

DIET AND HOME-RANGE SIZE OF CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

MONICA L. BOND, DEREK E. LEE, RODNEY B. SIEGEL, and MORGAN W. TINGLEY, The Institute for Bird Populations, P. O. Box 1346, Point Reyes Station, California 94956 (current address of Bond and Lee: Wild Nature Institute, P.O. Box 165, Hanover, New Hampshire 03755); rsiegel@birdpop.org

ABSTRACT: Fire is pervasive in forests used by California Spotted Owls (*Strix occidentalis occidentalis*) and their prey species. We assessed the diets and sizes of the breeding-season home ranges of seven Spotted Owls occupying burned forests in the southern Sierra Nevada 4 years after a fire and compared the results with data from previous studies in unburned forests within the range of the subspecies. Prey captured by owls in the burned area comprised 40.3% (by biomass) pocket gophers (*Thomomys* spp.) and 25.9% northern flying squirrels (*Glaucomys sabrinus*). In contrast, in unburned areas of the Sierra Nevada Spotted Owls fed primarily on flying squirrels, or on both flying squirrels and woodrats (*Neotoma* spp); in unburned southern California forests they fed overwhelmingly on woodrats. The owls' mean home range in the burned forest covered 402 ha, an area similar to that recorded in unburned forests of the Sierra Nevada. Our results are consistent with hypotheses that the burned habitat in our study area was rich in gophers and that Spotted Owls foraging on gophers in burned forests do not require home ranges substantially larger than do owls in unburned forests. With currently available data we could not conclusively attribute variation in diet or home-range size to the influence of fire, so further testing is warranted. Use of rodenticides and herbicides in managing burned Spotted Owl habitat may reduce the owl's key prey.

The California Spotted Owl (*Strix occidentalis occidentalis*) occurs in mixed-conifer and montane hardwood forests throughout the Sierra Nevada and the mountain ranges of southern California (Verner et al. 1992, Gutiérrez et al. 1995). Its vital rates are positively associated with large areas of older conifer-dominated forest and related conditions (Blakesley et al. 2005, Seamans 2005), and within its range the subspecies is viewed as an indicator for management of these forest types.

Forest fire is one of the most important issues affecting the Spotted Owl's habitat (Weatherspoon et al. 1992). California Spotted Owls typically occupy older forests with greater canopy cover (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004), and this has led to the presumption that fires of moderate and high severity reduce the owl's survival and pose a significant risk to its habitat (Weatherspoon et al. 1992, U.S. Forest Service 2001, 2004, 2005). However, Spotted Owls can occupy territories and continue to reproduce in burned habitats, including those with large severely burned patches (Gaines et al. 1997, Bond et al. 2002, Jenness et al. 2004, Bond et al. 2009). Franklin et al. (2000) hypothesized that fire could enhance the abundance of and access to prey for the Northern Spotted Owl (*S. o. caurina*) in California by creating patchy openings in the forest canopy and increasing habitat edges. Indeed, four years after a large, patchy fire in the southern Sierra Nevada, California Spotted Owls selectively foraged in burned forest rather than unburned forest, with the strongest selection for severely burned patches (Bond et al. 2009).

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

Prey composition is an important determinant of raptors' use of space (Peery 2000). Zabel et al. (1995) found that prey species predicted the size of the Northern Spotted Owl's home range in California better than the proportion of older forest in the home range, and Carey et al. (1992) reported that the prey base strongly influenced the size of the Northern Spotted Owl's home range in Oregon. In both studies, owls with a greater percent biomass of larger prey in their diet had home ranges smaller than those of owls that consumed more of the smaller prey species. Ward et al. (1998) documented that in California Northern Spotted Owls selected foraging sites according to the distribution of larger prey (e.g., woodrats), which provided an energetic benefit to the owls. The California Spotted Owl's major prey items by biomass are the dusky-footed and big-eared woodrats (*Neotoma fuscipes* and *N. macrotis*), northern flying squirrel (*Glaucomys sabrinus*), and pocket gophers (*Thomomys* spp.; Thraikill and Bias 1989, Williams et al. 1992, Smith et al. 1999, Munton et al. 2002).

Despite the importance of fire in shaping ecosystems in portions of the Spotted Owl's range, little is known about the diets and home-range sizes of owls occupying recently burned forests. Understanding the California Spotted Owl's prey base and space use in burned forests is important because fire is frequent in this subspecies' habitat, and it is not unusual for owls to continue to occupy and breed in burned forests (Bond et al. 2002, 2009, Roberts et al. 2011). Furthermore, forest management after a fire can include removal of fire-killed trees and applications of rodenticide and herbicide in efforts to enhance the growth of tree seedlings (McGinnis et al. 2010, Swanson et al. 2011), possibly to the detriment of foraging Spotted Owls and their prey. Our objective was to assess the breeding-season diet and estimate the sizes of the home ranges of California Spotted Owls occupying territories in recently burned mixed-conifer forests and compare the results with those of previous studies of owls in unburned forests. We note that the breeding-season home range may differ greatly from the year-round home range, as we have reported previously on the expanded winter movements of the same owls addressed in this study (Bond et al. 2010).

Our sample of owls in burned forests was relatively small (seven owls from four territories), our study included only a single breeding season, and the data from unburned forests we used for comparison were recorded in different years and in different areas. Therefore, rather than testing how fire affected diets and home-range sizes, we report for the first time basic information about the diet and home-range sizes of the California Spotted Owl in a burned forest and address differences from those in unburned forests qualitatively—a basis for developing hypotheses about fire effects to be tested in future studies.

METHODS

Study Areas

We estimated the diets and home ranges of California Spotted Owls during the breeding season of 2006 in forests burned by the 2002 McNally Fire in the Greenhorn Mountains and Kern Plateau in the Sequoia National Forest,

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

southern Sierra Nevada. Elevation ranged from 1500 m to 2500 m. 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 forest fires, the McNally Fire burned with variable severity, leaving a mosaic of severely burned, moderately burned, and unburned patches in the study area (Bond et al. 2009, 2010). Fires of high severity kill most existing vegetation and result in a forest structure dominated no longer by live trees but by herbs, shrubs, and dead trees, those of moderate severity cause patchwork mortality, and those of low severity rarely kill overstory trees and do not substantially alter the forest's structure (Smith 2000).

For comparison with our burned study area we obtained data from previous studies of the diets and home-range sizes of California Spotted Owls in unburned forests elsewhere within the subspecies' range (Thraillkill and Bias 1989, Call et al. 1992, Zabel et al. 1992, Smith et al. 1999, Zimmerman et al. 2001, Munton et al. 2002). Of these studies the nearest area matching ours in elevation was in the southern Sierra Nevada in the Sierra National Forest at 1220–2925 m elevation, 150 km north of the McNally Fire area. There Munton et al. (2002) studied the owl's diet and Zabel et al. (1992) estimated the sizes of home ranges of radio-marked owls during the breeding season of 1988. Farther north in the central Sierra Nevada, in the Eldorado (elevation 266–2257 m) and Tahoe national forests (670–1585 m), respectively, Thraillkill and Bias (1989) studied Spotted Owl diets during the 1986 and 1987 breeding seasons and Call et al. (1992) estimated the sizes of home ranges of radio-marked Spotted Owls during the 1987 breeding season. South of the McNally Fire area in the San Bernardino Mountains, Smith et al. (1999) assessed the owl's diet (elevation 1000–2500 m) and Zimmermann et al. (2001) estimated home-range sizes by radio telemetry (elevation 2000–2500 m).

In all the study areas summers are dry and hot, winters are wet and cold. At the Sierra Nevada study areas the vegetation is classified as Sierran Mixed Conifer (Allen 1988), dominated by ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and white fir (*Abies concolor*). Other common trees include sugar pine (*P. lambertiana*), incense-cedar (*Calocedrus decurrens*), canyon live oak (*Quercus chrysolepis*), and California black oak (*Q. kelloggii*). Above 2100 m, a transition zone is dominated by red fir (*A. magnifica*). Study areas in the central Sierra Nevada also included Douglas-fir (*Pseudotsuga menziesii*). In the San Bernardino Mountains study area the forest is dominated by bigcone Douglas-fir (*Pseudotsuga macrocarpa*), canyon live oak, coast live oak (*Quercus agrifolia*), and black oak below 1500 m, by Jeffrey pine, ponderosa pine, white fir, black oak, canyon live oak, sugar pine, incense-cedar, and western juniper (*Juniperus occidentalis*) above 1500 m (Stephenson and Calcarone 1999). Historically, fire regimes varied but most fires were of mixed severity (Skinner and Chang 1992, Weatherspoon et al. 1992, Minnich et al. 1995).

Field Methods

Prior to our study, U.S. Forest Service (USFS) personnel surveyed for and located California Spotted Owls within and near the McNally Fire's perimeter during three consecutive breeding seasons, 2003–2005 (W. Rannals and R. Galloway, unpubl. data). During the 2006 breeding season we surveyed for California Spotted Owls by standard methods described by Franklin et al. (1996). We selected four territories confirmed to be occupied by pairs of Spotted Owls. We selected these territories because they were inside or within 1 km of the fire perimeter, Spotted Owls had occupied them continuously since the fire, and there was sufficient road access for effective radio-tracking. We captured the adult owls with mist nets or noose poles and fitted them with color bands and backpack-style radio transmitters (batteries with a life expectancy of 1 year) that were designed to minimize contact with the owl's back (AVM Instrument Company, Colfax, CA). Radio transmitters were affixed with Kevlar ribbon (0.63 cm wide; Bally Ribbon Mills, Bally, PA). With the harness, the transmitter units weighed <20 g, or <4% of each owl's body mass. We considered each individual owl as a separate sample because Call et al. (1992) and Zimmerman et al. (2001) found that male and female California Spotted Owls forage independently. All four pairs attempted to nest in 2006, and we located each nest tree. Three attempts failed (Mill Creek, Speas Ridge, Burnt Ridge), and one pair successfully fledged one young (Poison Creek).

From 22 May to 15 August 2006 we radio-tracked the seven owls (4 males and 3 females) by locating each owl nightly or every other night between 21:30 and 04:00. We used a systematic design with a random start to record a representative sample of foraging locations. We randomly assigned each owl to a 1-hour time block on the first night we tracked it, then 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 night of sampling. To estimate the owls' locations, we triangulated on signals from the radio transmitters from established stations and used at least three compass bearings of the strongest signals, taking all bearings within approximately 30 minutes (Guetterman et al. 1991). For comparison of the sizes of home ranges in our burned study area with those of owls occupying unburned areas, D. Call, T. Munton, and G. Zimmerman provided us with locations of foraging radio-marked Spotted Owls in the Tahoe ($n = 7$), Sierra ($n = 8$), and San Bernardino ($n = 5$) national forests, respectively, during the same seasonal window of mid-May to mid-August. These studies used field methods similar to ours to estimate locations of foraging (Call et al. 1992, Zabel et al. 1992, Zimmerman et al. 2001).

In addition to estimating locations of nighttime foraging, every 7–10 days we recorded the location of each radio-marked owl's daytime roost. To assess the owls' diets, we collected regurgitated pellets at roost sites. We included multiple pellets found together in the same location as a single sample because remains of a single animal can be egested in more than one pellet (Forsman et al. 1984).

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

Data Analyses

We used digital maps and the GIS extension Fragstats (McGarigal et al. 2002) to calculate the area of suitable vegetation burned at high severity within a 2-km radius around the nest of each pair of owls. We chose this radius because >90% of each owl's foraging locations fell within it. We defined suitable vegetation as conifer and hardwood forest, which are those the California Spotted Owl typically uses (Verner et al. 1992). We report area burned at moderate and high severity because at these severities a fire alters a forest's structure substantially (Smith 2000) and because most managers consider these levels a threat to the California Spotted Owl (USFS 2004). Cover types and fire severity were derived from Landsat Thematic Mapper imagery developed by the USFS Pacific Southwest Region Remote Sensing Lab and available from the GIS Clearinghouse (<http://www.fs.fed.us/r5/rsl/clearinghouse/>).

We dissected all California Spotted Owl pellets collected from the McNally Fire study area and isolated all identifiable prey remains, including skulls, mandibles, other bones, bills, feathers, fur, and insect exoskeletons. We used the collection of the California Academy of Sciences, San Francisco, as a reference to identify remains of birds and mammals. We quantified the number of individuals of each species of prey in each sample as the highest count of diagnostic skeletal parts of each species. For example, if there were three right and two left maxillae of *Neotoma macrotis* in a pellet we considered the number of individuals of this species as three. We estimated the number of insects from the largest number of heads or paired mandibles. We identified two prey taxa (*Glaucomys sabrinus* and *N. macrotis*) to species and four others (*Thomomys*, *Peromyscus*, *Microtus*, and *Scapanus*) to genus only. The remaining prey items were identified to one of four broader taxonomic categories (diurnal squirrel, bird, bat, and insect). We calculated the percent frequency of each category in all pellet samples and estimated the percent biomass for each category from average weights (g) provided by Smith et al. (1999). For each of the four territories we tallied prey items by percent biomass but were unable to separate samples by sex because both members of a pair often roosted together in the same tree. The previously published studies of contents of California Spotted Owl pellets did not present the data by territory (Thraillkill and Bias 1989, Smith et al. 1999, Munton et al. 2002). Therefore, in addition to estimating the diet for each territory, we also pooled samples from all four territories for qualitative comparisons with those of other studies.

To estimate the sizes of the owls' home ranges, we used a kernel-density estimator, a widely used statistical method (Seaman and Powell 1996). Numerous methods for estimating home ranges with kernel estimators are available, but each method can generate a different estimate. In our analysis we used a fixed-bandwidth kernel estimator, which has been shown to have little bias in comparison to adaptive-bandwidth kernels (Seaman and Powell 1996). The choice of a smoothing parameter or bandwidth, h , to be used in an analysis affects the results critically, and there are several options for calculating the "optimal" bandwidth. The two most widely used methods for choosing h are the reference bandwidth, h_{ref} (Worton 1995) and least-

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

squares cross validation (LSCV; Silverman 1986, Wand and Jones 1995). The LSCV method produces more accurate estimates of simulated home ranges than does h_{ref} (Seaman and Powell 1996), but LSCV does not always converge, preventing its use in some cases.

We estimated the sizes of the owls' home ranges by kernel density in a two-step process. First, we analyzed sample sizes to test whether the number of points where each owl was relocated was sufficient for unbiased estimation of its home range. We used a bootstrapping algorithm in which, for each owl, we drew at random an increasing number of relocation points (n) from which we built a kernel-density utilization distribution resulting in an area estimate. We began by sampling 5 points and continued until all the available points for each owl had been drawn. At each n , we repeated the process 200 times, to calculate an incremental mean and standard deviation of kernel-density area. We used the simple h_{ref} method because small samples of points did not allow convergence with LSCV. We evaluated the simulation results for asymptotic convergence on home-range size as sample size increased, and if values for an individual did not converge, we excluded it from further analysis. We used owl locations from the unburned study areas that had been recorded during the same seasonal window of mid-May to mid-August, and ran the same power analyses by using bootstrapping simulations.

Second, after the sample-size analysis, we calculated the final home-range size as the 95th percentile of the fixed-kernel density estimated with LSCV. For all these calculations we used the package *AdehabitatHR* (Calenge 2006) in R, version 2.14.

RESULTS

The average area of suitable (conifer and hardwood) forest burned at moderate severity within 2 km of the four Spotted Owl nests we studied in or near the McNally Fire area was 237.9 ha (SD = 119.1, range 110.9–397.5); that which burned at high severity was 93.3 ha (SD = 35.5 ha, range 42.1–118.8 ha). Thus an average of 23% (range 10–39%) of suitable vegetation within the 2-km radius burned at moderate severity and 9% (range 4–12%) burned at high severity (Table 1).

We identified 199 individual prey items from 101 pellet samples from Spotted Owls in the McNally Fire area (range 7–35.5 pellet samples per owl territory). Samples from all four territories contained a substantial proportion of gophers and flying squirrels; big-eared woodrats were present in pellets at only two of the territories (Table 1). In the pooled sample of pellets from all four territories, the prey biomass comprised 40% gophers, 26% flying squirrels, and 11% woodrats.

The dominant species of prey that Spotted Owls captured in the closest unburned study area (Sierra National Forest, 1988) was the northern flying squirrel, 46% by biomass; gophers represented 18% and woodrats 12% (Munton et al. 2002; Table 2). In the Eldorado National Forest Spotted Owls primarily captured woodrats (38% of prey by biomass) and flying squirrels (31%; Table 2). In the unburned San Bernardino National Forest study area, woodrats were the overwhelmingly dominant prey, constituting 74% of the owls' diets by biomass (Smith et al. 1999; Table 2).

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

Table 1 Percent Each Category of Prey Contributed to Total Dietary Biomass, Estimated Home Range, and Severity of Fire within 2 km of Four California Spotted Owl Nests Four Years after the 2002 McNally Fire, Sequoia National Forest, California

Prey item	Site			
	Poison Creek	Mill Creek	Speas Ridge	Burnt Ridge
<i>Thomomys</i> spp.	18.9	48.6	40.4	53.3
<i>Neotoma macrotis</i>	35.4	0.0	0.0	8.3
<i>Glaucomys sabrinus</i>	20.7	35.9	35.3	11.6
<i>Peromyscus</i> spp.	5.2	8.6	2.4	1.6
scurid	8.1	6.7	9.8	10.5
<i>Microtus</i> spp.	4.1	0.0	6.5	0.0
No. prey items	83	13	44	59
Male home-range size (ha) (n) ^a	718.0 (40)	252.8 (51)	307.3 (48)	606.3 (53)
Female home-range size (ha) (n) ^b	129.8 (33)	—	606.0 (45)	197.3 (34)
Percent burned at moderate severity	38.9	9.8	19.3	23.5
Percent burned at high severity	11.6	3.7	9.0	11.5
Average elevation (m)	2167	1679	2052	1833

^an = Number of night-time relocation points per owl.

^bFemale at Mill Creek was not radio-marked.

The mean number of independent relocations we obtained for each foraging Spotted Owl in the McNally Fire area was 43 (range 33–53; Table 1). Simulation results for all owls in the McNally Fire converged and so we included them in the analysis (Figure 1). We excluded data from three Spotted Owls in the sample from unburned forests because of lack of asymptotic convergence (TH5, TH6, and SB1; Figure 1). The size of the home range of a Spotted Owl in the McNally Fire area averaged 402.5 ha (SE = 88.7, range 129.8–718.0 ha; Tables 1 and 3). The individual with the largest home range was the sole male that reproduced successfully that year (Poison Creek), while his mate's home range was the smallest (Table 1). Home-range sizes in unburned forests averaged 487.0 ha (SE = 63.9 ha) in the Tahoe National Forest, 529.0 ha (SE = 72.9 ha) in the Sierra National Forest, and 370.4 ha (SE = 58.7 ha) in the San Bernardino National Forest (Table 3).

DISCUSSION

Here we report the first data on the diet and the size of home ranges of the California Spotted Owl in a burned landscape. The size of an owl's home range varies with many factors, including but not limited to forest structure, fire severity, key prey species and temporal fluctuations in their numbers, the owl's foraging behavior, and whether it is nesting or feeding young (Carey et al. 1992, Zabel et al. 1995, Ward et al. 1998). We could not quantify home-range size rigorously as a function of diet, habitat, or other factors because our sample of owls and the length of our study were not sufficient.

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

Table 2 Average Percent Each Category of Prey Contributed to Total Dietary Biomass in Pooled Samples of Pellets Regurgitated by Spotted Owls in an Area Burned by the McNally Fire, Sequoia National Forest, and in Unburned Areas in the Eldorado, Sierra, and San Bernardino National Forests, California^a

	Eldorado NF ^b n = 139	Sierra NF ^c n = 1269	McNally Fire n = 199	San Bernardino NF ^d n = 8441
<i>Thomomys</i> spp.	7.8	18.4	40.3	10.4
<i>Glaucomys sabinus</i>	30.7	45.6	25.9	3.0
<i>Neotoma</i> spp.	38.1	11.8	10.9	74.0
Diurnal squirrel	6.6	0.9	8.8	1.3
Bird	12.4	12.9	4.0	3.5
<i>Peromyscus</i> spp.	1.3	5.5	4.5	4.0
<i>Microtus</i> spp.	0.7	1.2	2.6	1.3
<i>Scapanus</i> spp.	2.1	1.5	1.5	0.3
Bat	0.0	0.1	0.8	0.1
Insect	0.3	0.6	0.6	1.2
<i>Sylvilagus</i> spp.	0.0	0.0	0.0	1.0

^aSample size is number of individual prey items. Bold numbers indicate greatest percent biomass by study area.

^bData from Thraillkill and Bias (1989).

^cData from Munton et al. (2002).

^dData from Smith et al. (1999).

Previous studies of the California Spotted Owl's breeding-season diet (Thraillkill and Bias 1989, Smith et al. 1999, Munton et al. 2002) and home-range size (Call et al. 1992, Zabel et al. 1992, Zimmerman et al. 2001) were conducted in unburned areas. The dominant prey item we identified in pellets from the McNally Fire area was the pocket gopher; the northern flying squirrel and big-eared woodrat were also important. In comparison, the dominant prey California Spotted Owls took during the breeding season in an unburned area in the Sierra National Forest in the southern Sierra Nevada was the northern flying squirrel, proportions of pocket gophers and woodrats being smaller (Munton et al. 2002; Table 2). In the Eldorado National Forest in the central Sierra Nevada Spotted Owls consumed mainly woodrats and flying squirrels, while to the south in an unburned area in the San Bernardino National Forest, woodrats were the overwhelming prey (Smith et al. 1999).

In the McNally Fire area, owl pellets contained woodrat remains in amounts comparable to those in the nearest unburned study area at similar elevation (Sierra National Forest). But the average percent biomass of gophers in pellets from the McNally fire area was more than twice that in pellets from the unburned study area in the Sierra National Forest and more than 5 times higher than in pellets from the unburned Eldorado National Forest study area. Gophers are found in a variety of habitat types in the Sierra Nevada but are uncommon in mature and older forests with little or no herbaceous ground cover (Williams et al. 1992). They feed largely on

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

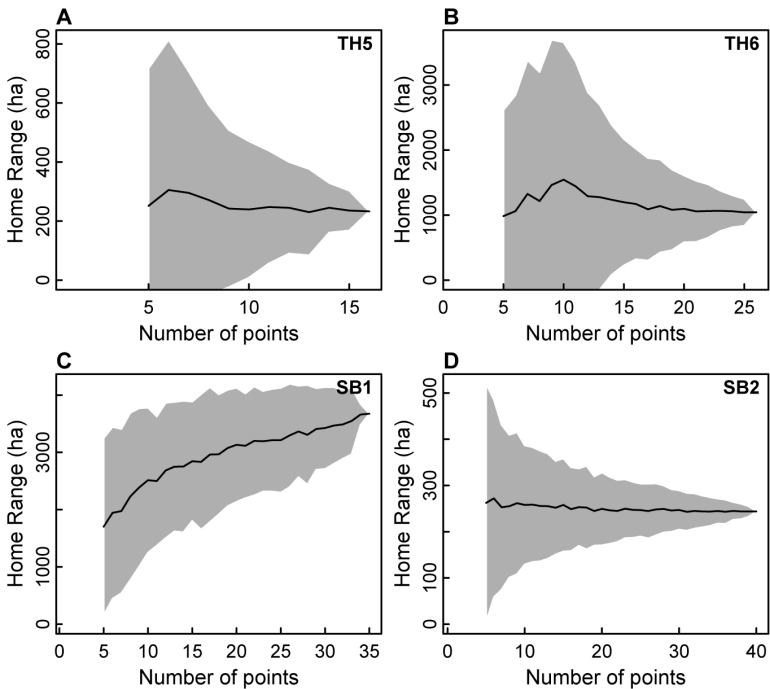


Figure 1. Mean (black line) and standard deviation (gray shading) of sizes of fixed-kernel home ranges for increasing random draws of n relocation points for representative radio-tracked California Spotted Owls from studies in multiple national forests in California. Plots were assessed for evidence of convergence in home range as n increased. Three home ranges did not converge, two in the Tahoe National Forest (A, B), and one in the San Bernardino National Forest (C). All other home ranges converged asymptotically (e.g., for a bird on San Bernardino National Forest, D).

herbaceous grasses and forbs and during the winter frequently consume mountain whitethorn (*Ceanothus cordulatus*) leaves and willow (*Salix* spp.) stems (Williams et al. 1992). Four years after the McNally Fire, stands of severely burned forest had significantly greater cover of shrubs and herbs and more dead trees than unburned stands or stands burned at moderate or low severity (Bond et al. 2009). Elsewhere we reported that California Spotted Owls selectively foraged in burned forest over unburned, with the strongest selection for severely burned patches (Bond et al. 2009). Forest fire may have enhanced the habitat for gophers (*sensu* Williams et al. 1992), and the standing fire-killed trees offered perches for foraging Spotted Owls, resulting in greater biomass of gophers in owl pellets from the McNally Fire area than in unburned areas of the Sierra Nevada.

In the McNally Fire area, Spotted Owl pellets contained less biomass of northern flying squirrels than did those from unburned areas of the Sierra

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

Table 3 Characteristics of Home Ranges Estimated by the Fixed-Kernel Method of California Spotted Owls Four Years after the 2002 McNally Fire, Sequoia National Forest, and in Three Unburned Areas

	Study area			
	Tahoe NF ^a	Sierra NF ^b	Sequoia NF McNally Fire	San Bernardino NF ^c
Latitude (° N)	40	37	36	34
Elevation (m)	670–1585	1220–2925	1500–2500	2000–2500
Mean home range (ha)	487.0	529.0	402.5	370.4
SE of home range	63.9	72.9	88.7	58.7
Range of home range	284.8–682.3	253.3–718.5	129.8–718.0	242.0–526.5

^aFrom D. Call, unpublished data.

^bFrom T. Munton, unpublished data.

^cFrom G. Zimmerman, unpublished data.

^dEstimated from locations of night-time foraging recorded 22 May–15 August 2006.

Nevada. Waters and Zabel (1995) found that the mean density of the flying squirrel in old-growth forest in northeastern California was greater than in young stands regenerating naturally after forest fire. On the basis of its habitat requirements (Waters and Zabel 1995, Meyer et al. 2007), the northern flying squirrel may take longer than the Spotted Owl's other prey to recover after severe forest fire. Future research should test the assumptions about the effects of fire on the California Spotted Owl's major prey species, with our results providing a basis for developing hypotheses.

The mean size of a home range in the McNally Fire area was 402 ha, similar to that in the unburned study areas, as evidenced by overlapping standard errors. The mean home range in our burned study area, however, was 24% smaller than in the nearest unburned area of similar elevation (Sierra National Forest), and pellets contained a greater biomass of gophers. In comparison, owls in the Sierra National Forest study area had the largest mean home ranges and were foraging primarily on flying squirrels.

Our results provide the basis for testable hypotheses on the effects of fire on the California Spotted Owl's use of space. As the biomass of an individual gopher and northern flying squirrel is similar (Smith et al. 1999), future studies could test the hypothesis that owls foraging primarily on gophers and flying squirrels may not need to forage as widely in burned forests as in comparable unburned forests. Studies could examine whether fire enhanced habitat for gophers and degraded it for flying squirrels, while controlling for any spatial and temporal differences in densities of these two prey species.

Our study of Spotted Owls occupying burned forests documented diets containing a majority of pocket gophers by biomass, with woodrats also a major prey item in one territory (Table 1). Shrubs and herbaceous vegetation provide important habitat for both of these key species of prey (Williams 1992), and these habitats can be abundant in a burned landscape (Bond et al. 2009). Therefore, post-fire management involving use of rodenticides to prevent damage to young trees or herbicides to suppress shrub growth within California Spotted Owl habitat may impair the owls' foraging.

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

ACKNOWLEDGMENTS

We thank K. Bruno and L. Kehas for field assistance and W. Rannals and R. Galloy of the Sequoia National Forest for providing Spotted Owl locations prior to our field work and valuable support during our study. We are indebted to D. Call, T. Munton, and G. Zimmerman for providing us with their telemetry data and to J. P. Ward for advice on field methods and data analysis. The California Academy of Sciences graciously allowed us access to its collection for our pellet analysis. We thank R. Gill, D. Herter, and D. Wiens for helpful comments on the manuscript. This study was funded by grants from Environment Now and the Resources Legacy Fund Foundation to The Institute for Bird Populations and was conducted by the Institute's Sierra Nevada Bird Observatory. This is contribution 377 of The Institute for Bird Populations.

LITERATURE CITED

- Allen, B. 1988. Sierran mixed conifer, in *A Guide to Wildlife Habitat Relationships* (K.E. Mayer and W.F. Laudenslayer, eds.), pp. 46–47. Calif. Dept. Fish and Game, Sacramento.
- Bias, M. A., and Gutiérrez, R. J. 1992. Habitat associations of California Spotted Owls in the central Sierra Nevada. *J. Wildlife Mgmt.* 56:584–593.
- Blakesley, J. A., Noon, B. R., and Anderson, D. R. 2005. Site occupancy, apparent survival, and reproduction of California Spotted Owls in relation to forest stand characteristics. *J. Wildlife Mgmt.* 69:1554–1564.
- Bond, M. L., Gutiérrez, R. J., Franklin, A. B., LaHaye, W. S., May, C. A., and Seamans, M. E. 2002. Short-term effects of wildfires on Spotted Owl survival, site fidelity, mate fidelity, and reproductive success. *Wildlife Soc. Bull.* 30:1022–1028.
- Bond, M. L., Gutiérrez, R. J., and Seamans, M. E. 2004. Modeling nesting habitat selection of California Spotted Owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada. *Forest Sci.* 50:773–780.
- Bond, M.L., Lee, D. L., Siegel, R. S., and Ward, J. P. 2009. Habitat use and selection by California Spotted Owls in a postfire landscape. *J. Wildlife Mgmt.* 73:1116–1124.
- Bond, M. L., Lee, D. E., and Siegel, R. B. 2010. Winter movements by California Spotted Owls in a burned landscape. *W. Birds* 41:174–180.
- Calenge, C. 2006. The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Modelling* 197:516–519.
- Call, D. R., Gutiérrez, R. J., and Verner, J. 1992. Foraging habitat and home-range characteristics of California Spotted Owls in the Sierra Nevada. *Condor* 94:880–888.
- Carey, A. B., Horton, S. P., and Biswell, B. L. 1992. Northern Spotted Owls: Influence of prey base and landscape character. *Ecol. Monogr.* 62:223–250.
- Forsman, E. D., Meslow, E. C., and Wight, H. M. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monogr.* 87:1–64.
- Franklin, A. B., Anderson, D. R., Forsman, E. D., Burnham, K. P., and Wagner, F. W. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. *Studies in Avian Biology* 17:12–20.
- Franklin, A. B., Anderson, D. R., Gutiérrez, R. J., and Burnham, K. P. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. *Ecol. Monogr.* 70:539–590.
- Gaines, W. L., Strand, R. A., and Piper, S. D. 1997. Effects of the Hatchery complex fires on Northern Spotted Owls in the eastern Washington Cascades, in *Proceedings of the Fire Effects on Rare and Endangered Species and Habitats Conference* (J. N. Greenlee, ed.), pp. 123–129. Int. Assoc. Wildfire and Forestry, Coeur d'Alene, ID.

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

- Guetterman, J. H., Burns, J. A., Reid, J. A., Horn, R. B., and Foster, C. C. 1991. Radio telemetry methods for studying Spotted Owls in the Pacific Northwest. U. S. Forest Serv. Gen. Tech. Rep. PNW-GTR-272.
- Gutiérrez, R. J., Verner, J., McKelvey, K. S., Noon, B. R., Steger, G. N., Call, D. R., LaHaye, W. S., Gingham, B. B., and Senser, J. S. 1992. Habitat relations of the California Spotted Owl, in *The California Spotted Owl: A Technical Assessment of its Current Status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, tech. coords.), pp. 79–99. U. S. Forest Serv. Gen. Tech. Rep. PSW-GTR-133.
- Gutiérrez, R. J., Franklin, A. B., and LaHaye, W. S. 1995. Spotted Owl (*Strix occidentalis*), in *The Birds of North America* (A. Poole and F. Gill, eds.), no. 179. Acad. Nat. Sci., Philadelphia.
- Jenness, J. J., Beier, P., and Ganey, J. L. 2004. Associations between forest fire and Mexican Spotted Owls. *Forest Sci.* 50:765–772.
- McGinnis, T. W., Keeley, J. E., Stephens, S. L., and Roller, G. B. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. *Forest Ecol. and Mgmt.* 260:22–35.
- Meyer, M. D., Kelt, D. A., and North, M. P. 2007. Microhabitat associations of northern flying squirrels in burned and thinned forest stands of the Sierra Nevada. *Am. Midland Nat.* 157:202–211.
- Minnich, R. A., Barbour, M. G., Burk, J. H., and Fernau, R. F. 1995. Sixty years of change in Californian conifer forests of the San Bernardino Mountains. *Conserv. Biol.* 9:902–914.
- Moen, C. A., and Gutiérrez, R. J. 1997. California Spotted Owl habitat selection in the central Sierra Nevada. *J. Wildlife Mgmt.* 61:1281–1287.
- Munton, T. E., Johnson, K. D., Steger, G. N., and Eberlein, G. P. 2002. Diets of California Spotted Owls in the Sierra National Forest, in *Proceedings of a symposium on the Kings River Sustainable Forest Ecosystems Project: Progress and current status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, tech. coords.), pp. 99–105 U.S. Forest Serv. Gen. Tech. Rep. PSW-183.
- Odion, D. C., and Hanson, C. T. 2006. Fire severity in conifer forests of the Sierra Nevada, California. *Ecosystems* 9:1177–1189.
- Peery, M. Z. 2000. Factors affecting interspecies variation in home-range size of raptors. *Auk* 117:511–517.
- Roberts, S. L., van Wagtenonk, J. W., Miles, A. K., and Kelt, D. A. 2011. Effects of fire on Spotted Owl site occupancy in a late-successional forest. *Biol. Conserv.* 144:610–619.
- Seaman, D. E. and Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- Seamans, M. E. 2005. Population biology of the California Spotted Owl in the central Sierra Nevada. Ph.D. dissertation, Univ. of Minn., St. Paul.
- Silverman, B. W. 1986. *Density Estimation for Statistics and Data Analysis*. Chapman and Hall, London.
- Skinner, C. N., and Chang, C. 1996. Fire regimes, past and present. *Sierra Nevada Ecosystem Project: Final report to Congress, vol II*, pp. 1041–1069. Centers for Water and Wildland Resources, Univ. of Calif., Davis.
- Smith, J. K. 2000. *Wildland fire in ecosystems: Effects of fire on fauna*. U.S. Forest Serv. Gen. Tech. Rep. RMRS-GTR-42, vol. 1.
- Smith, R. B., Peery, M. Z., Gutiérrez, R. J., and LaHaye, W. S. 1999. The relationship between Spotted Owl diet and reproductive success in the San Bernardino Mountains, California. *Wilson Bull.* 111:22–29.
- Stephenson, J. R., and Calcarone, G. M. 1999. Southern California mountains and

CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

- foothills assessment: Habitat and species conservation issues. U.S. Forest Serv. Gen. Tech. Rep. GTR-PSW-172.
- Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., and Swanson, F. J. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Frontiers Ecol. Env.* 9:117–125.
- Thraillkill, J. and Bias, M. A. 1989. Diets of breeding and nonbreeding California Spotted Owls. *J. Raptor Res.* 23:39–41.
- U.S. Forest Service. 2001. Sierra Nevada Forest Plan Amendment, Final Environmental Impact Statement. January 2001.
- U.S. Forest Service. 2004. Sierra Nevada Forest Plan Amendment, Final Supplemental Environmental Impact Statement. January 2004.
- U.S. Forest Service. 2005. Final Environmental Impact Statement for Revised Land Management Plans: Angeles National Forest, Cleveland National Forest, Los Padres National Forest, San Bernardino National Forest. U.S. Forest Service, Pacific Southwest Region. September 2005.
- Verner, J., Gutiérrez, R. J., and Gould, G. I., Jr. 1992. The California Spotted Owl: A technical assessment of its current status (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck, tech. coords.), pp. 55–77. U. S. Forest Serv. Gen. Tech. Rep. PSW-GTR-133.
- Wand, M. P., and Joes, M. C. 1995. Kernel smoothing. Chapman & Hall/CRC, Boca Raton, FL.
- Ward, J. P., Jr., Gutiérrez, R. J., and Noon, B. R. 1998. Habitat selection by Northern Spotted Owls: The consequences of prey selection and distribution. *Condor* 100:79–92.
- Waters, J. R., and Zabel, C. J. 1995. Northern flying squirrel densities in fir forests of northeastern California. *J. Wildlife Mgmt.* 59:858–866.
- Weatherspoon, C. P., Husari, S. J., and van Wagendonk, J. W. 1992. Fire and fuels management in relation to owl habitat in forests of the Sierra Nevada and southern California, in *The California Spotted Owl: A technical assessment of its current status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck, tech. coords.), pp. 207–221. U. S. Forest Service General Technical Report PSW-GTR-133.
- Williams, D. F., Verner, J., Sakai, H. F., and Waters, J. R. 1992. General biology of major prey species of the California Spotted Owl, in *The California Spotted Owl: A technical assessment of its current status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck, tech. coords.), pp. 207–221. U.S. Forest Serv. Gen. Tech. Rep. PSW-133.
- Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J. Wildlife Mgmt.* 59:794–800.
- Zabel, C. J., Steger, G. N., McKelvey, K. S., Eberlein, G. P., Noon, B. R., and Verner, J. 1992. Home-range size and habitat-use patterns of California Spotted Owls in the Sierra Nevada in *The California Spotted Owl: A technical assessment of its current status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck, tech. coords.), pp. 149–163. U. S. Forest Serv. Gen. Tech. Rep. PSW-GTR-133.
- Zabel, C. J., McKelvey, K. S., and Ward, J. P., Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of Northern Spotted Owls (*Strix occidentalis caurina*). *Can. J. Zool.* 73:433–439.
- Zimmerman, G. S., LaHaye, W. S., and Gutiérrez, R. J. 2001. Breeding-season home ranges of Spotted Owls in the San Bernardino Mountains, California. *W. Birds* 32:83–87.

Accepted 26 November 2012