



Effects of fire on spotted owl site occupancy in a late-successional forest

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ABSTRACT

The spotted owl (*Strix occidentalis*) is a late-successional forest dependent species that is sensitive to forest management practices throughout its range. An increase in the frequency and spatial extent of stand-replacing fires in western North America has prompted concern for the persistence of spotted owls and other sensitive late-successional forest associated species. However, there is sparse information on the effects of fire on spotted owls to guide conservation policies. In 2004–2005, we surveyed for California spotted owls during the breeding season at 32 random sites (16 burned, 16 unburned) throughout late-successional montane forest in Yosemite National Park, California. Our burned areas burned at all severities, but predominately involved low to moderate fire severity. Based on an information theoretic approach, spotted owl detection and occupancy rates were similar between burned and unburned sites. Nest and roost site occupancy was best explained by a model that combined total tree basal area (positive effect) with cover by coarse woody debris (negative effect). The density estimates of California spotted owl pairs were similar in burned and unburned forests, and the overall mean density estimate for Yosemite was higher than previously reported for montane forests. Our results indicate that low to moderate severity fires, historically common within montane forests of the Sierra Nevada, California, maintain habitat characteristics essential for spotted owl site occupancy. These results suggest that managed fires that emulate the historic fire regime of these forests may maintain spotted owl habitat and protect this species from the effects of future catastrophic fires.

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1. Introduction

Fire is an essential and dynamic process in many terrestrial systems throughout the world (Dickman and Rollinger, 1998). Whether on a 5-year or 200-year return interval, fire structures and maintains ecosystems (Wright and Bailey, 1982; Minnick et al., 2000). In western North America, fire regimes are so strongly correlated with the habitats they shape that it is difficult to ascertain whether fire regimes drive patterns in vegetation or vice versa (Agee, 1993; van Wagtenonk and Fites-Kaufman, 2006). The severity of fire can be quantified as a function of changes in vegetation after an area burned (van Wagtenonk, 2006). Attempts to exclude fire from these systems through a century of suppression have not been completely successful because continuing fuel accumulation (Kilgore, 1973; Vankat and Major, 1978; Agee et al., 2000) has led to more extensive high-severity fires (Skinner and Chang, 1996). While it is clear that unchecked wildfires in these forests are not an acceptable management option (Weatherspoon

et al., 1992), van Wagtenonk (1996) suggested the best tool for restoring and protecting these forests is carefully planned prescribed fire.

One species that is dependent on old-growth and late-successional forests is the spotted owl (*Strix occidentalis*) (Forsman et al., 1984; Gutiérrez and Carey, 1985; Gutiérrez et al., 1992; Verner et al., 1992a). Spotted owls are strongly associated with old forests, but are threatened by habitat loss and fragmentation (Bart and Forsman, 1992; Noon and Blakesley, 2006), the recent expansion of barred owls (*Strix varia*) into the range of spotted owls (Olson et al., 2005), and climate change (Glenn et al., 2010; Carroll, 2010). The old, and often dense, forests favored by spotted owls are economically desirable (Thomas et al., 1990; Verner et al., 1992a), but are at risk to stand-replacing fires due to heavy fuel loading (Agee et al., 2000). A century of fire exclusion and various management activities has transformed much of this forest into even-aged, early-successional forests that often contain large amounts of understory fuels (Husari et al., 2006; Stevens and Sugihara, 2006). This accumulated dead and down woody debris acts not only as fuel to carry the fire horizontally through the forest, but also vertically into the upper canopy (Weatherspoon and Skinner, 1995; Tappeiner and McDonald, 1996). Such high fuel loading and spatially continuous ladder fuels place adjacent

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old-growth forests at greater risk of catastrophic fire (Weatherspoon et al., 1992; Agee, 1993; Wright and Agee, 2004). The combination of logging and large-scale conversion of forests to human communities has resulted in dramatic declines in the extent and continuity of old-growth forests throughout western North America, causing concern for the persistence of spotted owls (Thomas et al., 1990; McKelvey and Weatherspoon, 1992). In the fire-adapted forests of the Sierra Nevada where California spotted owls (*S. o. occidentalis*) live and reproduce, habitat loss from wild-fire also is a concern as the risk of catastrophic fire steadily increases in the absence of periodic low to moderate severity fire (Miller et al., 2009). Skinner and Chang (1996) estimated that prior to Euro-American settlement, montane forests in the Sierra Nevada experienced low to moderate severity fires every 2–20 years.

In montane forests of the Sierra Nevada, California spotted owls typically nest and roost in stands with high canopy cover ($\geq 75\%$) and forage in stands with moderate ($\geq 40\%$) to high canopy cover (Call et al., 1992; Zabel et al., 1992). These owls use stands for nesting and roosting that have multilayered canopies and an abundance of large trees (>60 cm diameter at breast height [dbh]) (Bias and Gutiérrez, 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997). We wanted to determine if the low to moderate severity fires that reduce fuels would sustain functional spotted owl habitat by maintaining specific forest characteristics necessary for nesting and roosting. To do this, we investigated site occupancy patterns by California spotted owls within burned and unburned montane forests in Yosemite National Park. We had three primary objectives. First, we wanted to determine whether burned and unburned forests contained sufficient nesting and roosting habitat elements (e.g., canopy closure, basal tree area) for spotted owl site occupancy. We predicted that spotted owl occupancy would be positively influenced by canopy closure and tree basal area, and that these characteristics would be maintained in forests burned at low to moderate severity. Yosemite has a large area of relatively contiguous, mixed-conifer forest, leading us to predict that the density of spotted owl pairs would be higher in the park than in other mixed-conifer forest in the Sierra Nevada. Our second objective was to develop a model that land managers could use to accurately predict spotted owl site occupancy in a particular forest stand based on fire history and vegetation characteristics. Our final objective was to estimate spotted owl density within Yosemite. This was to provide baseline information in late-successional forests experiencing a frequent fire regime and not confounded by the effects of past forest management practices. To date, population estimation for this subspecies has been almost exclusively limited to National Forests in California that have experienced decades of fire exclusion and intensive timber harvest.

2. Methods

2.1. Study area

Located in the central Sierra Nevada, Yosemite National Park encompasses 3027 km², of which approximately 1580 km² was relatively contiguous montane forest (van Wagtenonk and Lutz, 2007) and potential habitat for spotted owls. This habitat occurred between 1000 m and 2500 m elevation on the western slope of the range and supports a diverse fauna (Graber, 1996). White fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), California black oak (*Quercus kelloggii*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*P. lambertiana*) dominated the lower montane forests. Red fir (*Abies magnifica*), white fir, sugar pine, and Jeffrey pine (*Pinus jeffreyi*) dominated the upper montane forests. The most prevalent forest type in our study area consisted of white fir with a mix of

Jeffrey pine (at higher sites) or ponderosa pine (at lower sites). More than half of the precipitation occurred from January through March, primarily as snow (van Wagtenonk and Fites-Kaufman, 2006). Between 1989 and 2004, 466 km² of the 1580 km² montane forest burned at least once.

At the time of this research, managers recognized three types of wildland fires, prescribed, wilderness, and wildfire. Managers purposefully set prescribed fires in order to meet defined objectives. In 1970, Yosemite National Park developed a prescribed burning program to reduce fuels and lower the risk of stand-replacing fires while conserving the selection pressures that fire historically imposed on these ecosystems (van Wagtenonk et al., 2002). Wilderness fires were naturally occurring lightning fires and since 1972, the park's wildland fire use program managed them under prescribed conditions. Since 1972, as long as these conditions were met, wilderness fires were typically not suppressed in Yosemite. Yosemite's Fire Management Program suppressed all wildfires, including human caused fires and wildland fires that did not meet management objectives. Researchers dated, mapped, and digitized for use with geographic information system (GIS) software all fires that occurred within Yosemite since 1930 (van Wagtenonk et al., 2002). Yosemite Park personnel also developed a digital vegetation map consisting of polygons of dominant overstory and understory vegetation types with cover classes assigned to each vegetation type polygon (National Park Service, 1997). Although our study area experienced all three types of fire, we did not have a large enough sample size to perform separate analyses on each type. Therefore, a "burned" forest in our study could have experienced any of the three fire types.

2.2. Data collection

2.2.1. Plot selection

Spotted owls in the Sierra Nevada rarely use forests with $<40\%$ canopy cover (Call et al., 1992; Gutiérrez et al., 1992; Zabel et al., 1992); therefore, we used 40% canopy cover as our cutoff criterion for mapping potential owl habitat. We used ArcMap 9.1 (ESRI, Redlands, California) and the digital vegetation map to delineate montane forest stands with $>40\%$ canopy cover within the park. We overlaid the digital fire history map onto the vegetation map to delineate all fires in the montane forest zone that burned since 1989, and had post-fire canopy cover $>40\%$. By this method, we delineated 466 km² of burned forest and 1113 km² of unburned forest, and we focused our surveys within these forests. We restricted our efforts to areas burned between 1989 and 2004 because this 15-year interval falls within the range of historic fire return interval (2–20 years) for these forest types (Skinner and Chang, 1996). We then generated 200 random points across that defined landscape (100 in burned, 100 in unburned areas) and selected the first 16 points in each stratum (total of 32 survey areas) that met logistical constraints of accessibility (≤ 2 days travel, including driving and hiking) and crew safety (Fig. 1).

2.2.2. Owl surveys

We used acoustic-lure and live-lure surveys (Reid et al., 1999) and mark-recapture methods (Franklin et al., 1996) to survey owls during the breeding season (April–July) in 2004 and 2005. We sampled each survey area at night three times during the breeding season and separated surveys by at least two weeks. We surveyed each site for only 1 year; 16 survey areas in 2004 and 16 different survey areas in 2005. Because these owls exhibit extreme site fidelity, we assumed if owls were present at a site in 1 year, they would continue to occupy that site until their death. To support this assumption, we conducted follow up diurnal visits (to observe annual reproduction) at each occupied site we located in the previous year and found all sites occupied by both or one of the same owls in

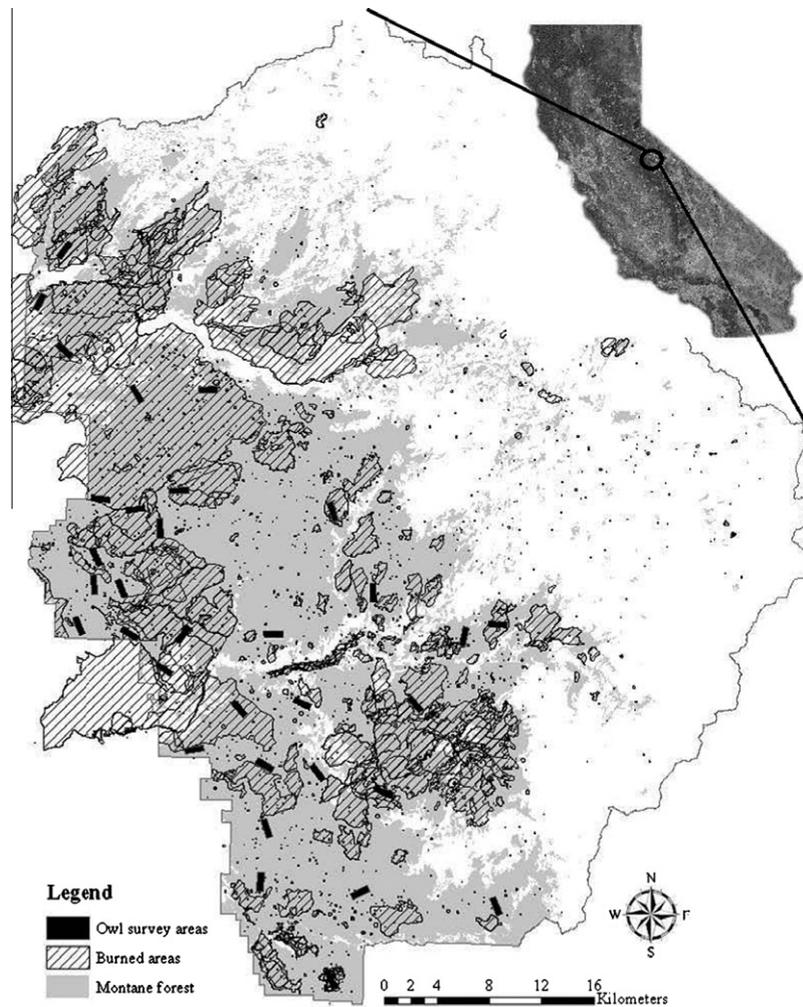


Fig. 1. Locations of 16 burned and 16 unburned California spotted owl survey areas (2004–2005) in Yosemite National Park, California. Burned areas experienced wildfires, managed wildland fires, or managed prescribed fires between 1989 and 2004.

repeated years (i.e., all sites occupied in 2004 were occupied in 2005). Therefore, we based our occupancy analyses on only the initial survey year and our results are not confounded by annual effects. Each survey area consisted of a rectangular grid with eight (four on each side) calling stations 500 m apart. We centered the grids on the 32 random points and thoroughly examined the entire survey area during grid establishment to ensure each survey area contained only one type of sampling strata (burned or unburned). We assumed that the effective sampling area was a 500 m wide buffer around each grid (Forsman, 1983) which converted to a sampling area of 3.75 km². In the rugged and remote terrain within the park, this was the largest area we could reasonably expect a field crew to survey in a single night. The combined area of the 32 transects we surveyed during the 2-year period was 120 km². We conducted systematic nocturnal surveys by vocally imitating spotted owl calls and listening for responses for 10 min at each station (Forsman, 1983; Franklin et al., 1996). Because spotted owls defend their territories by responding to “intruders” with hooting, we assumed owls responding to our vocally imitated calls were territorial (Forsman, 1983). We recorded the time, location (elevation and UTM [NAD27, Zone11 N]), sex, and species of all owl responses.

We identified, located, and captured spotted owls using the methods and protocols that were originally developed and published by Forsman (1983) and Franklin et al. (1996). When we detected spotted owls at night, we returned to the same locations the

next morning to try to determine the nest or roost location of each owl. We marked non-juvenile owls with a plastic colored leg band on one leg, and a numbered aluminum US Geological Survey Bird Banding Laboratory band on the other leg. To locate nests, we offered up to six live house mice (*Mus musculus*) to each pair and then observed what the owls did with each mouse. Reproductively active owls usually took mice to the nest or juvenile(s), allowing us to identify individual owls (band re-sighting), and locate nests or roosts (Reid et al., 1999). Through our diurnal band re-sighting, we were able to determine whether a particular owl pair’s territory overlapped >1 survey area. To avoid pseudoreplication, we only included one (chosen at random) of these overlapping survey areas. This situation occurred only once across the entire study area.

2.2.3. Habitat sampling

Following owl surveys each year, we measured spotted owl nesting and roosting habitat characteristics at all sites. We categorized owl activity sites as nests, roosts, or night survey observations (“night response”), and defined the geographic center for each site as the nest or roost tree used by the owls. Survey areas that did not yield spotted owl responses during nocturnal surveys we termed “no-response sites.” For no-response sites, we defined the geographic site center of the vegetation plot as the random point we used to locate the owl survey area during plot selection. At each site center, we recorded elevation (using Suunto wrist

altimeters) and location (UTM coordinates in NAD27 Zone 11 N). To characterize locations where we found owls, we compared the vegetation at those locations to vegetation at a random point at the no-response sites. We sampled vegetation at owl activity and no-response sites using nested circular plots oriented around the owl nest or roost tree (activity sites) or the largest tree closest to the random point (no-response sites). To measure the characteristics at the local stand level, we recorded tree species, diameter at breast height (dbh), and status (live tree or snag) in three concentric, nested, circular plots (0.05 ha, 0.1 ha, 0.2 ha) with the plot size expanding to quantify larger aspects of the habitat (i.e., larger trees) (Spies and Franklin, 1991; North et al., 1999, 2000). Within the plots, we measured all trees and snags in three size classes: 10–49 cm, 50–79 cm, and ≥ 80 cm dbh, respectively. We estimated the cover of downed coarse woody debris (CWD; logs ≥ 20 cm in diameter and ≥ 2 m long) using a 35.6 m line transect through the middle of the 0.1-ha plot. We measured shrub (>0.5 m tall) and sapling (<10 cm dbh and >0.5 m tall) ground cover using 8 m line transects at three locations: 2 m east, 8.6 m north, and 8.6 m south of the center tree. We estimated tree canopy closure using digital hemispherical photos taken 1 m above the ground surface at points 2 m north and south of the base of the center tree (Jennings et al., 1999). We used Gap Light Analyzer v 2.0 (Frazer et al., 1999) to estimate canopy closure from the photos.

Canopy closure is the proportion of the sky hemisphere obscured by vegetation when viewed from a single point, usually on the ground (Jennings et al., 1999). Closure is affected by tree heights and canopy widths and takes into account light interception and other factors that influence microhabitat. Canopy cover is a measure of the percent of ground covered by a vertical projection of the tree canopy (Jennings et al., 1999). Cover can be measured from multiple points on the ground or estimated from aerial photographs. We used remotely sensed canopy cover estimates to focus our survey efforts and used canopy closure estimates in the model estimations. We felt canopy closure was the best metric to use to measure the canopy for a particular nest or roost site in recent or current use by an owl.

2.3. Data analysis

We quantified fire severity for each of the 16 burned owl survey areas using the Relative differenced Normalized Burn Ratio (RdNBR) developed by Miller and Thode (2006). They used differential remote sensing imagery from before and after fire to create a map of polygons representing four levels of fire severity for all of the fires in Yosemite since 1973. Miller and Thode (2006) classified areas as unchanged if the severity was so low that a change could not be detected in the images one year post-fire. Low severity stands were generally lightly burned with only the fine fuels removed and some scorching of the understory trees. Moderate severity stands retained some fuels on the forest floor, but created some small tree mortality and scorching of the crowns of medium and large sized trees. High severity areas had near complete combustion of all of the litter, duff, and small logs, higher mortality of small to medium sized trees, and consumption of the crowns of large trees. Fire severity levels ranged from “1” (an unchanged area within the fire perimeter) to “4” (burned completely at high severity). We used ArcMap 9.1 (ESRI, Redlands, CA) to calculate the proportional area of each fire severity class within each of the 3.75 km² polygons that we surveyed for owls. If a survey area contained multiple fires with spatial overlap, we used the most recent fire for the overlapping areas. We then calculated the fire severity index for each survey polygon as the sum of the proportional area of each fire severity level within that survey polygon multiplied by the fire severity level (1–4) for that proportional area.

We calculated the total basal area (m² ha⁻¹) of live trees ≥ 10 cm dbh (BA_t), live trees ≥ 50 cm dbh (BA_{t50 cm}), and dead trees (snags) ≥ 80 cm dbh (BA_s). We estimated CWD cover (%) based on the percent of the 35.6 m line transect that was covered by CWD. We estimated shrub cover (%) in each plot as the mean across the three 8 m line transects.

In our analyses of owl pair site occupancy, we used nest sites when possible ($n = 15$), roost sites ($n = 3$) when we did not observe nesting at a particular owl site, and night response sites ($n = 1$) when we were unable to locate nests or roosts. We calculated the mean of each habitat variable (canopy closure, BA_t, BA_{t50 cm}, BA_s, shrub cover, CWD cover, and site elevation) within each owl activity type for sites where there was more than one nest ($n = 2$) or roost ($n = 2$) location for a territorial owl pair. In all analyses, we used only one site per owl pair to ensure independence among sites and followed established protocols when determining owl social status (G. Miller, Forest Service, unpublished paper).

We examined the correlation matrix for all of the habitat data to determine if any habitat variables were highly intercorrelated. To avoid collinearity in our models, we did not develop models that included highly correlated variables (e.g., correlation coefficient ≥ 0.70 ; Burnham and Anderson, 2002). Canopy closure and basal tree area tend to be highly correlated. To avoid including these two intercorrelated variables as separate variables in the same model (Burnham and Anderson, 2002), we standardized them using z-scores and summed them into a single derived variable (BA_{tCan}), which we believe provided an ecologically based (e.g., “owl-centric”) perception of forest density.

We defined spotted owl pair occupancy as the probability that a pair of territorial spotted owls will occupy a particular patch of habitat. Before conducting owl surveys, we developed a list of candidate models for predicting pair occupancy as a function of site burn history, all seven habitat variables, and survey year. We standardized habitat variables using z-scores because they were measured at different scales. We determined the model that best predicted spotted owl occupancy with program PRESENCE v 2.1 (Hines, 2006), which estimates site occupancy (Ψ) as a function of the probability of detection (ρ); therefore, ρ was included in each candidate model. By including habitat characteristics in the candidate models, we tested if Ψ varied as a function of habitat while also investigating if ρ varied as a function of survey time or fire history (burned vs. unburned). To include survey-specific detection rates, we employed the full identity function in PRESENCE and followed the procedures for single species, single season surveys detailed by MacKenzie et al. (2002). We considered only models with two to five parameters (including the intercept and probability of detection) to avoid the occurrence of spurious results by maintaining an approximate ratio of data to parameters >10 ($n = 32$ sites; maximum # parameters = $n/10$; Burnham and Anderson, 2002). We used Akaike’s Information Criteria (AIC) corrected for low sample size (AIC_c; Akaike, 1973; Hurvich and Tsai, 1989) to quantifiably and simultaneously compare candidate models (Burnham and Anderson, 2002).

We selected the “best” model on the basis of AIC_c values, Akaike weights (w_i), and evidence ratios as defined by Burnham and Anderson (2002). The Akaike weight (w_i) represents the probability that a particular model provides the best explanation of the data given the tested set of models. The difference in AIC_c values of alternative models relative to the model with the lowest AIC_c (ΔAIC_c) reflects the level of support for the alternative models. Models with $\Delta AIC_c \leq 2$ have “substantial” support, whereas models with ΔAIC_c of 4–7 have “considerably less” support, and models with $\Delta AIC_c > 10$ have essentially no support. To compare an alternative model to the best model, we calculated evidence ratios as w_1/w_2 , where w_1 and w_2 refer to Akaike weights for the two models being compared, with our best model always being the numerator.

Evidence ratios ≤ 2.7 are equivalent to a $\Delta AIC_c \leq 2$ and indicate substantial support for the model being compared to the best model, whereas evidence ratios ≥ 3 provide “little evidence” in favor of the alternative model (Burnham and Anderson, p. 79).

We applied the logistic model in program PRESENCE to incorporate habitat variables in our candidate models and to calculate the maximum likelihood estimates required for AIC calculations (Donovan and Hines, 2007). The logistic model employed by PRESENCE is

$$\log e[\Psi/(1 - \Psi)] = X\beta, \quad (1)$$

where Ψ refers to the probability of owl pair occupancy, X is the row vector of the habitat variables, and β is the column vector of model coefficients.

We applied a closed population model because of the short survey period (2 years) relative to the life span of adult California spotted owls (14 years; Steger et al., 2002) and their high adult annual survival rates (83%; Blakesley et al., 2001). We estimated the total population size (N) of California spotted owls in Yosemite, as well as the population size within areas characterized by different burn histories (burned and unburned) following Lancia et al. (1996):

$$\hat{N} = O_{\text{park}}/(a\hat{\rho}) \text{ with } \text{var}(\hat{N}) = \hat{N}^2 \times [(\text{var}O_{\text{park}}/O_{\text{park}}^2) \times (1 - a) + (\text{var}\rho/\rho^2)] \quad (2)$$

where O_{park} is the total number of owl pairs observed in the field from the surveys from both years, a is the proportion of the total area surveyed, and ρ is the probability of detecting a spotted owl pair from the surveys. We calculated the density of owl pairs at each survey area as

$$\hat{D}_{\text{site}} = O_{\text{site}}/A \quad (3)$$

where O_{site} is the number of owl pairs observed from the surveys for that survey site, and A is the area of the survey site (3.75 km²). To estimate owl density for the entire park (\hat{D}_{park}), we determined the grand mean and variance across all survey sites ($n = 32$)

$$\hat{D}_{\text{park}} = \left(\sum \hat{D}_{\text{site}} \right) / n \text{ with } \text{var}\hat{D}_{\text{park}} = (\text{SD}_{\text{site}})^2 \quad (4)$$

where SD is the standard deviation of owl pair density across all survey sites. For our population estimation, we only included individuals that we detected during the nocturnal surveys and if their nest or roost was inside the 3.75-km² survey area. We doubled our spotted owl density estimate to represent individual owls and compare it to other estimates in the Sierra Nevada, although owl pairs represent a more informative measure of owl density because pairs are the reproductive unit (Olson et al., 2005).

3. Results

3.1. Fire severity and habitat variability

The fire severity index of burned survey areas ranged from 0.4 to 3.1, with an overall mean (SE) of 2.0 (0.2). Across all burned survey areas, the mean (SE) proportion of area burned at unchanged, low, moderate, and high fire severity was 8% (2), 25% (4), 29% (4), and 14% (4), respectively. The maximum proportion of any given survey area that burned at high fire severity was 46%. Generally, survey areas burned at a low to moderate fire severity.

Canopy closure ranged from 28% to 94% ($\bar{x} = 77\%$) for burned sites and 63% to 96% ($\bar{x} = 87\%$) for unburned sites. The mean (SE) basal area of all trees (≥ 10 cm; BAT) was 42.8 (6.5) m² ha⁻¹ at burned sites and 56.3 (5.6) m² ha⁻¹ at unburned sites. In burned and unburned sites, the mean basal area for large snags (≥ 80 cm dbh) was 10.3 (2.0) m² ha⁻¹ and 9.0 (2.0) m² ha⁻¹, mean

coarse woody debris cover was 4.3% (1.2) and 6.6% (1.3), and mean shrub cover was 7.6% (2.2) and 12.9% (3.8), respectively.

The correlation matrix showed that BAT was highly correlated with BAT50 cm ($r = 0.89$) and canopy closure ($r = 0.70$). Consequently, neither of these appears as a separate variable together with BAT in the same model. The high correlation between BAT and BAT50 cm shows the BAT at our sites was driven by large trees and, on average, 74% of the BAT for any particular site comprised trees >50 cm dbh.

3.2. Spotted owl site occupancy

We detected 19 owl pairs and 2 single males (we did not include single owls in any analyses) after 116 h of nocturnal surveys confirmed by diurnal observations. Through the diurnal observations, we located 19 nests (9 in burned survey areas, 10 in unburned). We fitted 30 adults and 5 subadults with unique number and color leg bands. The unmodeled (naïve) site occupancy (Ψ) for owl pairs was 0.59 (SE = 0.09) across all site types and 0.50 (SE = 0.13) and 0.69 (SE = 0.12) for burned and unburned sites, respectively (Table 1). Detection rates at survey sites did not vary based on fire history.

The mean annual detection rates for spotted owl pairs (ρ) were consistently high, with $\rho = 0.47$ for 2004 and $\rho = 0.59$ for 2005 with the particular year in which we surveyed an area bearing no influence on site occupancy (Table 2). Within a year, owl pair detection rates (ρ) were similar across all sites within survey periods, but varied temporally, with $\rho = 0.52$ (SE = 0.11) in the first survey and 0.89 (SE = 0.05) thereafter. Because all pairs detected in the first survey were also detected in ≥ 1 subsequent survey within that survey year, we used only the second and third surveys in subsequent analyses (Table 1). We ran this same candidate model set using all three surveys and the results are exactly the same. Therefore, for brevity, we only present the most parsimonious model set (Table 2).

The best model for predicting the presence of owl pairs included basal area of trees >10 cm dbh and the ground cover of coarse woody debris in a model structured as:

$$\text{Logit}\hat{\Psi} = (3.92) + [41.81 \times \text{Zscore}(\text{BAT})] - [10.52 \times \text{Zscore}(\text{CWD})] + (2.13 \times \rho), \quad (5)$$

with an Akaike weight (w_i) of 0.40 (Table 2). The standard error of the parameter estimate for BAT was 84.29 and 24.94 for CWD. The second best model included the derived variable BATCan (Table 2), with structure as follows:

$$\text{Logit}\hat{\Psi} = (0.24) + 4.56 \times [\text{Zscore}(\text{BAT}) + \text{Zscore}(\text{canopyclosure})] + (2.12 \times \rho). \quad (6)$$

This model also had substantial support with w_i of 0.15 and an evidence ratio of 2.6 and ΔAIC_c of 1.90. The standard error (2.18) for the parameter estimate in this alternative model was much smaller than for either of the standard errors for the parameters in the “best” model. There was no support for a model that distinguished between burned and unburned sites ($w_i = 0.00$, $\Delta AIC_c = 35.09$) indicating that indirect complexities of post-fire effects on forest structure (e.g., changes in canopy closure) influence owl site occupancy rather than the direct effect of fire on the owls. Applying the best model, the mean and standard error (SE) of estimated occupancy rate was 0.46 (0.12) for burned sites 0.72 (0.11) for unburned sites, and 0.59 (0.08) across all sites. Total basal tree area (BAT) was higher both at burned and unburned sites with owls than at no-response sites (Fig. 2).

Table 1

Total counts^a and unmodeled mean (SE) occupancy and detection rate^b, population size^c, and density estimates of California spotted owls from random, systematic, nocturnal surveys in burned and unburned areas (April–July 2004–2005) in Yosemite National Park, California.

Burn treatment	Count of owl pairs ^a	Occupancy probability ^b	Detection probability ^b	Population size (pair) ^c	Density (owl pair km ⁻²)
Burned	8	0.50 (0.13)	0.89 (0.05)	123 (10)	0.15 (0.04)
Unburned	11	0.69 (0.12)	0.89 (0.05)	156 (13)	0.21 (0.04)
ALL	19	0.59 (0.09)	0.89 (0.05)	356 (20)	0.18 (0.03)

^a Count of owl pairs refers to the total number of pairs of owls observed in all survey areas within the burn treatment.

^b Occupancy and detection rates refer to the mean and standard error (SE) of the occupancy and detection rates for each owl survey areas calculated from program PRESENCE (Hines, 2006).

^c Population size refers to the total number of owl pairs calculated for each burn treatment with standard error representing the error rate in the estimate.

Table 2

Summary of model selection statistics^a from logistic model^b analysis of nesting and roosting habitat variables^c predicting the site occupancy of California spotted owl (*Strix occidentalis occidentalis*) pairs in Yosemite National Park, California, 2004 and 2005 ($n = 32$; 16 burned sites, 16 unburned sites).

Model description ^d	K	$\log(L)^a$	AIC_c	ΔAIC_c	w_i
Occupancy{BAT}{CWD}	5	-15.03	40.07	0.00	0.40
Occupancy{BATCan}	4	-16.99	41.97	1.90	0.15
Occupancy{BATCan}{Shrub}	5	-16.71	43.42	3.35	0.07
Occupancy{BAT}{Elevation}	5	-16.72	43.44	3.37	0.07
Occupancy{BATCan}{CWD}	5	-16.76	43.52	3.45	0.07
Occupancy{BAT}	4	-17.91	43.82	3.75	0.06
Occupancy{BATCan}{BAs}	5	-16.91	43.82	3.75	0.06
Occupancy{BATCan}{Elev}	5	-16.94	43.88	3.81	0.06
Occupancy{BAT}{Shrub}	5	-17.78	45.56	5.49	0.03
Occupancy{Canopy}{BAT50 cm}	5	-18.13	46.26	6.19	0.02
Occupancy{Canopy}	4	-22.63	53.26	13.19	0.00
Occupancy{Canopy}{Elevation}	5	-22.21	54.42	14.35	0.00
Occupancy{Canopy}{CWD}	5	-22.32	54.64	14.57	0.00
Occupancy{Canopy}{Shrub}	5	-22.47	54.93	14.86	0.00
Occupancy{Canopy}{BAs}	5	-22.59	55.18	15.11	0.00
Occupancy{BAT50 cm}	4	-24.52	57.04	16.97	0.00
Occupancy{Elevation}	4	-30.47	68.94	28.87	0.00
Occupancy{constant} (null model)	3	-34.17	74.33	34.26	0.00
Occupancy{Burned}	4	-33.58	75.16	35.09	0.00
Occupancy{Shrub}	4	-33.77	75.54	35.47	0.00
Occupancy{BAs}	4	-34.05	76.11	36.04	0.00
Occupancy{SurveyYear}	4	-34.10	76.20	36.13	0.00
Occupancy{CWD}	4	-34.15	76.30	36.23	0.00
Occupancy{constant}, detection rate{Burned}	2	-38.85	81.70	41.63	0.00

^a Statistics include: \log_e likelihood ($\log(L)$), Akaike's Information Criterion corrected for small sample size (AIC_c), relative AIC_c (ΔAIC_c), Akaike weights (w_i), and the number of parameters (K) in the model.

^b Logistic model used: $\log_e(\Psi/(1-\Psi)) = X\beta$, where Ψ refers to the probability of owl pair occupancy, X is the row vector of habitat variables, and β is the column vector of coefficient values.

^c 'BAT' refers to basal area of all live trees >10 cm diameter at breast height (dbh), 'BAs' refers to basal area of snags ≥ 80 cm, 'BAT50 cm' refers to basal area of all live trees >49 cm, 'canopy' refers to canopy closure estimated from digital hemispherical photos, 'BATCan' refers to the sum of BAT and canopy closure at the owl site, shrub refers to mean shrub cover, and 'CWD' is the cover of coarse woody debris.

^d Detection rate was survey-specific ("full identity") in every model except the last one, in which it varied by burn treatment.

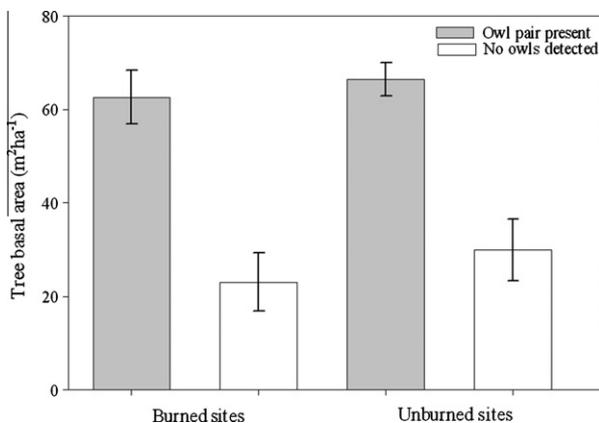


Fig. 2. Comparing the mean \pm SE basal area of all live trees (≥ 10 cm) at burned and unburned sites with owls (nest and roost sites) and without (random points) between April–July, 2004–2006 at Yosemite National Park, California.

3.3. Population estimation

Eighty-four percent of all of the nests or roosts we located were within the boundary of our 3.75 km² survey areas. Using the detection rate (ρ) estimated by PRESENCE and extrapolating across all potential habitat, we estimated the population size (SE) for Yosemite as 280 (16) pairs of California spotted owls, with 70 (6) pairs in the burned montane forest and 228 (18) pairs in the unburned forest (Table 1). The mean (SE) density of owl pairs was 0.15 (0.04) pairs km⁻² in the burned forest and 0.21 (0.04) pairs km⁻² in the unburned for an overall average of 0.18 (0.03) pairs km⁻² across the entire park (Table 1), or 1 pair 6.25 km⁻². This is a conservative estimate because there were three pairs of owls we did not include in the estimate because their nests were 0.2 km, 0.7 km, and 1.3 km outside of the survey areas. We also omitted an additional pair that we detected only during the diurnal follow-up surveys (while looking for another pair) and not during our nocturnal surveys. The roost for this "consequential" pair were within the same survey area as the nest of another pair (<1.5 km apart).

4. Discussion

The relatively low mean fire severity index documented for our burned forests (2.0) suggests a fire history similar to what existed before Euro-American settlement (Skinner and Chang, 1996). Although we characterized individual survey areas with a single fire severity index value, burned areas contained a mosaic of different fire severities. This mosaic reflects heterogeneity among burned forest patches and creates a complex matrix of habitat characteristics at multiple scales (e.g., microhabitat, stand, and landscape). This post-fire heterogeneity may be one of the most important aspects of the burned landscape to spotted owls. Franklin et al. (2000) showed that owls with territories that contained a mosaic of vegetation types infused within old-growth conifer forest had higher fitness. Bond et al. (2009) found that California spotted owls use this mosaic for a variety of different activities such as low severity for nesting and roosting and higher severities for foraging.

4.1. Spotted owl occupancy

Based on our modeling results, California spotted owl nest and roost site occupancy in montane forests of Yosemite National Park was best predicted by combining the positive effect of total basal area (BA_T), and the negative effect of coarse woody debris (CWD). However, there was substantial support for the alternative model that used the derived variable combined canopy closure and tree basal area (BA_TCan). The abundance of large trees has a clear association with spotted owl nest and roost sites (Bias and Gutiérrez, 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997). These results also indicate that fire does not reduce the probability of spotted owl occupancy, especially if numerous large trees remain after a fire. Clark (2007) showed northern spotted owl occupancy declined and local extinction increased immediately following fire. However, his results are confounded by post-fire salvage logging and large areas of early-seral forests in his study area. Also, the fire age of our study is variable (2–14 years) while his was only 1–2 years. However, it is important to note the disparity of these results with ours suggests that salvage logging may have detrimental effects on spotted owl occupancy. Jenness et al. (2002) found a weak negative association of fire to Mexican spotted owl occupancy. However, they collected no data on the habitat characteristics to allow investigation into the post-fire forest structure that potentially drove that association.

We included detection rates in our models because the California spotted owl home range is potentially larger than our survey area (MacKenzie, 2005). According to MacKenzie et al. (2002), however, high detection rates (e.g., >0.5), such as what we estimated from our nocturnal surveys ($\rho = 0.89$; Table 1), produce accurate and unbiased predictive models for occupancy.

In an earlier study on habitat associations of California spotted owls in northeastern California, site occupancy was positively associated with large trees (>61 cm dbh) and high canopy cover (>70%; Blakesley et al., 2005). However, the proportion of smaller trees (<60 cm dbh) around the nest, even with high canopy cover (>70%), was negatively associated with occupancy (Blakesley et al., 2005). By contrast, models incorporating only large trees (>50 cm dbh; BA_T50 cm) were not supported in our analyses (Table 2), indicating that a range of tree sizes influence site occupancy by spotted owls. Trees between 10 cm and 50 cm dbh contribute to a multilayered understory that presumably allows for efficient thermoregulation by owls (Barrows, 1981; Weathers et al., 2001). Large trees are important as nest sites for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel, 1995; Meyer et al., 2007),

an important prey species for spotted owls in the Sierra Nevada (Williams et al., 1992).

The disparity between our results and those of Blakesley et al. (2005) could reflect several key differences between our studies. Blakesley et al. (2005) measured their vegetation at a larger spatial scale than our study and consequently used categorical canopy cover data. At our smaller spatial scale, we were able to use continuous canopy closure data. Additionally, their study was conducted in the northern Sierra Nevada which has a more recent history of logging, and thus large trees may be more limited there than in the more pristine forests in Yosemite. Their study site also suffered from decades of fire suppression, which resulted in a dense understory of regenerating white fir. These thickets of young trees could interfere with owl foraging which could explain the negative association of small trees to owl occupancy. Furthermore, Blakesley et al. (2005) quantified habitat only at nest sites, whereas we included roost sites (when nests were unknown). The presence of large trees may be less important in the selection of owl roosts versus nest sites (Verner et al., 1992b). Including roost sites in spotted owl occupancy models provides a more robust model than those excluding such features because the owls may not nest every year (Blakesley et al., 2001, 2005; Steger et al., 2002).

The spatially invariant detection rates reported here compared to the highly variable rates reported for northern spotted owls in Oregon (Olson et al., 2005) could be explained by the disparity in forest management practices. For example, forest managers favored clearcutting in the Pacific northwest over much of the range of the northern spotted owl, while much of the range of the California spotted owl predominantly experienced selective logging. Only a small portion (18%) of our study area was logged during the 1930s (National Park Service, 1930), and none of the study area contained co-habiting, invasive barred owls (*S. varia*), a species that typically has negative effects on detection rates and site occupancy of spotted owls (Kelly et al., 2003; Olson et al., 2005). Consequently, the mean per visit detection rate for spotted owl pairs in our study (0.89 ± 0.1) was higher than in Oregon (0.51) where barred owls and logging were more common (Olson et al., 2005, p. 930). The main factors influencing habitat structure in the montane forests of Yosemite are natural processes, predominately fire. Our results evaluated the role of fire unconfounded by large-scale logging, development, or competition with an aggressive congener.

In a study in the Sierra Nevada, Gutiérrez et al. (1992) found that California spotted owl nest and roost sites had higher snag basal area than random sites. However, study areas of these authors were predominantly in forests with a history of consistent logging, such that large snags likely were limited in availability. In the predominantly unlogged forests of Yosemite, large snags are relatively common and burned and unburned forests had similar basal areas of large snags.

The lower AIC_c value for the BA_T-CWD model indicates that this model has the best fit to the data and, therefore, should reflect the best balance of precision (as measured by standard error) and bias (as measured by log-likelihood). In our candidate model set (Table 2), we hypothesized that CWD would be a positive influence on spotted owl site occupancy due its positive association with food for the northern flying squirrel in forests of the Pacific northwest (Amaranthus et al., 1994; Lehmkuhl et al., 2004). However, studies in the forests of the Sierra Nevada with typically lower fire return intervals have shown no relationship between CWD and northern flying squirrels (Pyare and Longland, 2002; Meyer et al., 2007). Fire transforms CWD into nutrient-loaded ash, resulting in less CWD in burned forests than unburned forests (Shaffer and Laudenslayer, 2006). It is possible that CWD interferes with owl foraging when attempting to extract prey from the ground.

Potentially unpredictable ephemeral effects (e.g., CWD or shrub cover) can be avoided by introducing variable(s) that measure

more temporally stable effects. Our derived variable, BATcan; is based on live trees that typically remain alive and upright for decades after the fire. Summing standardized total tree basal area ($\text{m}^2 \text{ha}^{-1}$) and canopy closure (%) at a site creates a single variable that depicts forest density in the overstory as well as the understory. The model comparisons showed BATcan was an acceptable alternative with greater precision for predicting spotted owl site occupancy in montane forest than the BA_t-CWD model. The consistent positive association of BATcan with site occupancy in our study is in agreement with the consensus that dense forest with large trees are important nesting and roosting habitat for spotted owls in the Sierra Nevada bioregion (Bias and Gutiérrez, 1992; Call et al., 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997; Zabel et al., 1992). An important benefit to managers in using the BATcan variable is the reduction in field data collection, as canopy closure is quickly and easily measured and requires little field or analysis training and minimal equipment. However, we caution the use of BATcan in models for forests where >70% of the total basal area of a stand is dominated by smaller trees (<50 cm dbh) because in that situation, increases in stand basal area typically indicate increases in tree density rather than tree size. This leads back to the idea that too many small trees negatively affect spotted owl occupancy (Blakesley et al., 2005).

4.2. Population estimate

Similar density estimates of spotted owl pairs in burned and unburned forests (95% confidence intervals, CI: 0.07–0.22 and 0.14–0.28 owl pairs km^{-2} , respectively) of the type that we examined (predominately low to moderate severity burns of a relatively small percent of the landscape) suggest that fire did not affect owl densities in Yosemite. Consequently, detection and occupancy rates were similar in burned and unburned forests. Based on density estimates in Noon et al. (1992, p. 175), we calculated the 95% CI individual owl density for the area surrounding Yosemite including two national forests and a national park. This estimate (0.10–0.21 owls km^{-2}) was markedly lower than our estimate of total individual owl density in Yosemite (95% CI = 0.25–0.46 owls km^{-2}) and suggests that Yosemite has a higher density of spotted owls than the surrounding national forests and nearby parks. However, this comparison is tentative because Noon et al. (1992) presented only 'crude densities' and did not correct for unsuitable areas within their total available habitat. Consequently, if the amount of suitable habitat was substantially lower than the total area they used in their calculations, their spotted owl density estimates could be lower than reported.

For our population size estimate for the park, we caution that these could be biased slightly high because we treated both forest types (lower montane and upper montane) equally in terms of occupancy and detection rates and this may not be true. It is for this reason that we discuss our results in terms of density rather than the overall population estimation for the park.

5. Conclusions

Our data suggest that the landscape-level prescribed burning and wildland fire use programs of Yosemite National Park may benefit California spotted owls by protecting their nesting and roosting habitat from catastrophic fires while simultaneously creating a large, contiguous, and diverse landscape conducive to population persistence for spotted owls. This is especially evident in Sierra Nevada montane forests that historically burned at low to moderate intensity and usually resulted in a mosaic of burn severity, with minimal mortality of medium and large trees (van

Wagtendonk and Fites-Kaufman, 2006). Our results are particularly relevant to forests where large aggregations of residual downed coarse woody debris create spatially continuous fuel loads and extremely flammable environments. Our results suggest that fire, particularly fire resulting in low to moderate tree mortality, can retain residual habitat features that are important for roosting and reproducing California spotted owls.

California spotted owl site occupancy rates and densities were similar in recently burned (<15 years) and unburned montane forests of Yosemite National Park. Our predictive model for site occupancy can assist managers in developing fire management plans with minimal impact and potential benefit to California spotted owls. Currently, the application of our site occupancy model relies heavily on local and site-specific data. A landscape scaled remote sensing and GIS model could assist in the evaluation of fire and land management plans both for Yosemite and more generally for the Sierra Nevada. Integrating remote sensing data with our derived variable, BATcan, would create a reliable and simple model that would allow managers to move beyond the limitations (in both money and time) of having to collect ground based data.

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