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Management and Conservation Article

Habitat Use and Selection by California Spotted Owls in a Postfire Landscape

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ABSTRACT Forest fire is often considered a primary threat to California spotted owls (*Strix occidentalis occidentalis*) because fire has the potential to rapidly alter owl habitat. We examined effects of fire on 7 radiomarked California spotted owls from 4 territories by quantifying use of habitat for nesting, roosting, and foraging according to severity of burn in and near a 610-km^2 fire in the southern Sierra Nevada, California, USA, 4 years after fire. Three nests were located in mixed-conifer forests, 2 in areas of moderate-severity burn, and one in an area of low-severity burn, and one nest was located in an unburned area of mixed-conifer–hardwood forest. For roosting during the breeding season, spotted owls selected low-severity burned forest and avoided moderate- and high-severity burned areas; unburned forest was used in proportion with availability. Within 1 km of the center of their foraging areas, spotted owls selected all severities of burned forest and avoided unburned forest. Beyond 1.5 km, there were no discernable differences in use patterns among burn severities. Most owls foraged in high-severity burned forest more than in all other burn categories; high-severity burned forests had greater basal area of snags and higher shrub and herbaceous cover, parameters thought to be associated with increased abundance or accessibility of prey. We recommend that burned forests within 1.5 km of nests or roosts of California spotted owls not be salvage-logged until long-term effects of fire on spotted owls and their prey are understood more fully. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1116–1124; 2009)

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KEY WORDS California spotted owl, fire severity, foraging habitat, forest structure, resource selection function, southern Sierra Nevada, *Strix occidentalis*, telemetry error.

Forest fire is a natural disturbance event and prominent management issue that can affect habitat of California spotted owls (*Strix occidentalis occidentalis*; Weatherspoon et al. 1992), a species that has driven many forest-management decisions in the Sierra Nevada and southern California, USA, for the past decade (U.S. Forest Service [USFS] 2001, 2004, 2005). Sierran mixed-conifer forests are a particularly important vegetation type for California spotted owls and are characterized by mixed-severity fire regimes, where complexes of lightly to severely burned patches at intermediate scales are common (Weatherspoon et al. 1992, Minnich et al. 1995, Centers for Water and Wildland Resources 1996, Tefler 2000). California spotted owls evolved in an environment that included a heterogeneous landscape partially shaped by fires that produced mixed patches of unburned, low-, moderate- and high-severity burned forest (Weatherspoon et al. 1992, Centers for Water and Wildland Resources 1996). Vital rates of spotted owls are positively associated with forest characteristics, including the amount of older conifer-dominated forest in an area (Blakesley et al. 2005, Seamans 2005).

Beginning in the early 20th century, natural and human-caused processes changed fire regimes of forests in the western United States. Changes in climate resulted in periods of increased moisture and warmer temperatures (Centers for Water and Wildland Resources 1996). Extensive harvesting shifted the size distribution of trees within forested stands from larger, older trees with greater inter-tree gaps to denser forests with more smaller sized trees (McKelvey and Johnston 1992, Centers for Water and Wildland Resources 1996). By the mid–20th century, policies of vigorous fire suppression led to exclusion of this once more frequent and widespread disturbance process (Weatherspoon et al. 1992).

Because California spotted owl nests and roosts are associated with older forests and high tree-canopy cover (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004), many forest managers postulate that high-severity fires could have a negative impact on persistence of the species and, therefore, believe that fire poses the greatest risk to owl habitat (Weatherspoon et al. 1992; USFS 2001, 2004, 2005). Reducing fire risk by modifying owl habitat is considered necessary to help conserve the species. In addition, burned forests that once provided habitat for spotted owls may be presumed unusable and trees harvested as salvage.

Results from past studies of fire impacts on spotted owls are equivocal. Fires with large patches burned at high severity seemed to adversely affect occupancy rates in some owl territories, whereas in other territories experiencing high-severity fire, spotted owls have remained and continued to reproduce (see e.g., MacCracken et al. 1996, Gaines et al. 1997, Bond et al. 2002, Jenness et al. 2004). Franklin et al. (2000) hypothesized that fire could enhance prey abundance and access to prey by creating patchy openings within otherwise closed forest canopy and by increasing habitat edges.

Although spotted owls continue to occupy burned landscapes, few data have been published that describe how owls use burned landscapes. Managing burned

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landscapes for the benefit of California spotted owls requires understanding how owls use burned portions of their territories for nesting, roosting, and foraging. We report on habitat use and selection by 7 California spotted owls occupying a landscape that burned 4 years previously in the 2002 McNally Fire in the southern Sierra Nevada, California. Our study objectives were to determine whether this sample of California spotted owls nested, roosted, and foraged differentially according to vegetation burn severity. Specifically, we sought to 1) characterize nesting and roosting sites of California spotted owls relative to burn severity and conventional microhabitat descriptors, 2) quantify the probability that a spotted owl in our sample would select a roost site according to burn severity, 3) develop and contrast multiple resource selection probability functions (RSPF; Manly et al. 2002) to quantify the probability of foraging habitat use by owls according to burn severity and other ecologically pertinent covariates, and 4) quantitatively describe and compare structural characteristics of vegetation within the burn-severity categories.

STUDY AREA

We conducted our study at 2 areas, the Greenhorn Mountains and the Kern Plateau, both in Sequoia National Forest, southern Sierra Nevada Mountains, California. The Greenhorn Mountains are approximately 20 km northwest, and the Kern Plateau is approximately 20 km north–northeast, of the town of Kernville, California. These 2 areas are separated by Kern River Canyon and are approximately 13 km apart.

Elevations at both areas ranged from 1,500 m to 2,500 m. The nearest National Weather Service weather station at Johnsondale (1,427 m) recorded an annual average precipitation of 57 cm from 1971 to 2000 (National Climate Data Center 2008). Vegetation was classified as Sierran Mixed Conifer (Allen 1988), dominated by ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and white fir (*Abies concolor*). Above 2,100 m, a transition zone was dominated by red fir (*A. magnifica*). Other common tree species included sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), canyon live oak (*Quercus chrysolepis*), and California black oak (*Q. kelloggii*).

In July and August 2002, the McNally Fire burned approximately 60,985 ha in the Sequoia and Inyo National Forests, including 33,704 ha of conifer-dominated forests (Odion and Hanson 2006). Like most fires, the McNally Fire burned with variable severity, leaving a mosaic in the 2 study areas. Using USFS vegetation burn-severity maps (USFS 2006), we estimated that 31% of conifer forest types remained unburned in foraging ranges of the spotted owls that we studied, whereas 29%, 27%, and 13% were burned at low-, moderate-, and high-severities, respectively.

METHODS

Spotted Owl Habitat Use

We collected location data from sites used by California spotted owls for roosting, nesting, and foraging, and vegetation data from sites available to owls. We defined selection as use of a particular forest burn-severity class at a greater frequency than expected given its availability.

Our field procedures for sampling habitat use by California spotted owls entailed 1) surveying and locating spotted owls at previously occupied sites near or within the McNally Fire, 2) capturing owls and affixing radiotransmitters, and 3) relocating owls at daytime roosts or in nests and at nighttime foraging sites using radiotelemetry. Prior to our study, USFS personnel surveyed for and located California spotted owls occurring within and adjacent to the McNally Fire perimeter during 3 consecutive breeding seasons 2003–2005 (W. Rannals and R. Galloway, USFS, unpublished data). We selected 4 territories confirmed to be occupied by pairs of spotted owls during the 2006 breeding season. We selected these 4 territories because 1) territory juxtaposition was inside or within 1 km of the fire perimeter, giving occupying owls access to burned and unburned forest; 2) these territories were occupied by spotted owls continually since the fire; and 3) there was sufficient road access for effective radiotracking.

We located, captured, and classified sex of California spotted owls using standard techniques (Forsman 1983, Franklin et al. 1996). We also affixed backpack-style radiotransmitters designed to minimize contact with the owl's back (AVM Instrument Company, Ltd., Colfax, CA; J. P. Ward, New Mexico State University, unpublished data) using Kevlar ribbon (0.63-cm wide; Bally Ribbon Mills, Bally, PA). Our transmitter units with harness weighed <20 g, or $<4\%$ of each owl's body mass.

We considered individual owls as sampling units because previous studies of California spotted owls found that males and females foraged independently (Call et al. 1992, Zimmerman et al. 2001). We located each owl nightly or every other night between 2130 hours and 0400 hours. We also located each owl during the day every 7–10 days to obtain roosting locations and measure our telemetry-location error. We used a systematic design with a random start to collect a representative sample of foraging locations. We randomly assigned each individual owl to a 1-hour time block in the first night that we tracked the owl, then we systematically shifted each owl's time block by 1 hour (or back to the first time block when the sequence was completed) on each subsequent sampling night.

We estimated owl locations by triangulation on signals from the affixed radiotransmitters. We used ≥ 3 compass bearings of the strongest signals with all bearings taken within approximately 30 minutes for estimating each owl location (Guetterman et al. 1991). We used handheld 3-element collapsible directional Yagi antennas and portable receivers supplied by AVM Instrument Company, Ltd. and Telonics (Telonics, Inc., Mesa, AZ) for deciphering signal strength and direction. We used a Geographic Positioning System (error <10 m) to determine Universal Transverse Mercator (UTM) coordinates of telemetry monitoring stations and spotted owls visually observed at roosts or nests and Program LOCATE III (Pacer Computing, Tatamagouche, NS, Canada) to estimate the most likely point-location of the radiomarked owls from observer location and direction of the radio signals using a

maximum likelihood estimator (Nams 2006). We plotted and analyzed all spatial data using ArcMap 9.1.

Available Habitat Types

To quantify habitat selection, we needed to estimate the amount of different habitat types available to owls during the study. We used spatially explicit data generated by the USFS (USFS 2006) to estimate amounts of habitat and vegetation burn severity within foraging ranges of owls that we approximated for the primary period for rearing young (May through mid-Aug) using a circle with radius that extended from a nest or roost center to the furthest documented foraging location for each radiomarked owl. We used a nest location as the center of the approximated foraging range if young were produced and fledged during the study. Otherwise, we used a harmonic mean of roost locations for each individual owl generated in Animal Movement Program (Hooge et al. 1999). For analyzing selection of foraging sites, we quantified available habitat by intersecting a systematic sample of grid-points in each owl foraging range with the digital habitat maps (see Foraging Habitat Selection).

We classified habitat within foraging ranges according to digital data layers of existing vegetation type and burn severity from the McNally Fire using Geographic Information System (GIS) maps. The vegetation map we used (EVEG Tile; Goudy and Smith 1994) was updated by USFS analysts in 2001 using a combination of automated-systematic procedures, remote sensing classification, photo editing, and ground surveys. Minimum mapping size was 1 ha and 30-m pixel size (Allen 1988). California Wildlife Habitat Relations (CWHR; Mayer and Laudenslayer 2002) vegetation type was derived from EVEG data.

To create a GIS layer of severity of vegetation burned by the McNally Fire, USFS analysts used Landsat Thematic Mapper data before and after the fire and field data on vegetation collected 1 year following several Sierra Nevada fires that occurred from 2001 to 2004 for ground verification of the remote sensing data. The resulting map showed 4 classes of fire severity: 1) Unburned–unchanged—areas in which conditions 1 year after the fire were indistinguishable from prefire conditions; 2) Low severity—areas of surface fire with little change in cover and little mortality of dominant vegetation; 3) Moderate severity—areas between low- and high-severity classes and representing a mixture of effects on dominant vegetation; and 4) High severity—areas where dominant vegetation had high to complete mortality due to fire. We considered including clearcut areas as an additional category because there were scattered pre- and postfire clearcuts within 5 of the owl foraging ranges. However, we calculated after mapping that <3% of all available habitat as defined by our owl foraging ranges had been clearcut and considered this habitat class too limited for detecting use given our sample of foraging sites for each owl.

Available Habitat Structure

We described vegetation in each burn-severity category using structural measures of owl habitat (e.g., Gutiérrez et al. 1992). We measured structural features at 5 randomly selected sites within each of the 4 GIS-classified burn-severity categories of conifer and mixed-conifer forest types within the largest foraging range of each of 4 owl pairs. Ground-truthing of GIS-classifications indicated slight errors, which resulted in unequal sample sizes among burn-severity categories, mostly between the unburned and low-severity burn (n = 15, unburned; 26, low severity; 20, moderate severity; 19, high severity; for 80 sites across all 4 pairs).

At each of the 80 sites, we measured tree-canopy cover, tree size by condition (dead or alive), herb and shrub cover, and size and number of fallen logs, and we assessed vegetation burn severity. We established a center for each sampling plot at a tree ≥30 cm diameter at breast height nearest to the random UTM location because we assumed that large trees provided perches for foraging spotted owls. At each center tree, we centered 2 perpendicular transects 25 m long with the direction of the first transect determined by a spin of a handheld compass. We measured canopy cover by taking a spherical densitometer reading every meter for 50 readings. We recorded species and number of all live trees and fire-killed or prefire snags >15 cm diameter at breast height within a variable circular plot using a 20-basal-area-factor prism from the center tree. We measured the diameter of each tallied tree or snag with a Biltmore stick (Forestry Suppliers, Inc., Jackson, MS) or diameter tape. We measured herb and shrub cover by recording the length (cm) of transect intersected by shrub, bare ground, and herbaceous vegetation. We indexed amount of downed wood in each plot by counting the number of segments in each of 3 diameter categories (15–29 cm, 30–59 cm, ≥60 cm) that intersected the transect. Lastly, we assigned burn severity of the stand based on a visual, qualitative estimation of the amount of vegetation burned and the definitions used by the USFS to produce the burn-severity map.

We measured the same microhabitat vegetation characteristics at all 4 nest sites and a sub-sample of 33 roost sites distributed among all 4 owl territories. At these sites, we used the actual nest or roost trees as plot-center.

Data Analyses

To quantify accuracy of burn-severity mapping, we constructed an error matrix (Story and Congalton 1986, Congalton and Green 1993) structured to report user and producer errors for each burn-severity class. We combined accuracy values from each class to determine overall accuracy of the burn-severity map.

We assessed accuracy of telemetry methods by first estimating locations of radiomarked owls while they were stationary at roosts or nests every 7–10 days using telemetry signals and compass bearings and then by subsequently finding the actual locations by following the strongest radio signal until we observed owls visually. We then used distance and direction vectors from estimated to actual observed radio locations to calculate radiotelemetry bias. From the distance–direction vectors, we estimated the long-axes (m) of a 95% Hotelling's confidence ellipse (Batschelet 1981) for each of 5 owls for which we amassed ≥5

distance–direction samples. We used overall mean of the 5 mean values for each owl as a radius of a telemetry-error circle, which we circumscribed around each estimated foraging location. Establishing the telemetry-error circle around each point also allowed us to account for instances where owls foraged at habitat edges (Zabel et al. 1995, Ward et al. 1998). We classified foraging sites that included <90% of the same habitat within an associated telemetry-error circle as an edge site.

We described nesting and roosting habitat according to the burn-severity class that defined the location of the observed nest or roost tree for each individual or pair of owls. We tested for selection of roosting habitat using resource selection ratios ($\hat{w}$), which in this case were ratios between the proportion of roost sites found in a burn-severity class divided by the proportion of that class estimated to be available (Manly et al. 2002). We took the latter proportions from GIS maps of estimated owl foraging ranges. We used Bonferroni-corrected 95% confidence limits to denote selection ($\hat{w} > 1$), use equal to availability ($\hat{w} = 1$), or avoidance ($\hat{w} < 1$) of a burn-severity class. We based this analysis on combined use of all 7 owls in the sample.

We analyzed selection of foraging habitat by California spotted owls by comparing frequency of used and available habitat utilizing logistic regression to estimate a RSPF (Manly et al. 2002). We quantified used habitat with telemetry-estimated foraging locations. We calculated available habitat for each owl from a systematic sample of all telemetry-error circles within its approximated foraging range with centers spaced at twice the error-circle radius.

For the RSPFs, we developed a series of logistic regression models to estimate probabilities that a particular burn severity was used (Manly et al. 2002) using Stata 8.0 (Stata Corporation, College Station, TX). Our model structure identified each individual owl's data as a group of used and available sites with owl treated as a random effect, with distance, burn severity, and other covariates as fixed effects. Thus, we compared each owl's foraging points only with its own available habitat. In addition to owl identity and burn severity, we analyzed other variables believed to affect the owls' selection of foraging habitat. Spotted owls are central-place foragers during the breeding season (Carey and Peeler 1995) so we modeled foraging-habitat selection as a function of distance and distance^2 from the center of the foraging-range circle (Rosenberg and McKelvey 1999, Glenn et al. 2004). Laymon (1988) found that random sites had steeper slopes than foraging sites, so we included percent slope as a variable. Franklin et al. (2000) reported that northern spotted owl survival and reproduction were positively associated with amount of edge in the territory, so we also included an edge effect as a binomial variable indicating that a foraging point telemetry-error circle included <90% of one burn-severity class. Lastly, although Zimmerman et al. (2001) found evidence that members of a California spotted owl pair foraged independently, we included a sex effect to account for possible negative association, sex-specific foraging patterns, or within-territory habitat partitioning. Thus, our global model included effects of owl, burn severity, distance from center of foraging range, this distance^2, edge, and slope. We also included 2-way interactions of owl, burn severity, and distance to investigate whether selection of different burn severities varied independently according to owl and distance.

We established 30 a priori models that included various nested and nonnested subsets of the global model. Our primary focus was to assess the influence of burn severity on foraging site selection. This model set also included sex, slope, and edge effects mainly as possibly confounding parameters to be controlled for, but we did not model these parameters with great complexity. We followed an information-theoretic approach (Burnham and Anderson 2002) using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and assigning AIC_c weights to rank candidate models and formalize evidence that a particular model is supported by the underlying data.

We limited our analysis of structural conditions in burn-severity classes to those variables that previous researchers determined to be key components of spotted owl foraging habitat. California spotted owl foraging locations have been characterized by greater basal area of medium (28 cm) to large trees (>61 cm), high canopy cover, lower basal area of smaller trees (<28 cm), higher snag basal area, gentler slopes, greater conifer basal area, greater shrub cover, and more coarse woody debris than random sites (Gutiérrez et al. 1992). Northern spotted owls (North and Reynolds 1996, McDonald et al. 2006) and California spotted owls (Call et al. 1992, Gutiérrez et al. 1992, Irwin et al. 2007) also selected foraging sites with greater hardwood basal area and multiple canopy layers. Shrub and herbaceous ground cover and downed wood are associated with prey of spotted owls like woodrats (*Neotoma* spp.), northern flying squirrels (*Glaucomys sabrinus*), and white-footed mice (*Peromyscus* spp.; Williams et al. 1992, Block et al. 2005, Innes et al. 2007). Thus, our independent variables included tree-canopy, shrub, and herbaceous cover, coarse woody debris >15 cm diameter, basal areas of various combinations of live and dead conifer and hardwood trees of different size classes, mean and variance of tree diameter at breast height, and percent slope.

Using an information-theoretic approach, we described differences in habitat structure among burn-severity categories with a parsimonious model that best fit the microhabitat data we collected in the field. According to AIC_c and associated weights, we selected a top model from a set of 26 a priori candidate models developed from previous studies on spotted owl foraging habitat and biological knowledge. We modeled the 4 burn-severity categories as a function of multiple continuous or discrete independent variables (microhabitat measurements) with multinomial logistic regression, also known as polytomous logistic regression (North and Reynolds 1996).

RESULTS

We located, captured, and radiomarked 4 male and 3 female California spotted owls on 4 territories between 22 May and 12 June 2006. From 22 May through 15 August 2006, we identified all 4 nest trees and 60 roost sites (range = 4–11

Table 1. California Wildlife Habitat Relationship (CWHR) vegetation type, burn severity, number of spotted owl foraging locations in each burn-severity category, percent of foraging points and 4.1-ha circles in each category, and mean percent of each category that was available within foraging ranges of 7 California spotted owls in the McNally Fire, Sequoia National Forest, California, USA, during the 2006 breeding season. Blank indicates quantities <1%. We excluded 17 locations from vegetation types that comprised <4% of total available habitat.

CWHR vegetation type	Burn severity	Total no. of foraging points in category	% of foraging sites		Average % available in foraging ranges
			Points	Error circles	
Sierran mixed conifer	Unburned	26	9	10	15
	Low	107	35	34	16
	Moderate	69	23	23	14
	High	35	12	12	7
Montane hardwood	Unburned	10	3	3	4
	Low	3	1	2	3
	Moderate	6	2	2	4
	High	1			2
Red fir	Unburned	2	1		5
	Low	1		1	3
	Moderate	0			2
	High	0			1
Montane hardwood–conifer	Unburned	4	1	2	2
	Low	4	1	2	2
	Moderate	7	2	2	2
White fir	Low	7	2	2	2
	Moderate	1			1
	High	1			

roosts/owl) and estimated 301 foraging locations (range = 32–53 locations/owl). Distance from nest or harmonic mean of roost locations to the owl's farthest foraging point during this period ranged from 1,149 m to 3,444 m ($\bar{x}$ = 2,149 m). Areas within owls' foraging ranges that we calculated from these distances ranged from 415 ha to 3,726 ha ($\bar{x}$ = 1,451 ha) for this period.

Overall accuracy of the burn-severity map was 93% correct (n = 80 sites). User's accuracy of the 4 burn-severity classes on this map ranged 75–100% and producer's accuracy ranged 81–100%. We observed 6 misclassifications in the field. Of 20 sites classified as unburned 5 were actually burned at low severity and 1 of 20 sites classified as moderate severity was actually burned at high severity.

Average telemetry error (linear distance between estimated and actual roost locations) among all owls was 82 m (SD = 65.4 m, n = 34 locations among 7 owls). Population mean value of the long-axis of the 95% Hotelling's confidence ellipse from 5 owls with $\geq$5 locations each was 114 m (SE = 60.6 m). We used the 114-m error-radius to calculate a 4.1-ha telemetry-error circle around each estimated owl foraging location and we used 2 times the radius (228 m) to space the systematic sample of circle centers for obtaining available habitat amounts.

All burn-severity classes were utilized by spotted owls for roosting. We classified 17 of 60 roosts on the GIS vegetation burn-severity map as unburned (28%), 34 as burned at low severity (57%), 9 as burned at moderate severity (15%), and none in high severity. Vegetation surveys at a sub-sample of roost sites (n = 33) documented one roost classified on the GIS map as moderate severity that was actually in high-severity burned forest. Selection ratios indicated that forest burned at low severity was selected for roosting (95% CI of $\hat{w}$ = 1.31–2.60), unburned forest (0.36–1.46) was used for roosting in proportion to its availability, and forest burned at moderate severity (0.02–0.97) was avoided for roosting. We recorded only one incidence of roosting in the high-severity burn class. Sampled roost sites averaged tree-canopy cover of 63% (SE = 3.5), similar to unburned forests, a mean tree diameter at breast height of 63 cm (SE = 3.6), and a high basal area of large trees, averaging 30 m^2/ha (SE = 3.2).

Spotted owl pairs in all 4 territories attempted to nest in spring 2006 as determined by behavior and evidence of brood patches on females. Nests in 3 territories were located within the boundaries of the fire, and the nest in one territory was located approximately 500 m outside the fire boundary. We documented one nest tree in unburned mixed conifer–hardwood, one in conifer forest burned at low severity, and 2 in conifer forest burned at moderate severity. One pair, nesting in a stand burned at moderate severity, produced the only fledgling of the 4 nesting attempts. All 4 nest trees were large ($\geq$72 cm) conifers, including one apparently killed by the fire within a moderately burned stand.

Twelve CWHR vegetation types were used by foraging owls, but most (78%) foraging locations were in Sierran Mixed Conifer vegetation, with 12% in Montane Hardwood and Hardwood–Conifer vegetation (Table 1). We assessed 301 foraging sites, an average of 43 (SD = 7.6) sites/owl, and an average of 305 available sites/owl (SD = 195.5) for a total of 2,433 sites. All burn-severity classes were utilized by foraging spotted owls. Proportions of availability for the 4 burn-severity classes were not highly variable among individual owls (CVs were $\leq$29% in all categories, mean CV = 19%).

Our global model with individual owl effects, including owl $\times$ distance, owl $\times$ burn severity, and distance $\times$ burn severity interactions, fit best (AIC_c wt = 1.0; all other models were >13 AIC_c values of the top model). The RSPFs indicated that selection probabilities varied among owls, with all burn-severity classes influencing selection of foraging habitat. A mean RSPF generated by combining RSPFs from individual

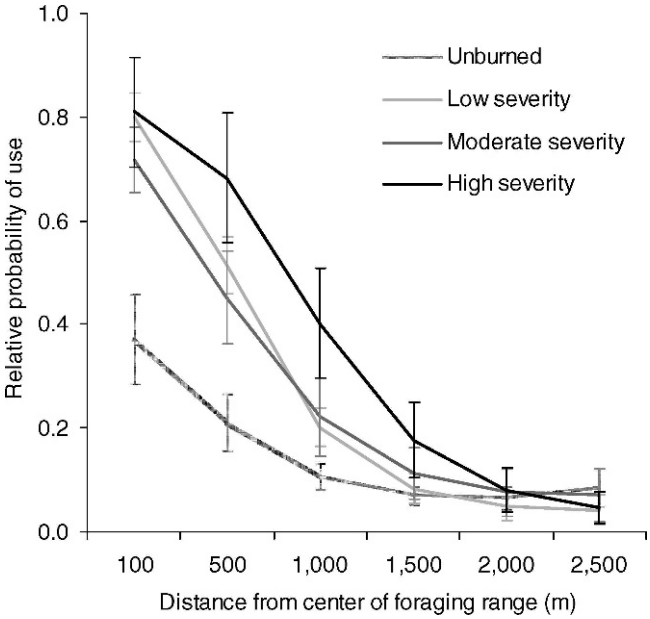

Figure 1. Mean resource selection probability functions (±SE) for 7 California spotted owls foraging at different distances from the center of the owls' breeding foraging range in forest burned at different severities (unburned, low, moderate, and high) in the McNally Fire, Sequoia National Forest, California, USA, 2006. Probabilities generated from coefficients in top-ranked model.

owls includes a curvilinear reduction in probability of use with distance from the center of foraging range that varied with severity of burn (Fig. 1). Probability that any of these 7 owls would use a site for foraging was greatest when the site was burned and was located within approximately 1 km of a nest or roost center (Fig. 1). For 5 of 7 owls, strongest selection for foraging areas was in high-severity burned forest within 1.5 km from the center of their foraging ranges. Although selection of burned forest for foraging was strong, high standard errors indicate selection was variable among owls. Conversely, unburned forest generally had lower probability of use for foraging, although 2 owls showed increased use of unburned forest at locations furthest from the center of their foraging ranges. No discernable difference in use patterns among burn severities was evident beyond 1.5 km. Both steepness of slope and edge affected selection of foraging sites, as they were included in the top model; probability of a foraging site being used was negatively related to steepness of slope and positively related to presence of an edge between burn-severity classes.

The model that best described differences in habitat variables among the 4 burn severities (AIC_c wt = 0.99) included percent tree-canopy cover, percent shrub and sapling cover, percent herbaceous cover, amount of coarse woody debris, basal area of snags, mean tree diameter at breast height, variance of tree diameter at breast height, and percent slope (Table 2). Canopy cover was highest at unburned sites and lowest at high-severity burned sites. Unburned sites were characterized by many pieces of coarse woody debris >15-cm diameter and small live trees 15–27-cm diameter at breast height. Low-severity burned sites had the highest basal area of large live trees with diameter at breast height >53 cm, although this metric was not included in the top-ranked model. Moderate-severity burned sites were characterized by the highest mean diameter at breast height and greatest variance of diameter at breast height of all trees, live and dead. High-severity sites had the highest herb and shrub cover, highest basal area of snags, and steepest slopes (Table 2).

DISCUSSION

The California spotted owls we studied used all severities of burned forest for nesting, roosting, and foraging during the breeding season 4 years after a large forest fire. We detected a negative effect of distance from the center of an owl's foraging range on utilization of habitat for foraging, regardless of burn severity, as expected for central-place foragers. However, we documented one owl traveling >3.4 km from the center of a foraging range, indicating that an owl will travel at least this distance while foraging during the breeding season. After accounting for distance, spotted owls selected burned areas for foraging over unburned forest, with the greatest selection for high-severity burned areas.

Vegetation characteristics of different burn-severity categories provide insight into why these spotted owls might be

Table 2. Conventional measures of spotted owl microhabitat estimated ($\bar{x}$ with SE) from a sample of randomly selected plots in each of 4 burn categories available to 7 California spotted owls for roosting, nesting, or foraging in the McNally Fire, Sequoia National Forest, California, USA, from May to August 2006.

	Burn severity							
	Unburned		Low		Moderate		High	
	n = 15		n = 26		n = 19		n = 20	
Habitat variable	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
% canopy	62.5	4.76	51.4	3.26	27.9	3.64	14.7	2.26
% herb	14.5	4.41	12.6	2.13	17.8	5.11	32.3	5.72
% shrub and sapling	19.5	2.70	11.2	1.99	12.4	2.94	39.8	5.80
No. of pieces coarse woody debris >15 cm	4.3	1.02	1.7	0.41	1.9	0.43	1.8	0.39
Basal area of live trees 15–27 cm (m^2/ha)	11.4	2.83	2.7	0.81	1.9	1.01	0	0
Total snag basal area (m^2/ha)	5.8	2.96	15.0	3.94	13.8	2.65	48.4	5.15
Basal area of live trees and snags >53 cm (m^2/ha)	23.9	5.96	34.3	6.02	24.5	3.05	19.9	4.39
Mean dbh (cm)	53.2	5.04	58.5	3.54	72.5	4.34	54.0	4.17
Variance of dbh (cm)	756.4	199.36	713.6	101.26	1,224.4	208.02	1,033.3	306.30
% slope	14	1	16	2	16	1	24	2

selecting burned forest for foraging and low-severity burned forest for roosting 4 years postfire. Several of the parameters in our best model for distinguishing owl habitat structure among burn-severity classes may be associated with increased abundance or accessibility of prey. Spotted owl prey species, including dusky-footed woodrats (*N. fuscipes*), are more abundant in plant communities with greater understory hardwood, shrub, and herbaceous cover (Carey et al. 1992, Williams 1992, Lee and Tietje 2005, Innes et al. 2007). Understory plants, particularly shrubs and forbs, provide food for woodrats (Williams et al. 1992) and dense shrubs provide excellent cover. Both of these factors may contribute to greater abundance of this key prey species and stimulate attraction by spotted owls to high-severity burned sites after postfire vegetation regrowth has produced a modest understory. In the northern Sierra Nevada, northern flying squirrels and deer mice (*P. maniculatus*) are most abundant in areas with open canopy and high shrub cover (Coppeto et al. 2006). Deer mice have also shown strong affinity to forest openings where conifer seeds may become more accessible or stronger competitors may be limited in number (Gashwiler 1979, Galindo and Krebs 1985).

Another important vegetation difference among burn-severity categories in our study was the greater number of snags in high-severity burned areas relative to other categories. Snags provide shelters for prey species like woodrats and flying squirrels. In the southern Sierra Nevada, dusky-footed woodrat nests are common where shrubs encircle rock outcrops or snags (Lawrence 1966). Bushy-tailed woodrat (*N. cinerea*) densities in dry forests of eastern Washington, USA, were strongly correlated with arboreal and terrestrial cover in the form of large snags, mistletoe, and large soft logs (Lehmkuhl et al. 2006). Northern flying squirrel population densities in Oregon, USA, were correlated with the occurrence of suitable nesting cavities in trees and early decay–stage snags with diameters >50 cm (Volz 1986).

Although we found no reports on the direct effects of fire on common spotted owl prey in Sierran mixed-conifer habitat, we suspect on the basis of habitat requirements that northern flying squirrels may suffer the greatest or take longer to recover than woodrats or forest-dwelling mice (Waters and Zabel 1995). Adult dusky-footed woodrats do not suffer reduction in survival or abundance from understory fire of low to moderate intensity and patchy distribution in oak woodlands (Lee and Tietje 2005), but reductions in survival and abundance can occur immediately after hotter, more complete burns for chaparral-dwelling (Wirtz 1977, Wirtz et al. 1988) and desert-dwelling (Simons 1991) woodrats. However, low-severity burned or unburned patches may serve as refugia from which animals can recolonize areas with a recovering understory like that observed in patches of forest that burned at high severity. In addition, a number of studies have concluded that populations of deer mice increase after fire (Tevis 1956, Gashwiler 1959, Bendell 1974, Ream 1981, Converse et al. 2006). In summary, the most likely explanation for the greater probabilities of use by spotted owls of forest patches burned at high severity was increased presence of prey promulgated by enhanced habitat conditions, which we documented as increased shrub and herbaceous cover, and number of snags. Additional research is needed to determine precise effects of different severities of fire and associated patch sizes on populations of California spotted owl prey, whether increased prey abundance or access ultimately provides an ecologically significant benefit to spotted owls or other predators, and the duration of any such effects.

Spotted owls in our study area selected low-severity burned forest for roost sites, avoided roosting in higher severity burns, and used unburned roost sites in proportion to their availability. Our field-sampled roost sites had an average tree-canopy cover >60% and were dominated by large trees. California spotted owl roost sites in previous studies also were characterized by higher canopy cover and larger diameter trees (Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997). These characteristics may serve such functions as predator avoidance, protection from mobbing, and thermoregulation (Gutiérrez et al. 1992, Franklin et al. 2000).

The range of burn severities used by spotted owls in our study illustrates that a mosaic of burn severities in California spotted owl territories apparently can satisfy owl habitat requirements for ≥ 4 years postfire. Investigations into the influence of spatial characteristics of different burn severities such as patch size and shape on probability of postfire occupancy from a larger sample of spotted owls may provide insight into the reason results from previous studies on impacts of fire on this species were equivocal.

Although RSPFs describe habitat selection, habitat conditions identified by our modeling should not necessarily be considered definitive indicators of population requirements. Longer term studies should be conducted to quantify vital rates of spotted owls in burned versus unburned landscapes over multiple years in conjunction with prey studies and without the confounding effect of postfire salvage-logging. Evaluating long-term impacts of fire on spotted owls will also require a better understanding of postfire habitat change over time and whether those changes will further affect habitat suitability for spotted owls.

MANAGEMENT IMPLICATIONS

California spotted owls whose territories included unburned and burned Sierran mixed-conifer forest of low- to high-severity made use of all burn severities, with high probability of foraging in burned areas, including high severity, within 1.5 km of nests or roosts, and selectively roosted in low-severity burned areas. Accordingly, we implore restraint in assuming all fire has a negative impact on late-seral forest habitat specialists like spotted owls. The assumption that moderate- and high-severity burned forest is not suitable spotted owl habitat has provided a basis for risk assessments of timber harvesting as fuels treatments (e.g., Lee and Irwin 2005) but may be inappropriate in the development of pre- and postfire management prescriptions. Because our sample of California spotted owls in the McNally Fire did not avoid burned areas for nesting, roosting, and foraging, burned forest may have provided some benefits to this species. We

recommend that burned forests within 1.5 km of nests or roosts of California spotted owls not be salvage-logged until long-term effects of fire on spotted owls and their prey are understood more fully.

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