068	0.738	1.011
Slope	0.983	0.009	0.966	1.001	--	--	--	--
Elevation	--	--	--	--	--	--	--	--
Intercept	0.485	0.069	**0.348**	**0.623**	--	--	--	--

Bold values indicated 95% CI that did not overlap 1.

[a] HCEdge = high contrast edge, LCEdge = low contrast edge.

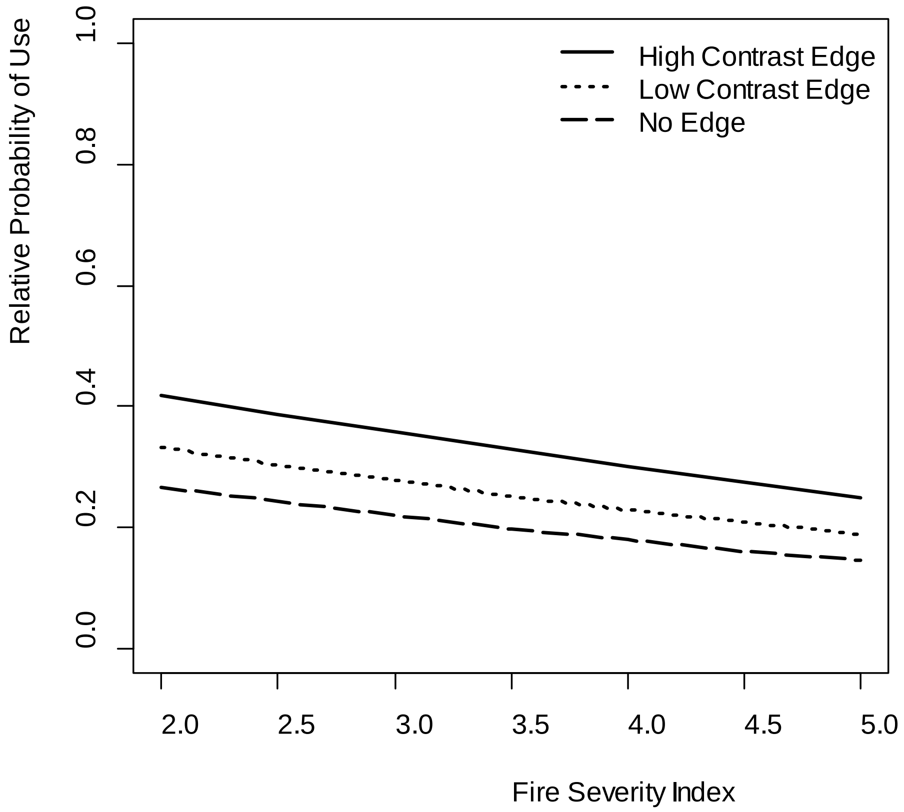

Figure 5. Modeled relative probability of California spotted owl habitat use as a function of fire severity index and edge type in Yosemite National Park, CA. Note: x-axis only displays possible fire severity index values.

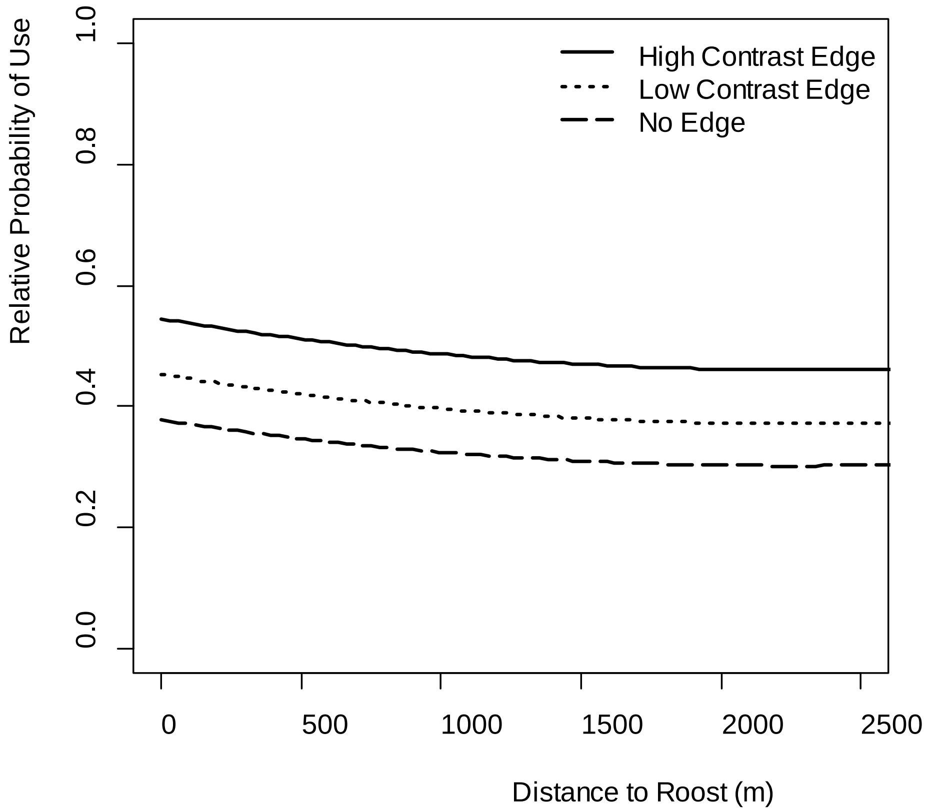

Figure 6. Modeled relative probability of California spotted owl habitat use as a function of distance to roost and edge type in Yosemite National Park, CA.

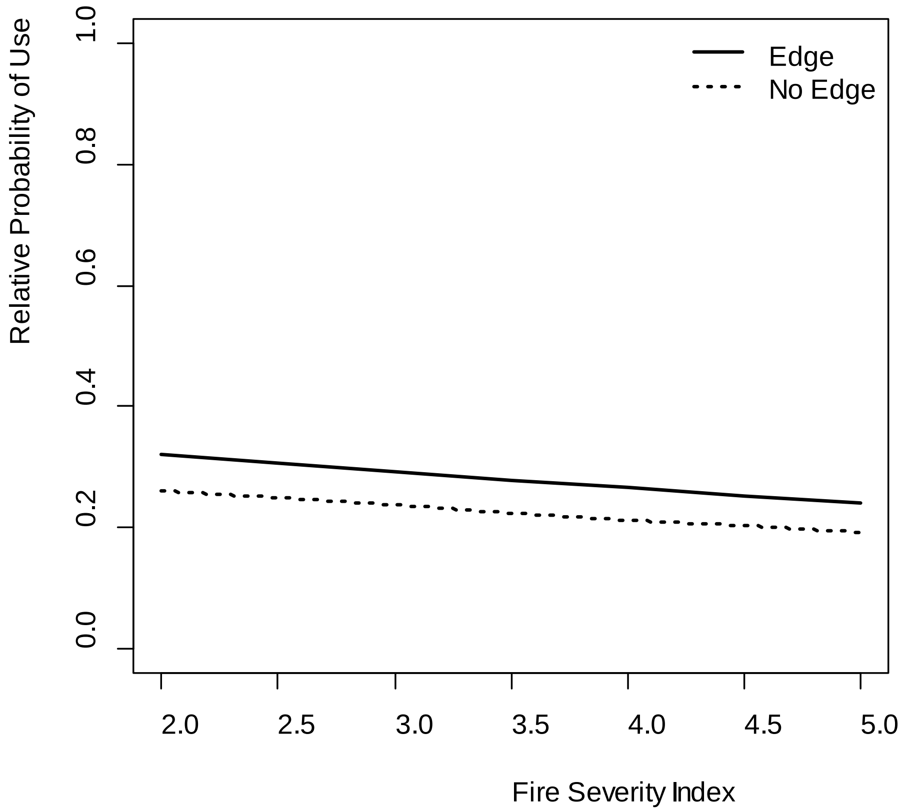

Figure 7. Modeled relative probability of California spotted owl habitat use as a function of edge in Yosemite National Park, CA. Note: x-axis only displays possible fire severity index values.

DISCUSSION

Overall, California spotted owls avoided high severity forest patches and used lower severity patches, consistent with my predictions and previous research on northern spotted owls (Clark 2007, Comfort 2013). Contradictory to this, Bond et al. (2009) suggested California spotted owls in the southern Sierra Nevada preferentially foraged in high severity forest patches. Further complicating deciphering owl habitat use, my results indicate owls selected high contrast edges (abrupt transitions in vegetation structure and composition compared with patches burned at other severities), contrary to my a priori predictions, but comparable to the findings of Comfort (2013). In addition, I found that owls foraged closer to their roosts and selected less steep slopes, similar to my predictions, but confidence intervals on the slope parameter slightly overlapped zero and indicated poor strength in the covariate effect. Although I predicted that spotted owls would forage near streams and more northerly aspects, I found no influence of these variables on their habitat use.

California spotted owls may be adapted to low and moderate severity fires that are characteristic of mixed-conifer zones of the Sierra Nevada (Skinner and Chang 1996, Collins et al. 2011, Thode et al. 2011). 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). In unburned forests, California spotted owls selected mature forest with an abundance of large trees, multiple canopy layers, and 40-70 percent overstory canopy closure (Williams et al. 2011). Forests burned at low and moderate severities in Yosemite typically retain all of these characteristics (Thode et al. 2011) and may explain the spotted owl foraging patterns I observed in my study. Further, the largest high severity patch (36 ha) owls used in my study was adjacent to a nest that failed early that season. This close proximity to a large high severity patch may have influenced owl use of that larger patch and the failure of the nest. Without any live trees in the high severity patch, there was a lack of cover over the nest and greater exposure to inclement weather and depredation by great horned owls inhabiting the adjacent high severity patch.

Many studies have demonstrated that fires of low to moderate severity retained habitat characteristics required by spotted owls and that owls continued to occupy and use these types of post-fire habitats (Clark 2007, Keane et al. 2010, Roberts et al. 2011). Further, other studies showed spotted owl occurrence (Comfort 2013) and colonization (Tempel et al. *In press*) both decreased with increasing fire severity. Spotted owls not only used high severity patches less often than low severity (Clark 2007), but Keane et al. (2010) also showed large high severity patches supported fewer owls than those same areas did pre-fire. In contrast, Lee et al. (2012) examined colonization probabilities and concluded that fires with up to 32 percent high severity fire had no effect on extinction or colonization probabilities for California spotted owls in burned forests of the Sierra Nevada. Likewise, California spotted owls in southern California with less than 50 ha of severely burned habitat within core areas had extinction probabilities similar to unburned sites, but extinction probability increased if severely burned habitat was greater than 50 ha (Lee et al. 2013). However, Lee et al. (2012 and 2013) could not randomly select owls and the confounding effects of salvage logging and fire suppression may have influenced their results; therefore, their results should not be extrapolated outside of their particular study area.

Franklin et al. (2000) proposed that older forests provide nesting sites and refuge from predators while young forests and edges provide more diverse foraging opportunities. Therefore, California spotted owls may be selecting forest sites that burned with low severity fire that have correspondingly greater canopy closure for avoiding predators. In my study, I found a radio-tagged owl dead with signs of raptor depredation (cut and plucked feathers) in a recently burned area with greater proportions of high severity fire than other owl home ranges (10 percent vs. average of 5 percent). Further, I observed more great horned owls in this area than any other spotted owl home range in my study area, perhaps because these very large raptors could fly more freely with more open forest from high severity burns. For further antidotal evidence to support this, I also found another radio-tagged owl dead with the same signs of raptor depredation near a high contrast edge, but inside a high severity patch. I did not include this owl in my analyses because we only had a few observations of it before it died. California spotted owls are large raptors (average adult weight is 610 g (Sibley 2000)) and are typically too heavy to be carried far in one piece by another raptor (adult great horned owl average weight is 1,400 g (Sibley 2000)). Therefore, I assumed the mortality locations of these two dead spotted owls were close to the actual location where they were killed; also documented for black kites (*Milvus migrans*) depredated by eagle owls (*Bubo bubo;* Sergio et al. 2003).

My results suggest that owls show a higher relative probability of selection for edge sites than non-edge sites (Table 5 and Figure 7). These results are supported by Williams et al. (2011) finding that owls foraged closer to edges in unburned forests with greater than 70 percent canopy closure. However, the literature is unclear regarding the effect of the amount of edge. For example, the amount of edge had no effect on site occupancy for California spotted owls (Chatfield 2005), but Tempel et al. (*In press*) concluded that the amount of edge positively influenced owl demographic rates. Collectively, recent research revealed that northern and California spotted owl survival and reproduction 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 2013) which may explain owl use of edges associated with fire. However, northern spotted owls in southwestern Oregon had larger home ranges and decreased survival due to fragmented habitat from edges (Schilling et al. 2013). The complexities of these results from many different studies suggests that more research addressing spotted owl habitat use of edges is necessary, especially in burned landscapes.

More importantly, it appeared that high contrast edges greatly influenced the importance of edge (Figure 5 and 7) and my results are similar to research on spotted owl use of edge types in other burned temperate conifer forests. Northern spotted owls foraged in edges and, at large spatial scales (12.9-207 ha), appeared to select diffuse or low contrast edges created by fire, while owls selected hard edges at smaller spatial scales (<0.8 ha) (Comfort 2013). Although I found relative probability of use greater for high contrast edges, similar to Comfort (2013), my confidence intervals slightly overlapped zero, suggesting lack of precision in the estimate. Perhaps given a larger sample size of owls and telemetry locations, I would have found more support for owl use of high contrast edges. Furthermore, Comfort (2013) used continuous metrics for describing edge types within burned landscapes, whereas I treated edges as categorical predictors; perhaps another possible explanation for less support for high contrast edge use in my study area. Although spotted owls foraged in high contrast edges, California spotted owls located their nests further from high contrast edges (Phillips et al. 2010), highlighting the differences between owl foraging and nesting habitat selection.

Combined, the importance of edge type and fire severity index suggest that California spotted owls in Yosemite may be avoiding large patches of high severity fire, similar to research on the northern spotted owl (Comfort 2013). Although high contrast edges had higher relative probability of use, owls also used areas with lower fire severity index (FSI) values (Figure 5). FSI incorporates the area of each fire severity patch within an owl foraging location, while edge type simply indicates whether the location contained high severity fire of any proportion. For example, an edge was classified as a high contrast edge if it contained 10 percent high severity fire or 80 percent high severity fire in combination with other fire severity types. Because I incorporated telemetry error in the analysis, I used the 92 m buffered owl location to define edge types and FSI, and have confidence in my findings that show consistent use of locations with multiple fire severity patches; indicating edge types are important to the owl. However, it does not indicate the owl actually used the interior of the high severity patch. Owls may have been using the lower severity patch neighboring the high severity patch (i.e., the lower severity side of the edge) which would be supported by my finding that owls used lower fire severity patches more often than areas with higher FSI. Therefore, perhaps small proportions of high severity fire nested within a larger matrix of low and moderate severity fire may be beneficial for owl foraging by creating high contrast edges. More importantly, owls may avoid large patches of high severity fire since I documented owls using areas with lower fire severity index values. Further, other research in Yosemite found that areas with the lowest FSI values had greater amounts of edge and that as FSI increases, moderate and high severity patch sizes increase, leading to a decrease in the amount of overall edge (Roberts et al. 2008).

Spatial complexity created by fire may affect owl foraging due to vegetation changes, but can also affect small mammal prey communities (Roberts et al. 2008). Spotted owl foraging patterns can be influenced by prey abundance, diversity, and biomass (Carey et al. 1992, Carey and Peeler 1995, Zabel et al. 1995). Research on the northern spotted owl found that owls select habitat based on prey availability and that owls forage in forest edges where prey availability is high (Zabel et al. 1995, Ward Jr. et al. 1998). Sakai and Noon (1997) observed northern spotted owls foraging at edges where they detected woodrats. Although these observations occurred in unburned forests, prey availability may also be higher in edges created by fire that burned forests at variable severities.

Fire severity patterns change vegetation structure and increase habitat complexity which influence small mammal distributions and abundances across the landscape (Converse et al. 2006, Roberts et al. 2008). A landscape mosaic of variable burn severities, including unburned patches, can ensure that individual owls have access to different seral stages, thereby potentially increasing their access to different prey species within their own territories. Studies have shown that individual owls consumed both flying squirrels and woodrats in burned and unburned forests of the Sierra Nevada (Keane et al. 2010, Bond et al. 2013) indicating that owls have access to many different habitat types. Research suggests that flying squirrels are found in areas with greater canopy cover and litter depths ≥ 3 cm (Meyer et al. 2007*a*); conditions more common in unburned and low severity burned forest. Innes et al. (2007) found dusky-footed woodrats in areas with high California black oak density and large logs and stumps, factors that are also influenced by fire and more specifically promoted by higher severity fire (Cocking et al. 2014). Collectively, fire variably affects owl prey habitat and different fire severity patterns create a matrix of different habitat types that may promote owl prey diversity, abundance, and stability (Roberts et al. *In review*). Therefore, fire may also influence spotted owl foraging habitat selection by altering prey availability and perhaps contributed to the habitat use patterns I observed in my study.

On the contrary, Bond et al. (2009) concluded that California spotted owls in Sequoia National Forest selected high severity patches for foraging, perhaps due to higher density of snags and increased shrub cover that provides refuge for owl prey. However, they only examined habitat use for a single breeding season in only four owl territories, while I examined habitat use in eight owl territories over a period of three breeding seasons. For Bond et al. (2009), all study owl territories experienced fire severity effects from a single fire that had fire severity patterns that were not representative of the natural range of variation for that habitat type (Meyer *In review*). My study encompassed a much larger area with over a dozen fires burning throughout owl home ranges with all of them burning within the natural range of variation. Furthermore, Bond et al. (2009) examined habitat use four years post-fire, while fires in my study area ranged from 2-15 years post-fire. Overall, fire severity proportions also differed between the two study areas since, on average, only 5 percent of owl home ranges in Yosemite contained high severity fire, while foraging ranges in their study area contained 13 percent burned at high severity. The unburned forest matrix differs between their study area, Sequoia National Forest, and mine, Yosemite, as well. The National Forest has a history of timber harvest and much more aggressive fire suppression programs; whereas Yosemite, a National Park, experienced only minimal harvesting from the 1900s-1930's and, since 1970, implemented prescribed fires and allowed some wildfire to burn unsuppressed (van Wagtendonk 2007, Lutz et al. 2009). Collectively, these differences may contribute to our contradictory results.

In addition to fire severity and edge metrics, distance to roost was also important for explaining owl habitat selection. Many studies found distance to roost or nest important in foraging habitat selection for spotted owls (Glenn et al. 2004, Irwin et al. 2007, 2012, Wiens 2012) and two in particular also documented a non-linear trend in selection (Glenn et al. 2004, Wiens 2012). Only two spotted owls in my study had successful nests so I used distance to roost because most roosts were within 500 meters of nest sites (personal observation). Forsman et al. (1984) documented male northern spotted owls consistently roosting within 200 meters of nest sites. Therefore, although other studies found distance to nest important, distance to roost may exert a similar level of influence on foraging and may explain why distance to roost was an important variable in top models. However, two radio-tagged owls had active nests and those individual owls could be contributing to the importance of distance to roost; but, I only attached a transmitter to one nesting female and most of her locations were collected after the chicks fledged.

Spotted owls have high site fidelity to nest and roost sites and in breeding seasons tend to roost near the eventual nest site (Forsman et al. 1984). Furthermore, spotted owls are central-place foragers and often remain near the nest site in non-breeding seasons, so nest and roost location may play a significant role in owl foraging habitat selection (Forsman et al. 1984, Carey and Peeler 1995). Rosenberg and McKelvey (1999) argue that not including distance to nest or roost in habitat selection models may bias selection for habitat characteristics near the central place. Therefore, in my study, edge sites and fire severity patterns may have been important to owl foraging based on the initial selection of a roost site, since owls are central-place foragers. However, owls also select their nest sites based on certain surrounding characteristics so perhaps investigating fire severity and edge patterns near nest and roost sites can provide further insight.

Although other studies found distance to stream and aspect important in explaining owl habitat selection (Clark 2007, Irwin et al. 2007, 2012, Underwood et al. 2010, Loehle et al. 2011), I failed to detect the same pattern. I expected distance to stream to be an influence due to increased prey near water (Doyle 1990, McComb et al. 1993, Meyer et al. 2007*a*) and cooler microclimates (Van de Water and North 2010). However, owl home ranges in my study area consistently contained several streams and while at the landscape scale distance to water may be important, owls appeared to eliminate this as a factor by consistently delineating their home ranges around streams (Figure 8). I also was unable to differentiate between seasonal and permanent streams. I expected aspect to be important given that south- and west- facing slopes tend to have greater fire intensity and decreased stem density and canopy closure (Underwood et al. 2010). It is likely I failed to detect a difference because I classified eight categories for aspect, however, *post-hoc* I reclassified aspect into four categories and still detected no effect on habitat selection. Perhaps treating aspect as a continuous variable with the appropriate transformation may have altered the importance of this predictor variable.

Although I discovered that fire severity patterns, edge metrics, and distance to roost explained California spotted owl foraging habitat selection, I recommend that top models be interpreted with caution since models had low values for deviance R^2 (i.e. close to zero). Other model evaluation methods indicated that the model was reasonable at predicting used observations since the correlation coefficient was relatively close to one and the linear regression had modest R^2 values, a slope significantly different from zero, and an intercept close to zero (Johnson et al. 2006). The main reason I exert using caution with my model results is that perhaps other factors I did not measure, such as vegetation characteristics or prey availability, may be important in explaining spotted owl foraging habitat selection. Future studies investigating microscale habitat characteristics associated with foraging locations or prey abundance and movement can help shed more light on owl habitat use patterns.

Protecting the remnant mixed-conifer forests in the Sierra Nevada from stand-replacing fires via mechanical thinning or prescribed fire is a priority for management agencies. Researchers conclude that active management, such as prescribed fire and silvicultural treatments, that promote a matrix of age classes can reduce fire threat and decrease owl habitat loss to stand-replacing fire (Irwin et al. 2004, Calkin et al. 2005, Ager et al. 2007, Roloff et al. 2012, Comfort 2013). For example, the Rim Fire, one of the largest fires in California history, burned five of my study sites and two 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 to sensitive wildlife, such as California spotted owls. Maintaining closed canopy forest within owl home ranges with variable-sized patches of low, moderate, and smaller patches (< 36 ha) of high severity fire may be beneficial for owls since my study found that fire severity index and edge type were important in explaining owl habitat selection. My results suggest that sustaining forests burned with a mosaic of lower fire severities burned in different years interspersed with large unburned patches may help sustain California spotted owls in Yosemite National Park.

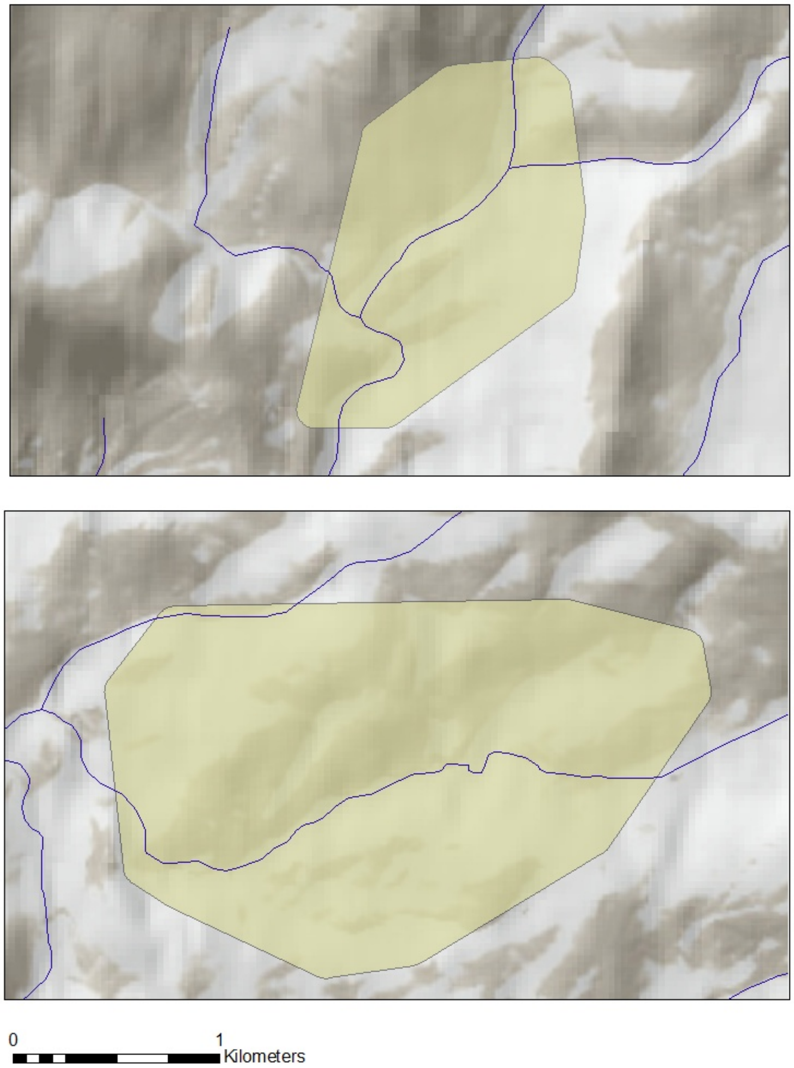

Figure 8. Example of two California spotted owl home ranges showing distribution of streams within home ranges in Yosemite National Park.

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