Research Article

Foraging Habitat Selection by California Spotted Owls After Fire

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ABSTRACT Forest fire is one of the most important ecological disturbances affecting habitat of the declining California spotted owl (*Strix occidentalis occidentalis*) population in southern California. We analyzed foraging location data collected 3 and 4 years post-fire, from 8 radio-tagged California spotted owls whose home ranges included forest burned in the 5,176-ha Slide Fire in the San Bernardino Mountains, California, USA. We analyzed foraging habitat selection with sensitivity analysis using 3 different spatial extents to define available resource area: utilization distribution, minimum convex polygon, and capture radius. At all 3 extents of available habitat these spotted owls selected foraging sites close to their territory centers and riparian areas. Resource selection functions indicated burned forests were generally used in proportion to their availability, with the exception of significant selection for moderate-severity burned forests farther from territory centers at the largest available habitat extent (capture radius). Riparian habitats should be preserved for California spotted owls in southern California, and forests burned by high-severity fire should be considered potentially suitable foraging habitat. We suggest researchers perform habitat selection analyses at multiple spatial extents of availability and describe the sensitivity of their results. © 2016 The Wildlife Society.

KEY WORDS foraging habitat selection, forest fire, resource selection function, riparian habitat, sensitivity analysis, spotted owl, *Strix occidentalis*.

The use of radio-telemetry data to quantify space- and resource-use patterns is helpful for management of animal populations, and is especially valuable for conservation of declining species facing natural and anthropogenic habitat disturbances (Sawyer and Brashares 2013). Forest fire is one of the most important ecological disturbances affecting habitat for the California spotted owl (*Strix occidentalis occidentalis*). The California spotted owl is a rare, medium-sized (400–600 g) raptor that uses mid- and late-seral forests for nesting and roosting throughout its range in the Sierra Nevada, southern California mountains, and coastal mountains from the Santa Barbara area north into Monterey County (Gutiérrez et al. 1995). The owl uses a broader range of habitats for foraging (Bond et al. 2009, Williams et al. 2011). The affinity of this subspecies for mature forests has placed it at the center of socioeconomic conflicts over forest management including timber harvest and vegetation management intended to reduce fire risk (Verner et al. 1992). It is uncertain whether or how wildfires influence habitat selection by California spotted owls in the southern part of the subspecies' range.

In southern California, spotted owls occur in upper elevations of forested islands in the Transverse and Peninsular mountain ranges, which are surrounded by extensive chaparral, desert, and semi-desert communities (LaHaye et al. 1994). Wildfire is particularly important in this region because extremely dry and windy weather conditions can result in large forested areas burned at high severity by intense fires (Keeley et al. 2009). High-intensity fires (i.e., stand-replacement or crown fires) cause widespread mortality of existing vegetation. Fire intensity is a measure of energy output, whereas fire or burn severity refers to aboveground effects to vegetation (Keeley 2009). High-intensity fires change forest structure from one dominated by live trees to one dominated by herbs, shrubs, and standing dead trees, or snags (DellaSala et al. 2014). Fires in southern California's mountains create heterogeneous landscapes composed of a mosaic of intermixed patches of unburned to severely burned forest, known as a mixed-severity regime (Weatherspoon et al. 1992, Minnich et al. 2000). This fire mosaic likely enables wildlife species dependent upon late-seral forests, such as the spotted owl, to co-exist with intense fires (Lee et al. 2012, Baker 2014). Indeed, intense fire may enhance foraging opportunities for California spotted owls when it occurs close to nest or core roost stands (Bond et al. 2009). However, intense fire can result in loss of closed-canopy forests that owls select for nesting and roosting (Bond

et al. 2009) and exceptionally large areas burned by intense fire during extreme weather conditions may trigger territory abandonment at lower quality owl sites (Lee and Bond 2015). Wildfires over the past 2 decades have affected California spotted owl habitat to a greater extent in southern California than elsewhere in the range of the subspecies (Lee et al. 2013). However, no studies have yet examined post-fire selection of foraging habitat in this part of the subspecies' range, where the regional population is in decline.

Resource-selection studies quantify specific factors that increase or decrease the probability that an animal will use a particular resource, for example, a late-seral or severely burned forest stand (Rota et al. 2013). A habitat feature is considered to be selected if it is used disproportionately more than it is available (Johnson 1980, Beyer et al. 2010), and a variety of statistical methods can quantify which specific habitat features are preferred or avoided relative to other types (Rettie and McLoughlin 1999, Aarts et al. 2013). However, results of resource-selection analyses may vary depending upon the spatial extent used to define available resources, and studies should examine the sensitivity of selection results to variable definitions of availability (Beyer et al. 2010, Northrup et al. 2013).

In October 2007, a series of wildfires burned across southern California, USA, ultimately affecting >202,343 ha extending from Santa Barbara County to the border of Mexico. The Slide Fire in the San Bernardino Mountains burned 5,176 ha, including 4,591 ha of tree-dominated vegetation types potentially suitable for California spotted owls. We analyzed foraging location data collected in 2010 and 2011 from 8 radio-tagged California spotted owls captured within or near the perimeter of the Slide Fire. Our objective was to assess factors influencing foraging habitat selection at 3 different spatial extents of availability in burned or partially burned territories: utilization distribution (UD), minimum convex polygon (MCP), and capture radius (CR).

STUDY AREA

We used data from radio-tagged owls within and near the 2007 Slide Fire on the Mountaintop Ranger District of the San Bernardino Mountains. These mountains rise above the surrounding lowlands approximately 140–150 km east of Los Angeles, California, USA (Stephenson and Calcarone 1999). Climate of the study area was Mediterranean with most precipitation falling during the winter as rain at lower elevations and rain and snow at higher elevations. Average annual precipitation in these mountains ranged from 500 mm to 1,000 mm with substantial local variability due to aspect, elevation, topography, rain-shadow patterns, and seasonal storm patterns (Minnich 1988).

Elevation ranged approximately 1,121–2,525 m. Vegetation was montane coniferous forest in more xeric settings, dominated by Jeffrey pine (*Pinus jeffreyi*) or ponderosa pine (*P. ponderosa*), with California black oak (*Q. kelloggii*) a common understory tree, or mixed-conifer forests in more mesic settings, including combinations of Jeffrey and ponderosa pines, white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*P. lambertiana*; Stephenson and Calcarone 1999). The study area was a mix of public lands managed by the United States Forest Service (USFS) and small communities on private inholdings. The forests historically were subjected to commercial timber harvesting, but current management emphasizes public recreation, habitat protection, and fuels reduction around the communities.

We used Monitoring Trends in Burn Severity (MTBS) vegetation burn-severity geographic information system (GIS) data from the United States Geological Survey and USFS (www.mtbs.gov, accessed 15 Jul 2013) in conjunction with USFS Existing Vegetation (EVEG) maps created in 2002 and 2003 to characterize the study area. The MTBS vegetation burn-severity data were created with pre- and post-fire Landsat 5 Thematic Mapper satellite imagery from 6 July 2006 and 9 June 2008. These images were used to create a differenced Normalized Burn Ratio (dNBR) map with a 30-m pixel size that was then categorized into burn categories. For tree-based fire severity variables, percentage change in canopy cover and basal area was 0–25% in the low-severity and unburned category, 25–75% in the moderate-severity category, and >75% in the high-severity category (Miller et al. 2009). We estimated that 21.8% of tree-dominated vegetation types (i.e., forest types) remained unburned in the Slide Fire, whereas 19.3%, 30.8%, and 28.1% burned at low, moderate, and high severities, respectively (Fig. 1).

METHODS

Field Methods

Prior to our study, all California spotted owl breeding territories within the boundaries of the San Bernardino National Forest had been located by annually surveying all forested stands beginning in 1989 (LaHaye et al. 2004, Lee et al. 2013). Selection of owls for this study was based on their proximity to the Slide Fire. Contracting biologists for the USFS captured and radio-tracked spotted owls occupying all known territories with historical nest trees within or closely adjacent to the fire perimeter. Biologists located, captured, and classified sex of owls using standard techniques (Forsman 1983, Franklin et al. 1996) and fitted each owl with a Holohil RI-2CP backpack transmitter (Holohil Systems, Ltd., Ontario, Canada) using Kevlar ribbon (0.63 cm wide; Bally Ribbon Mills, Bally, PA). Transmitters with the harness weighed <16 g, or less than 3% of the owl's total weight. Animal care and use procedures were part of a study plan approved by the USFS and the California Department of Fish and Wildlife.

Biologists estimated owl locations by triangulating on signals from the affixed radio transmitters (Guetterman et al. 1991). An extensive road system in the area enabled trackers to acquire most signals <400 m from owls. After the conclusion of the study in December 2011, all remaining radio-tagged owls were recaptured to remove transmitters (R. Tanner, Tanner Environmental, personal communication). We considered individual owls as sampling units and
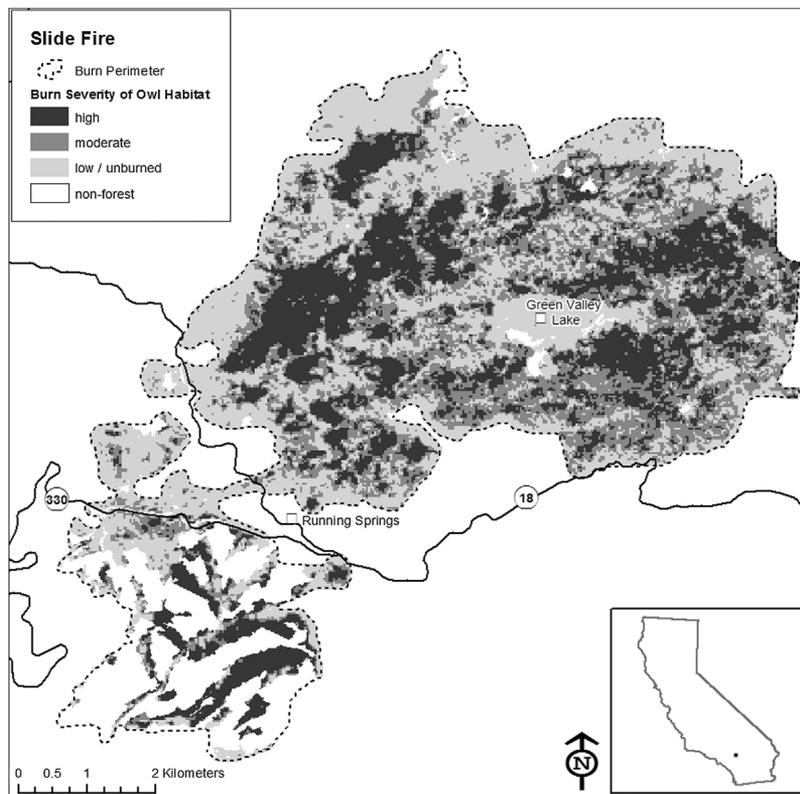
Figure 1. Burn severity of hardwood, conifer, and mixed-forest types in California spotted owl habitat from the 2007 Slide Fire, San Bernardino Mountains, southern California, USA.

modeled males and females of a pair separately because their foraging was most likely independent (Forsman et al. 1984, Zimmerman et al. 2001, Irwin et al. 2007, Bond et al. 2009). During the breeding season (1 Mar–31 Aug) radio-trackers attempted to obtain a foraging location for each radio-tagged owl between sunset and sunrise 1–2 nights per week with >48 hours between attempts, to provide a reasonably large sample of temporally independent locations (Guetterman et al. 1991). Sampling was less intensive during the non-breeding season (1 Sep–28 Feb) because of weather conditions. Trackers attempted to collect locations for each owl at different times throughout the night to attain a range of sampling times. Owls were tracked from 1 month to 29 months, with variation in tracking effort resulting from 1) death of owl; 2) radio-tagged owl could not be located; or 3) transmitter unit stopped working and could not be replaced.

Used and Available Habitat

The USFS provided us with data on receiver station locations, bearings to radio-tagged owls, date and time, and signal strength and gain. We considered all locations obtained between sunset and sunrise to be foraging locations (Forsman et al. 1984). We used the maximum likelihood estimator in LOAS software (Version 4.0, Ecological Software Solutions, Sacramento, CA) to generate estimated spotted owl foraging locations and calculate error ellipses from receiver stations and bearings. We used only triangulated locations that generated error ellipses <5.0 ha (Williams et al. 2011). We assessed linear

telemetry location error by having trackers triangulate on a roosting owl to obtain an estimated location and then walk in to confirm actual location, and by conducting blind tests (i.e., placing transmitters in locations unknown to trackers) within several owl territories. Most of the points with error ellipses >5.0 ha generally overlapped with the points we included in our analysis, thus we were confident our data did not contain systematic spatial bias from telemetry error.

We defined the available foraging habitat sample for each radio-tagged owl at 3 different spatial extents each year: 1) a UD defined as the year-round 95% fixed-kernel home-range (Silverman 1986; McDonald et al. 2006; Irwin et al. 2007, 2012; Williams et al. 2011); 2) year-round 100% MCP (Mohr 1947, Carey et al. 1992); and 3) 100% CR, a circle with a radius that extended from the nest or territory center to the farthest documented foraging location for that owl in that year (Glenn et al. 2004, Bond et al. 2009). The UD is the most conservative representation of the availability sample and may underestimate the area of true availability because it omits even some areas known to be used. In contrast, the CR represents all habitats presumed to be accessible but may include areas with constrained availability because of the presence of conspecifics, predators, inhospitable terrain, or other factors (Buskirk and Millspaugh 2006). The MCP is an intermediate representation of the availability sample between the UD and the CR.

To calculate UDs, we used 95% isopleths of the fixed-kernel density and applied least squares cross validation (Worton 1989) to select the kernel bandwidth. Fixed kernels

are less biased than adaptive kernels at outer contour levels and have better surface overlap when compared to the true distribution (Seaman et al. 1999). We applied a bootstrap procedure to determine whether sufficient numbers of points were collected for unbiased estimation of the UD home-range size (Worton 1995, Bond et al. 2013, Tingley et al. 2014; Supplemental Materials S1 and Fig. S1, available at www.onlinelibrary.wiley.com).

Average telemetry error distance (i.e., linear distance between estimated and actual transmitter locations), calculated from 5 walk-ins on roosting owls and 22 blind tests, was 80 m (SD = 58, $n = 27$ locations). To account for location estimation error, we quantified used habitat with 80-m-radius (2.01 ha) telemetry-error circle buffers surrounding estimated foraging locations (i.e., used plots rather than used points; Rettie and McLoughlin 1999, Frair et al. 2010). We quantified available habitat from a systematic sample of all non-overlapping 2.01-ha telemetry-error circles (available plots) that fit within each owl's UD, MCP, or CR.

Covariates

We created a GIS database for the study area consisting of 5 categories: non-forest (e.g., water, meadow, shrub, rock, urban), low severity burned or unburned forest, moderately burned forest, highly burned forest, and post-fire logged forest. We obtained layers from MTBS (burn severity), EVEG (forest or non-forest), and Google Earth (Mountain View, CA) aerial imagery (human infrastructure [non-forest], post-fire logging) maps. We combined forest-type polygons burned by low-severity fire with unburned polygons because low-severity fire has little effect on key spotted owl habitat elements such as density of large trees and snags, downed logs, and canopy cover (Bond et al. 2009) and because it is difficult to distinguish low-burned from unburned forest using remote-sensed data. Additional covariates were slope, elevation, aspect, and riparian areas (streams).

To designate the vegetation composition at each foraging or available location, we calculated proportion of forest burned at high, moderate, or low or unburned severity within each 2.01-ha used or available plot. Using proportion of each burn-severity category within a plot rather than a point location estimate for habitat-selection analysis explicitly acknowledges and accounts for the inherent error and potential bias in radio-telemetry (Rettie and McLoughlin 1999, Frair et al. 2010). Thus, we modified the representation of habitat use at each location from a binary data set (the use of each burn-severity category is either 1 or 0) to a set of continuous burn-severity variables that sum to 1 (a composition). This methodology results in a more conservative habitat-selection analysis, with a diminished ability to detect selection, but one that is less biased (Rettie and McLoughlin 1999, Frair et al. 2010). This methodology also allowed us to identify instances where owls foraged at edges between different forest burn severities (Bond et al. 2009). We classified foraging sites without a dominant (>90%) burn category as an edge site (Bond et al. 2009). For all other covariates, we made measurements at the used point or center point of the available plot.

For robust resource-selection analyses, a sufficient amount of the resource of interest must be available for selection or avoidance by individuals (Northrup et al. 2013). Our primary foraging habitat selection covariate of interest for our sample of spotted owls was forest burn severity. We quantified amount of the 3 forest burn-severity categories within each of 42 spotted owl available habitat areas (3 available habitat extents × 7 owls/year × 2 years; Table 1). We found that 13 of the 42 available habitat areas (5 in 2010 and 8 in 2011) included <5% forest burned at high severity (Table 1), which we considered to be insufficient for reasonably unbiased selection analyses. We censored data from these 13 available habitat areas.

We considered 9 covariates for analysis: distance from territory center (km), distance from stream (km), aspect (west = 1 north, south, or east = 0), elevation (standardized to units from the mean), slope (%), high-severity burn (proportion in plot), moderate-severity burn (proportion in plot), low-severity or unburned (proportion in plot), and edge (defined above). Spotted owls are central-place foragers, so we expected the probability of use to be negatively correlated with distance from the nest or territory center, in either a linear or a quadratic manner (Carey and Peeler 1995, Rosenberg and McKelvey 1999, Bond et al. 2009). During the non-breeding season, relative use of the territory center may decline in California spotted owls (Irwin et al. 2007), so we tested whether foraging habitat selection as a function of distance from the center of the foraging range differed between breeding and non-breeding seasons by examining a model with a seasonal effect. We found no significant seasonal effect, so we analyzed all foraging data together within a year-round range to maximize our used sample size. Laymon (1988) reported that random sites had steeper slopes

Table 1. Hectares of coniferous and mixed conifer-hardwood forest, and proportion of high-severity burned forest in 3 extents of available habitat areas (95% fixed-kernel home range [UD], 100% minimum convex polygon [MCP], and 100% capture radius [CR]) for 8 California spotted owls during 2010 and 2011 in the area of the 2007 Slide Fire, San Bernardino National Forest, California, USA. We excluded available habitat areas with <5% high-severity burned forest from selection analysis. Owls with the same alpha code are paired.

Year	Owl	Forested area (ha)			Proportion high severity		
		UD	MCP	CR	UD	MCP	CR
2010	DC441	266	532	1,398	0.08	0.04	0.14
	DC521	211	782	6,839	0.07	0.12	0.12
	GVLR341	378	931	2,441	0.11	0.21	0.22
	GVLR360	398	1,403	8,749	0.12	0.17	0.16
	LEFCC482	25	148	585	0.04	0.02	0.01
	SC238	134	196	2,055	0.13	0.44	0.18
	SC321	211	262	2,419	0.12	0.02	0.17
2011	DC441	150	124	556	0.03	0.05	0.01
	DC521	240	1,088	10,914	0.06	0.23	0.12
	GVLR341	204	363	3,143	0.10	0.19	0.18
	GVLR360	92	116	384	0.03	0.08	0.12
	SC238	158	96	284	0.03	0.01	0.28
	SC321	103	87	335	0.03	0.02	0.28
	CC282	522	851	3,765	0.28	0.43	0.19
	$\bar{x}$	221	499	3,133	0.09	0.15	0.16

than foraging sites in the central Sierra Nevada, so we included percent slope as a variable. California spotted owls in the northern Sierra Nevada selected foraging sites at lower elevations and closer to streams (Irwin et al. 2007); thus, we incorporated distance to riparian vegetation and elevation. Preliminary examination of our data using kernel density plots (Kabacoff 2011) suggested a possible quadratic relationship with distance to riparian, so we also included distance to riparian^2. Finally we postulated owls would avoid foraging sites with western-facing aspects because these areas are more arid than other aspects. California spotted owls could be more likely to select foraging sites with forest that burned at moderate and high severity (Bond et al. 2009), or at sites with low-severity burns or unburned forest (Zabel et al. 1992, Irwin et al. 2007). Previous research reported selection (Zabel et al. 1995, Ward et al. 1998, Williams et al. 2011) or avoidance (Glenn et al. 2004) of edges. We were unable to test for avoidance of post-fire logged or non-forested areas because available habitat areas contained too little of these categories (i.e., <5%).

Foraging Habitat Selection Analysis

Our main objective was to estimate foraging habitat selection in burned or partially burned territories by identifying preferred or avoided vegetation types within the available foraging range (Johnson et al. 2006). We analyzed selection of foraging habitat by comparing used and available resources with mixed-effects logistic regression to estimate a resource selection function (RSF) in a type III study design (Manly et al. 2002:7). Logistic regression is a relatively simple method for enabling inferences about selection or avoidance of covariates (Johnson et al. 2006, Aarts et al. 2013, Northrup et al. 2013). Following the 2-sample, Type III logistic-regression procedure outlined by Manly et al. (2002:99), we obtained a sample of used resource units and generated a separate sample of available resource units for each owl in each year in each spatial extent (UD, MCP, or CR).

We performed all mixed-effects logistic regression analyses in Program R (R Development Core Team 2013) using the glmer (family = binomial, link = logit) form in the package lme4 (Bates et al. 2012). We used mixed-effects models as an approximating function to obtain estimates of coefficients for variables to include in exponential RSF models for each available habitat area using the formula:

$$w(x_i) = \exp(\beta_1 x_1 + \ldots + \beta_i x_i) \tag{1}$$

where $w(x_i)$ is the relative probability of selection given the predictor variables, $x_1 \ldots x_i$, and $\beta_1 \ldots \beta_i$ are the coefficients to be estimated (McDonald et al. 2006, Irwin et al. 2012). We then calculated selection ratios (selection ratio = exp [coefficient]) from the coefficients in the top models, or average of competitive top models, for interpretation. Selection ratios measure the multiplicative change in relative probability of use when the covariate changed by 1 unit, assuming all other variables remain constant (McDonald et al. 2006). We computed confidence intervals for the selection ratios as exp(coefficient + 1.96[coefficient SE]).

Our model structure identified each individual owl's data as a group of used and available sites with individual owl ($n = 8$) treated as a random effect, and the vegetation and physiographic covariates as fixed effects. We compared each owl's foraging points only with its own availability sample each year by also treating year as a random effect. We found no evidence that habitat conditions changed significantly within each year (e.g., no major timber harvest or urban development).

We followed an information-theoretic approach (Burnham and Anderson 2002) using Akaike's Information Criterion (AIC) and assigning AIC weights to rank candidate models and formalize evidence that a particular model was supported by the underlying data, and to evaluate the strength of evidence for each model considered. We examined correlation matrices of fixed effects and used only variables in the same models that were not highly correlated (i.e., $|r| > 0.5$). We considered models with ΔAIC < 2 to be competitive, and we examined the degree to which 95% confidence intervals of beta coefficients overlapped 0 and selection ratios overlapped 1 to determine the direction and precision of evidence for covariate effects. We calculated model-averaged beta estimates by averaging from all weighted models and assuming $\beta = 0$ for models in which a predictor variable did not appear (Burnham and Anderson 2002).

We conducted model selection independently for each of the 3 spatial extents of available habitat. In each case, we began with the global model that included random effects of owl and year and fixed effects of distance from territory center, distance from territory center^2, 3 terms for females having different distance from center curves than males (female, female × distance from territory center, female × distance from territory center^2), distance to riparian, distance to riparian^2, elevation, slope, west aspect, high-severity burned forest, moderate-severity burned forest, low-severity burned and unburned forest, interactions of each burn severity and distance to territory center, and edge. We simplified the global model by removing all physiographic and sex variables with non-significant coefficients ($P > 0.05$) and ranked 2 additional candidate models that included various combinations of burn severities and distance, as well as the null model. Our final list of models included 1) the global model; 2) a model with all significant physiographic and sex variables and edge, all 3 burn severities, and burn severities × distance to center interactions; 3) a model with all significant physiographic and sex variables and edge, and all 3 burn severities, but without any burn severity × distance to center interactions; 4) a model with all significant physiographic and sex variables and edge; but without any burn severities or their interactions with distance; and 5) the null model, with only owl and year. We determined that coefficient estimates from the 3 logistic regressions of available habitat spatial extents converged with significance if they had the same sign, standard errors that excluded 0, and overlapping standard errors (Northrup et al. 2013).

RESULTS

United States Forest Service contracting biologists located, captured, and radio-tagged 11 California spotted owls (6 M

Table 2. Model selection results from censored data for describing probability of use by 8 foraging California spotted owls during 2010–2011 in the area of the Slide Fire of 2007, San Bernardino National Forest, California, USA, based on maximum likelihood estimation. Results are from separate analyses using 3 spatial extents to define available habitat area, and censored to exclude available habitat areas with <5% high-severity fire. We considered models with difference in Akaike's Information Criterion (ΔAIC < 2.0) to be competing.

Model name[a]	Model structure[b]	ΔAIC	Weight	K[c]
Utilization distribution				
Sigphys+burn	$DC + DC^2 + EL + DR + DR^2 + HI + MOD + LO$	0.0	0.44	11
Sigphys+noburn	$DC + DC^2 + EL + DR + DR^2$	0.2	0.40	8
Sigphys+burn+burn×dc	$DC + DC^2 + EL + DR + DR^2 + HI + MOD + LO + HI × DC + MOD × DC + LO × DC$	2.2	0.15	14
Global	$DC + DC^2 + FEM + FEM × DC + FEM × DC^2 + SLO + EL + ASPW + DR + DR^2 + HI + MOD + LO + HI × DC + MOD × DC + LO × DC + EDGE$	7.0	0.01	20
Null		117.6	0.00	3
Minimum convex polygon				
Sigphys+burn	$DC + DC^2 + FEM + FEM × DC + FEM × DC^2 + DR + DR^2 + HI + MOD + LO$	0.0	0.89	13
Sigphys+burn+burn×dc	$DC + DC^2 + FEM + FEM × DC + FEM × DC^2 + DR + DR^2 + HI + MOD + LO + HI × DC + MOD × DC + LO × DC$	4.3	0.10	16
Global	$DC + DC^2 + FEM + FEM × DC + FEM × DC^2 + SLO + EL + ASPW + DR + DR^2 + HI + MOD + LO + HI × DC + MOD × DC + LO × DC + EDGE$	8.7	0.01	20
Sigphys+noburn	$DC + DC^2 + FEM + FEM × DC + FEM × DC^2 + DR + DR^2$	45.8	0.00	10
Null		507.6	0.00	3
Capture radius				
Sigphys+burn+burn×dc	$DC + DC^2 + FEM + FEM×DC + FEM×DC^2 + EL + ASPW + DR + DR^2 + HI + MOD + LO + HI×DC + MOD×DC + LO×DC + EDGE$	0.0	0.40	19
Global	$DC + DC^2 + FEM + FEM×DC + FEM×DC^2 + SLO + EL + ASPW + DR + DR^2 + HI + MOD + LO + HI×DC + MOD×DC + LO×DC + EDGE$	1.0	0.38	20
Sigphys+burn	$DC + DC^2 + FEM + FEM×DC + FEM×DC^2 + EL + ASPW + DR + DR^2 + HI + MOD + LO$	14.0	0.20	15
Sigphys+noburn	$DC + DC^2 + FEM + FEM×DC + FEM×DC^2 + EL + ASPW + DR + DR^2$	63.5	0.02	12
Null		1,898.2	0.00	3

[a] Sigphys = all significant physiographic effects, burn = burn severity effects, noburn = no burn severity effects, dc = distance from territory center effect.

[b] All models include random terms for individual owl and year. DC = distance from territory center, DC^2 = distance from territory center[2], FEM = female, SLO = slope, EL = elevation, ASPW = western aspect, DR = distance to riparian, DR^2 = distance to riparian[2], HI = proportion high-severity burned forest, LO = proportion low-severity burned and unburned forest, MOD = proportion moderate-severity burned forest, EDGE = edge (sites without a dominant [>90%] burn category).

[c] K = number of parameters in the model.
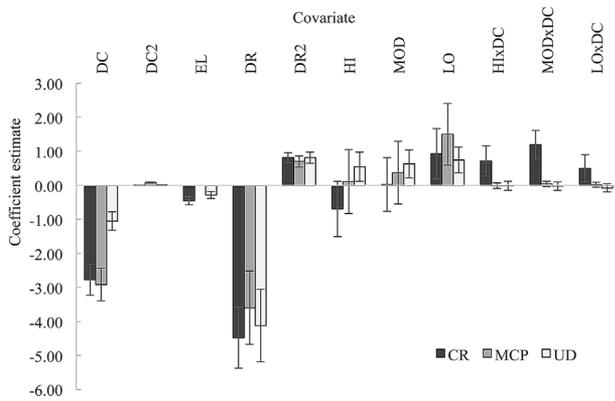
Figure 2. Model-averaged coefficient estimates and standard errors for 11 covariates of foraging habitat selection from 8 radio-tagged California spotted owls, 2010–2011, in the area of the 2007 Slide Fire, San Bernardino Mountains, southern California, USA using 3 available habitat extents: circle radius (CR), minimum convex polygon (MCP), and fixed-kernel utilization distribution (UD). DC = distance from territory center, DC2 = distance from territory center^2, EL = elevation, DR = distance to riparian, DR2 = distance to riparian^2, HI = proportion high-severity burned forest, MOD = proportion moderate-severity burned forest, LO = proportion low-severity burned and unburned forest, HI×DC, MOD×DC, and LO×DC = interactions of each burn severity and distance to territory center.

and 5 F) from 7 territories between June and September 2009. We excluded all data from 2009, and used data only from 2010 and 2011 in our analysis. This was to allow trackers sufficient time to learn the study area and become proficient in radio-tracking, and because the 2009 data did not incorporate that year's entire breeding season. We obtained a sufficient sample of locations for 8 owls (5 M and 3 F) from 5 territories to include in habitat-selection analysis. Seven owls were tracked for 2 years, but 1 male shifted territories mid-breeding season, so we excluded his data for that year. Another male was tracked for 1 year only. We obtained 765 independent foraging locations for all owls, with 464 locations in 2010 and 301 in 2011 (average/owl/year = 58 in 2010 and 43 in 2011, range: 35–76/owl/year).

Foraging Habitat Selection

Histograms of proportion of different burn severities within the available habitat plots showed the majority of plots with the low-severity and unburned condition were either 0 or 1 and the majority of plots with moderate and high severity were 0, but all other proportions were uniformly distributed at all 3 spatial extents (Fig. S2, available online in Supporting Information). There were no plots with a proportion >0.85 moderate severity.

We considered the number of parameters in our models to be adequate (i.e., models were not over-fitted) because standard errors were estimable and reasonable. Results for post-fire selection of foraging habitat indicated slightly different models best described selection in each of the spatial extents (Table 2). Coefficient estimates for variables describing foraging location selection from the 3 extents (Fig. 2) revealed some areas of agreement (convergence of coefficient estimates), and some areas of disagreement (non-convergence of coefficient estimates) based on our definition

of convergence. At all spatial extents, coefficients converged and indicated significant selection for locations close to riparian vegetation (Table 3; Fig. 2). At the MCP and CR spatial extents, coefficient estimates converged and indicated significant selection for foraging locations that were close to the nest or home range centroid (Table 3, Fig. 2). For the UD, the sign of the coefficient for distance from center was the same as the MCP and CR, but standard errors did not overlap. Coefficient estimates for most variables related to forest burn severity varied among spatial extents, did not converge, and were not significant, with the exception of proportion of moderate-severity × distance from center in the CR analysis (Table 3, Fig. 2).

When we used UD as the available habitat, the top-ranked and second-ranked models had nearly the same weight (0.44 and 0.40; Table 2), and differed only in the presence or absence of forest burn-severity covariates, indicating forest burn severities were not significant effects. Confidence intervals of selection ratios for high and moderate burn severity included 1 (Table 3), meaning they were used in proportion to their availability. The lower confidence interval of the selection ratio for unburned or low severity forest was slightly above 1, suggesting possible selection for this condition at this spatial extent, but none of the model-averaged beta estimates for any of the forest burn-severity effects were statistically significant (Table 3).

The top model using MCP as the available habitat carried a majority of the weight (0.89) and was far superior to the second-ranked model (Table 2). This model included forest burn-severity effects, but the confidence intervals of selection ratios for burn-severity effects included 1 (Table 3), which meant all burn severities were used in proportion to their availability.

When we used CR as the available habitat, 2 competing top models with similar weights (0.40 and 0.38; Table 2) both included effects of forest burn severity and interactions between burn severity and distance from center. Confidence intervals of selection ratios for forest burn-severity effects indicated most burn severities were used in proportion to their availability, but owls positively selected moderately burned forest farther from the center (Table 3).

Foraging locations were negatively correlated with elevation in the smallest (UD) and largest extents (CR) of available habitat (Table 3). Moreover, females foraged at different distances from the center than males in the 2 largest extents (MCP and CR) of available habitat (Table 3). Using model-averaged parameter estimates and standard errors from top and competing models, we estimated final RSFs for the 3 available habitat extents. All RSFs included significant variables for distance from center (DC) and distance to riparian (DR), but only the RSF for the CR included any significant variables for burn severity (moderate [MOD]). We estimated RSFs for each habitat area as:

UD $w(x) = \exp(-1.048(DC) + 0.015(DC^2) - 0.286$ (elevation) $- 4.120(DR) + 0.813(DR^2))$,

MCP $w(x) = \exp(0.108(female) + 0.009(female \times DC) - 0.039(female \times DC^2) - 2.911(DC) + 0.086(DC^2) - 3.594(DR) + 0.701(DR^2))$, and

$$\begin{aligned} \text{CR } w(x) = \exp(&0.503(\text{female}) - 1.605(\text{female} \times \text{DC}) \\ &+ 0.044(\text{female} \times \text{DC}^2) - 2.771(\text{DC}) + 0.004(\text{DC}^2) \\ &- 0.449(\text{elevation}) - 4.474(\text{DR}) + 0.815(\text{DR}^2) + 0.027 \\ &(\text{MOD}) + 1.194(\text{MOD} \times \text{DC})). \end{aligned}$$

DISCUSSION

For millennia, wildfire in southern California has been a primary natural disturbance shaping forests inhabited by California spotted owls (Minnich et al. 2000). From 2003 to 2007, spotted owl territories in the region were especially affected by wildfire, with >40% of 168 breeding sites monitored by USFS biologists in the San Bernardino and San Jacinto mountains experiencing ≥1 fire (Lee et al. 2013). Despite the strong influence of fire in the region's forests and concern over the conservation status of the subspecies (LaHaye et al. 2004), we are unaware of any previous study to describe foraging habitat selection by radio-tagged spotted owls in southern California.

Table 3. Model-averaged beta estimates, standard errors, P-values, and selection ratios for models describing probability of use by 8 foraging California spotted owls during 2010–2011 in the area of the Slide Fire of 2007, San Bernardino National Forest, California, USA, based on maximum likelihood estimation. Results are from a censored dataset excluding owls with <5% high-severity fire in their available habitat areas. Asterisks are significant explanatory variables ($P < 0.05$). We investigated foraging habitat selection for 3 spatial extents of available habitat: utilization distribution, minimum convex polygon, and capture radius.

Covariate[a]	Estimate	SE	P	Selection ratio	95% selection ratio CI Lower	95% selection ratio CI Upper
Utilization distribution						
(Intercept)	−0.486	0.516				
DC*	−1.048	0.269	0.020	0.351	0.207	0.594
DC²*	0.015	0.004	0.017	1.015	1.008	1.023
Elevation*	−0.286	0.103	0.036	0.751	0.614	0.919
DR*	−4.120	1.067	0.020	0.016	0.002	0.131
DR²*	0.813	0.166	0.013	2.255	1.629	3.123
HI	0.547	0.430	0.122	1.727	0.743	4.014
MOD	0.631	0.412	0.095	1.879	0.838	4.215
LO	0.745	0.377	0.065	2.106	1.006	4.409
HI×DC	−0.014	0.131	0.315	0.986	0.763	1.274
MOD×DC	−0.023	0.125	0.308	0.977	0.765	1.249
LO×DC	−0.074	0.119	0.230	0.929	0.735	1.174
Minimum convex polygon						
(Intercept)	−0.495	0.943				
Female	0.108	0.309	0.284	1.114	0.608	2.039
Female×DC	0.009	0.503	0.318	1.009	0.376	2.706
Female×DC²*	−0.039	0.016	0.049	0.962	0.932	0.994
DC*	−2.911	0.484	0.009	0.054	0.021	0.140
DC²*	0.086	0.016	0.010	1.090	1.057	1.124
DR*	−3.594	1.077	0.026	0.027	0.003	0.227
DR²*	0.701	0.168	0.017	2.017	1.452	2.800
HI	0.111	0.939	0.314	1.117	0.178	7.034
MOD	0.373	0.922	0.274	1.452	0.238	8.848
LO	1.497	0.904	0.085	4.467	0.760	26.252
HI×DC	−0.010	0.079	0.313	0.990	0.848	1.156
MOD×DC	0.041	0.076	0.246	1.042	0.897	1.211
LO×DC	0.017	0.074	0.302	1.017	0.880	1.175
Capture radius						
(Intercept)	−0.044	0.760				
Female	0.503	0.254	0.065	1.653	1.005	2.720
Female×DC*	−1.605	0.306	0.011	0.201	0.110	0.366
Female×DC²*	0.044	0.008	0.010	1.045	1.029	1.061
DC*	−2.771	0.457	0.008	0.063	0.026	0.153
DC²	0.004	0.005	0.185	1.004	0.994	1.014
Elevation*	−0.449	0.119	0.021	0.638	0.505	0.806
Slope	0.003	0.002	0.094	1.003	0.999	1.008
Aspect	−0.234	0.126	0.072	0.791	0.618	1.014
DR*	−4.474	0.895	0.012	0.011	0.002	0.066
DR²*	0.815	0.144	0.010	2.258	1.705	2.992
HI	−0.693	0.812	0.184	0.500	0.102	2.458
MOD	0.027	0.789	0.318	1.027	0.219	4.819
LO	0.927	0.735	0.123	2.527	0.598	10.682
HI×DC	0.718	0.444	0.088	2.051	0.859	4.896
MOD×DC*	1.194	0.419	0.035	3.299	1.452	7.496
LO×DC	0.499	0.404	0.126	1.647	0.746	3.638
Edge	−0.250	0.122	0.061	0.779	0.613	0.989

[a] DC = distance from territory center, DR = distance to riparian, HI = proportion high-severity burned forest, MOD = proportion moderate-severity burned forest, LO = proportion low-severity burned and unburned forest.

We found at all extents of available habitat, these spotted owls strongly selected foraging sites close to their territory center, and close to riparian areas. Resource selection functions suggested forest burn severity was not significantly associated with probability of use, meaning burned forests were generally used in proportion to availability, with the exception of selection for moderate-severity burned forests farther from the territory center at the largest available habitat extent (CR).

Foraging Habitat Selection

The influence of distance from territory center was expected because spotted owls are central-place foragers (Rosenberg and McKelvey 1999; Glenn et al. 2004; Irwin et al. 2007, 2012; Bond et al. 2009). Results from studies of foraging spotted owls that do not include this effect should be interpreted with caution.

Our results suggest that riparian habitats are especially important to spotted owls in southern California. Riparian habitats also were significant foraging areas for California spotted owls (Irwin et al. 2007) and northern spotted owls (Irwin et al. 2012) in long-unburned forests in more northerly regions. Woodrats (*Neotoma* spp.) often are associated with streamside forests; mean woodrat densities in the San Gabriel Mountains of southern California were highest in riparian-hardwood communities (Horton and Wright 1944), and streamside forests in the relatively dry eastern Olympic Peninsula, where streams were narrow, deeply cut, and near boulder fields, had the highest average densities of bushy-tailed woodrats (*N. cinerea*) of all sites sampled in western Oregon and Washington (Carey et al. 1999). Verner et al. (1992:7) noted that diverting surface water and mining ground water in southern California threaten the associated riparian woodlands. Loss or degradation of riparian habitat as a consequence of anthropogenic water diversions, as well as reduced snowpack levels, drought, and warmer temperatures linked to climate change, is likely to adversely affect the spotted owl in southern California and throughout its range.

The owls in our study in southern California used high-severity burned forest, and all other burn severities, generally in proportion to availability during the third and fourth year after fire. The lone significant selection factor for forest burn severity that we observed was positive selection for moderate-severity burned forest farther from the territory center when availability was defined at the largest extent. Even within high-severity fire areas, considerable numbers of overstory trees can survive the fire, often containing no green needles immediately after fire when satellite imagery is taken for fire-severity mapping, but flushing with new foliage 1 year post-fire (Hanson and North 2009). The USFS typically maps forests with ≥75% basal area mortality as high severity (Miller et al. 2009), which incorporates some stands with surviving overstory trees into the high-severity category. Thus, a substantial amount of vegetation heterogeneity can occur even within areas mapped as high severity, potentially contributing to habitat structure used by foraging spotted owls in these areas.

The only other published study of California spotted owl habitat selection in a burned landscape used the CR as available habitat in the southern Sierra Nevada, and reported owls selected high-severity burned forest for foraging (Bond et al. 2009). Bond et al. (2009) recommended burned forests within 1.5 km of spotted owl nests and roosts in the Sierra Nevada be protected from post-fire logging. Because spotted owls also foraged in severely burned forests in our southern California study area, we suggest that complex early seral forests (DellaSala et al. 2014) within California spotted owl home ranges in both regions be considered potentially suitable foraging habitat.

Available Habitat Extent, Censoring Data, and Buffer Circles

A graphical comparison of model-averaged covariate coefficients from the 3 spatial extents of availability samples revealed some disagreement regarding forest burn-severity effects (Fig. 2), underscoring the importance of spatial extent when defining available habitat. In this study, high-severity burned forest was our primary vegetation condition of interest, but between the largest and smallest extents of our availability samples, the coefficient sign for this parameter differed. Beyer et al. (2010) illustrated how quantifying preference for one habitat over another is sensitive to the researcher's subjective decision about how available habitat is sampled. In their simulated dataset using different extents of availability, used points remained unchanged, but regression coefficients for selection varied according to extent—even differing in sign. Their statistical preference changed only because the relative availability of the vegetation types changed across extents. Thus, positive or negative preference for a given habitat is conditional upon the defined sample of availability. Beyer et al. (2010) described how selection coefficients can be negatively correlated with the proportion of a given habitat being available. However, in our study, we found no trend of high-severity burned conditions increasing or decreasing as spatial extent increased (Table 1); therefore, we contend our coefficients were not significantly biased by spatial extent of the availability sample.

Our methodology also involved censoring individuals if high-severity burned forest (the main condition of interest to us) was largely unavailable to them. Frair et al. (2010) noted that in selection analyses, rare habitats are subject to false negatives (type-II errors), whereas common types are subject to false positives (type-I errors); therefore, we think our methodology of censoring owls whose available habitat areas contained <5% high-severity forest fire provided us with a more robust selection probability for this type and reduced our probability of type-II error. Our parameter estimates from the kernels were similar between full and censored datasets, because the kernel extent is already restricted to used areas.

Using point location estimates increases the probability of incorrect conclusions about habitat preference relative to buffered telemetry-error circles (Rettie and McLoughlin 1999). Our methodology of replacing point locations with buffered error circles and analyzing composition of the area

of the plot rather than the point, accounted for the inherent imprecision of telemetry locations and increased the accuracy of determining habitat selection but reduced precision and may have diminished our power to detect statistically significant selection (Rettie and McLoughlin 1999, Frair et al. 2010). A buffer usually will contain variation unless vegetation patch size is much larger than error circle size (i.e., includes only 1 vegetation category). However, the inclusion of different burn severities within a buffered circle enabled us to determine whether owls were selecting edges between forest burn-severity categories. We found no statistically significant evidence that spotted owls selected edges in this burned landscape.

MANAGEMENT IMPLICATIONS

We suggest researchers perform selection analyses at multiple spatial extents of availability and report the sensitivity of coefficient estimates, censor individuals with unacceptably low amounts of a particular habitat of interest within their availability sample, and use buffered circles rather than point location estimates to decrease the probability of type-II errors. We found that extent of defined availability affected selection of burned forest categories, but not in terms of distance to center or distance to riparian, the strongest effects in these data. Our preferred method was to use the more-inclusive MCP or CR, which represents most habitat theoretically available based on the sample of radio-telemetry locations, while excluding non-habitat, such as treeless areas in the case of spotted owls, within the boundaries of the MCP or CR. Non-habitat should be defined by previous studies of habitat selection or expert opinion, but we urge the researcher to be open to re-defining suitable habitat as information on selection in previously unstudied vegetation associations becomes available.

High-severity fires may eliminate some nesting and roosting stands for California spotted owls, but they can enhance foraging opportunities during breeding (Bond et al. 2009) and non-breeding seasons (Ganey et al. 2014). The present study provides additional evidence that forests burned by high-severity fire should be considered potentially suitable foraging habitat for California spotted owls because they were used in proportion to their availability. We documented significant selection for riparian areas in all available habitat extents. We recommend maintaining or, if necessary, implementing protective measures and management activities that conserve water and streamside forests, and monitoring the effects of land management activities on the owl's riparian-associated small-mammal prey.

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