Home Range and Habitat Selection of Spotted Owls in the Central Sierra Nevada

Author(s): Perry J. Williams, R.J. Gutiérrez, Sheila A. Whitmore
Source: Journal of Wildlife Management, 75(2):333-343. 2011.
Published By: The Wildlife Society
URL: http://www.bioone.org/doi/full/10.1002/jwmg.62

Journal of Wildlife Management 75(2):333–343; 2011; DOI: 10.1002/jwmg.62

Research Article

Home Range and Habitat Selection of Spotted Owls in the Central Sierra Nevada

PERRY J. WILLIAMS,[1,2] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1980 Folwell Avenue, Saint Paul, MN 55108, USA*

R.J. GUTIÉRREZ, *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1980 Folwell Avenue, Saint Paul, MN 55108, USA*

SHEILA A. WHITMORE, *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 200 Hodson Hall, 1980 Folwell Avenue, Saint Paul, MN 55108, USA*

ABSTRACT We studied home range and habitat selection of radio-marked adult California spotted owls (*Strix occidentalis occidentalis*) randomly selected from among the breeding population of owls in the central Sierra Nevada, California from June to October 2006. The most parsimonious home-range estimate for our data was 555 ha (SE = 100 ha). Home-range size was positively correlated with the number of vegetation patches in the home range (habitat heterogeneity). We used resource selection ratios to examine selection of vegetation types by owls within our study area. Owl home ranges contained a high proportion of mature conifer forest, relative to its availability, although the confidence interval for this estimate overlapped one. We also used resource selection functions (RSF) to examine owl foraging habitat selection. Relative probability of selection of foraging habitat was correlated with vegetation classes, patch size, and their interaction. Owls showed highest selection rates for large patches (>10 ha) of pole-sized coniferous forest. Our results suggested that spotted owls in the central Sierra Nevada used habitat that contained a high proportion of mature conifer forest at the home-range scale, but at a finer scale (foraging site selection) owls used other vegetation classes interspersed among mature forest patches, consistent with our hypothesis that spotted owls may use other forest types besides old growth and mature forests when foraging. Our study provides an unbiased estimate of habitat use by spotted owls in the central Sierra Nevada. Our results suggest that forest managers continue to protect remaining mature and old-growth forests in the central Sierra Nevada because owl home ranges contain high proportions of these habitats. However, our results also showed that owls used younger stands as foraging habitat so that landscape heterogeneity, with respect to cover types, may be an important consideration for management but we did not attempt to relate our findings to fitness of owls. Thus management for some level of landscape heterogeneity for the benefit of owls should proceed with caution or under an adaptive management framework. © 2011 The Wildlife Society.

KEY WORDS California spotted owls, radio-telemetry, random sampling design, resource selection function, Sierra Nevada, *Strix occidentalis occidentalis*.

Management of California spotted owls (*Strix occidentalis occidentalis*) has been predicated on identifying and protecting their primary habitat (Verner et al. 1992, U. S. Forest Service 2004). Their management has been controversial because there is incomplete knowledge of their habitat and home-range use patterns. For example, much effort has been devoted to identifying California spotted owl nest and roost habitat selection patterns (Bias and Gutiérrez 1992, LaHaye et al. 1997, Moen and Gutiérrez 1997, Bond et al. 2004, Chatfield 2005), but much less effort has been directed toward understanding their foraging habitat (Call et al. 1992, Zabel et al. 1992). Emphasizing nesting and roosting habitat selection for management may result in a limited view of habitat use by spotted owls because this subspecies appears to use a greater variety of habitats for foraging than for nesting and roosting (Verner et al. 1992, Gutiérrez et al. 1995). Thus, we studied California spotted owl home range and foraging habitat selection using a random selection of owls within the central Sierra Nevada, California. Our main objectives were to 1) estimate home-range sizes of owls, 2) estimate habitat characteristics associated with differences in home-range size, 3) estimate second-order (home-range) habitat selection based on vegetation-class selection by owls relative to the entire study area, and 4) estimate third-order (foraging) habitat selection based on foraging locations of owls within their home range.

STUDY AREA

Our study area (3,188 km^2) was located on the Eldorado and Tahoe national forests. The study area was characterized by cold, wet winters and hot, dry summers. Topography was mountainous and bisected by steep river drainages; elevation ranged from 233 m to 3,041 m. At lower elevations vegetation was Sierran mixed-conifer montane forests dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies*

Received: 1 October 2009; Accepted: 29 July 2010

---

[1] *E-mail: perry_williams@fws.gov*

[2] *Present Address: Big Oaks National Wildlife Refuge, Madison, IN 47250, USA.*

concolor), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), California black oak (*Quercus kellogii*), and, at higher elevations, California red fir (*Abies magnifica*) forest was dominant (Küchler 1977). Vegetation was influenced by aspect, climate, fire, logging, livestock grazing, edaphic conditions, and elevation, which resulted in a diverse pattern of forest types (Verner et al. 1992, Skinner and Chang 1996).

METHODS

The owls we used were randomly selected from all known owl territories ($n = 146$) in the central Sierra Nevada as part of an experiment on effects of logging on owls (R. J. Gutiérrez, University of Minnesota, unpublished data). This was a constrained random selection required by the design of the logging experiment (e.g., owl territories having recent, concurrent, or scheduled tree harvest during the study were excluded from sampling because harvest would have confounded experimental treatments; reasons such as legal constraints precluded sampling on some territories). Once owl territories met selection criteria we placed them in the sampling pool. Originally, we randomly selected 12 territories representing 24 owls (12 pairs) from this pool, which was the number of owls we considered feasible to monitor given available funding. We surveyed selected owl territories following methods described by Forsman (1983).

Owl Capture and Radio-Telemetry Monitoring

Once we located owls, we determined their sex by voice (Forsman et al. 1984), their age by plumage characteristics (Forsman 1981), and their pair status (Franklin et al. 1996). We attempted to capture all adult owls detected on territories. We marked captured owls using a locking United States Geological Survey aluminum band on one leg, a uniquely-colored plastic band and tab on the other leg (Franklin et al. 1996), and a backpack radio-transmitter (Holohil Systems Ltd. Model RI-2C, Ontario, Canada) secured with Teflon® (Dupont, Wilmington, DE) coated Kevlar® (Dupont) ribbon. Total mass of transmitters (including harness) was 14.4–15.4 g, which was <3.0% of the adult body mass of a male spotted owl (Gutiérrez et al. 1995).

Concurrently with telemetry monitoring, we conducted extensive blind tests (known locations of radio transmitters unknown to observers) on observers in several owl territories to estimate bearing error of locations. Absolute bearing error of the naïve observers was 7.2°, which we used to estimate quality of owl telemetry locations. We developed our monitoring procedures a priori to data collection to improve owl (transmitter) location estimates. To triangulate radio signals to estimate an owl's location we first used handheld directional 3-element Yagi antennae and R-1000 handheld receivers (Communication Specialists, Inc., Orange, CA) to receive signals from transmitters. We recorded compass directions on detected signals based on signal strength and quality at ≥3 monitoring stations spaced >160 m apart. We triangulated from permanent monitoring stations precisely located using a Trimble Pathfinder Global Positioning System (GPS) capable of ±3 m accuracy. Second, we triangulated all locations within 30 min. Third, we immediately plotted compass bearings on 1:15,000-scale topographic maps. Fourth, after we obtained a location we paused for 10 min and then repeated the process. Fifth, we later analyzed the quality of each location using the arithmetic mean estimator in LOAS software (version 4.0b, Ecological Software Solutions, Urnäsch, Switzerland) to calculate the 95% confidence ellipse of all locations for use in habitat selection analyses. Finally, we only used locations for analysis that had confidence ellipses <5 ha.

We partitioned the night into 3 hr segments for monitoring each owl and randomized the night and time each segment's monitoring would begin. Time segments for monitoring started between 30 min before sunset to 30 min after sunrise. The logistics of traveling long distances between owl territories precluded a completely randomized temporal sampling design, so we stratified owls into groups that could be monitored by one person based on the relative proximity of the first randomly selected owl to nearby owls. We randomly assigned each observer 2 owl territories to survey per night, excluding owls that were too remote to allow sufficient travel time to another owl territory during a night, in which case we monitored the owl for 6 hr. We monitored owls for 4 consecutive nights, followed by 3 nights with no monitoring. If we were unable to locate owls because we did not detect a signal or the signal was too faint to determine a direction, we searched adjacent areas using a vehicle mounted RA-5A omni-directional antennae (Telonics, Mesa, AZ). If we were unable to locate an owl for ≥2 weeks, we attempted to locate it using aircraft with 2 wing-mounted directional antennae. At the conclusion of the study we recaptured all owls to remove transmitters. Our study was approved by the University of Minnesota (Institutional Animal Care and Use Committee Protocol no. 0512A78787).

Home-Range Size Estimation

We defined a foraging home range as the area used by an owl during its nightly activities between June and October (Burt 1943). Studies of spotted owl breeding-season home range usually end after juveniles fledge (usually late Aug–Sep); however, none of the owls on either our study area or an adjacent demographic study area nested successfully during our study. We calculated the 100% minimum convex polygon (MCP) using Hawth's Analysis Tools (Beyer 2004) for ArcGIS. The MCP estimator has been criticized for many reasons; therefore, several authors have recommended that the MCP never be used (see review in Laver and Kelly 2008). However, we calculated it for comparative purposes because it was the only home-range estimator that had been used in all other California spotted owl home-range studies (Laymon 1988, Call et al. 1992, Zabel et al. 1992, Zimmerman and Gutiérrez 2001). We did not use it to draw inference about home-range size of owls.

To estimate home-range size of owls, we first estimated each owl's home range using 5 home-range estimators (95% isopleths of the adaptive-kernel density, 95% isopleths of the fixed-kernel density, 1-mode bivariate normal, 2-mode bivariate circle, and 2-mode bivariate normal). We then selected the most parsimonious of the 5 estimators for each owl using an information-theoretic model-selection approach (Horne and Garton 2006*a*) in Program Animal Space Use 1.2 Beta (Horne and Garton 2007) using the likelihood cross-validation criterion (CVC). We used the CVC because the number of model parameters was not explicit, and, therefore, could be used for non-parametric home-range models (i.e., kernel models). We estimated relative support for each home-range model by the difference in CVC between each model and the model with the lowest CVC value (i.e., ΔCVC). We used only the home-range size estimates from the most parsimonious home-range models for analyses because we assumed these models gave the best estimate of owl home ranges given our data (Horne and Garton 2006*a*). We used the likelihood-cross-validation (CVh) smoothing parameter in kernel estimates of home ranges calculated in Animal Space Use 1.2 Beta (Horne and Garton 2007) because it produced home-range estimates with better fit and less variability than did other smoothing parameters (e.g., least-squares cross-validation) in simulation studies (Horne and Garton 2006*b*).

Correlates of Home-Range Size

We developed alternative hypotheses based on spotted owl literature that might explain variation in spotted owl home-range size (Table 1). Our first model was a null (intercept-only) model (model 1). We assumed that small home ranges reflected better habitat conditions or configurations than did large home ranges because the higher the quality of the habitat, the shorter the distance an owl would need to travel to meet its requirements (McNab 1963, Zabel et al. 1995). Therefore, we hypothesized that spotted owls having more mature forest within their home range would have smaller home-range sizes because mature forest has been presumed to be their primary habitat (model 2; Gutiérrez et al. 1995). We hypothesized that owls having larger core habitat areas would have smaller home ranges because core habitat in close proximity should reduce travel distances of this central-place forager (model 3; McNab 1963, Carey and Peeler 1995, Zabel et al. 1995). We estimated core habitat by summing the area of all vegetation patches, including and contiguous to a traditional (most-used) roost patch, that have been shown to be selected habitats (medium- and mature-sized conifer vegetation with medium and high canopy cover) by California spotted owls (Verner et al. 1992). We hypothesized that owls having higher proportions of selected habitat within their home range would have smaller home ranges than owls having lower proportions of these habitats (model 4; Gutiérrez et al. 1992) because this would also reduce travel time and present owls with more selection options. Model 4 differed from model 3 because model 3 included only habitat adjacent to roost sites and was independent of home range size, whereas model 4 included the proportion of all habitat within the home range. We hypothesized that owls having high habitat heterogeneity (many types of vegetation classes) would have large home ranges because heterogeneity should increase separation of suitable habitat (model 5; Solis 1983, Carey et al. 1992). We hypothesized that males and females may have different home-range sizes, that pair status may affect home-range sizes, and that sex may only affect the home-range size depending on the pair's breeding status because of division of duties between the sexes, sexual dimorphism (females are larger), and greater potential exploratory behavior of single birds within a territory (models 6, 7, and 8, respectively). We hypothesized that topography might influence home-range size (average elevation, SD of elevation, and slope [models 9, 10, 11, respectively]; Irwin et al. 2004) because it influences owl's primary prey base. Northern flying squirrels (*Glaucomys sabrinus*) are the dominant prey base at higher elevations and occur at low density relative to other prey at lower elevations (Gutiérrez et al. 1995, Zabel et al.

Table 1. Model selection results for estimation of home-range size by California spotted owls ($n = 14$) in the central Sierra Nevada, California, June–October 2006 based on likelihood estimation.

Model no.	Model[a]	$-2\log_e(\mathcal{L})$[b]	K[c]	ΔAIC_c[d]	w_i[e]	R^2
5	PPA	193.06	3	0	0.615	0.55
3	CORE	195.62	3	2.56	0.171	0.43
12	AVGELEV + EDGE + AVGELEV × EDGE	188.04	5	4.09	0.08	0.68
8	SEX + PAIR	194.41	4	5.4	0.041	0.52
10	STDEVELEV	199.27	3	6.22	0.027	0.31
11	AVGSLOPE	200.23	3	7.18	0.017	0.26
6	SEX	200.56	3	7.51	0.014	0.24
1	NULL	204.26	2	7.9	0.012	
7	PAIR	201.12	3	8.06	0.011	0.21
2	PROP (MATURE)	202.41	3	9.36	0.006	0.13
4	PROP (SUITABLE)	203.33	3	10.27	0.004	0.05
9	AVGELEV	204.15	3	11.09	0.002	0.01

[a] PPA = an index of relative patchiness of each owl's home range; CORE = total amount of area (in ha) of vegetation classes 4, 5, 6, and 7 immediately adjacent to the roost site; AVGELEV = the average elevation of 1,000 random points within each owl's home range; EDGE = an index of the relative amount of edge in each owl's home range; SEX = sex of the owl; PAIR = pair status of the owl; STDEVELEV = SD of the elevation of 1,000 random points within each owl's home range; AVGSLP = average slope of 1,000 random points within each owl's home range; NULL = no effects (means) model; PROP = proportion of each vegetation classification relative to the home-range size of each owl.

[b] $-2 \times \log_e$(likelihood).

[c] No. of parameters in the model.

[d] Difference between model Akaike's Information Criterion adjusted for small sample size (AIC_c) and AIC_c value of the best model.

[e] AIC_c wt.

1995). Therefore, we hypothesized that owl home ranges would be larger at higher elevations. We hypothesized that owls that prey primarily on woodrats (*Neotoma fuscipes*) used edges whereas owls that prey on flying squirrels used interior forests and, therefore, home-range size would be associated with the amount of edge per area, elevation, and their interaction (model 12; Zabel et al. 1995).

To quantify habitat metrics we created a vegetation classification map because existing United States Forest Service (USFS) vegetation maps of the study area were <60% accurate (M. Bond, University of Minnesota, personal communication). We mapped the vegetation of every owl home range and classified the vegetation polygons encompassing 2,161 random locations throughout the study area to estimate available habitat in the study area (see habitat selection analysis below). We used 8 vegetation classes consistent with the California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988). These vegetation classes were: 1 = hardwood forest, 2 = areas with low (<40%) canopy cover, 3 = pole-sized (15–28 cm dbh) conifer forest with medium to high (≥40%) canopy cover, 4 = medium-sized (28–60 cm dbh) conifer forest with medium (40–70%) canopy cover, 5 = medium-sized conifer forest with high (>70%) canopy cover, 6 = mature (>60 cm dbh) conifer forest with medium canopy cover, 7 = mature conifer forest with high canopy cover, and 8 = water. We used the United States Department of Agriculture, National Agriculture Imagery Program's (2005) County Compressed Mosaics (multi-resolution seamless image database of natural-color, 1 m resolution orthophotographs) and a Geographical Information System (GIS; ArcINFO) to map vegetation classes. We first visually compared the orthophotographs to randomly select sites in the field to train ourselves to correctly identify vegetation classes using the orthophotographs. We continued training until we were confident that we could estimate tree size, canopy cover, and hardwood or conifer forest sufficiently (with minimal error; see below) to define the boundaries of vegetation patches and place patches into vegetation classes using the orthophotographs. We then used the GIS interfaced with the orthophotographs to classify 1) each vegetation patch (polygon) within each owl home range, and 2) each vegetation patch containing 1 of the 2,161 random points. We defined vegetation patches as contiguous areas of the same vegetation class. We assigned 1 of the 8 vegetation classes to each vegetation patch. Minimum mapping unit = 0.5 ha.

We assessed the user and producer map accuracy following Story and Congalton (1986); user accuracy was an estimate of the map's representation of the true vegetation classes, and producer accuracy was an estimate of the efficacy of mapping a specific geographic region. We randomly selected 161 points from the 2,161 random vegetation patches we classified from orthophotographs throughout the study area and measured vegetation at these points. At each of these 161 random locations we estimated the dominant species composition, dominant size class (i.e., dbh), percent canopy cover, and distance to a different vegetation class (if one was visible from our sampling plot), within 0.5 ha plots and assigned each vegetation patch to a vegetation class based on structure. We then estimated classification accuracy from percent agreement between these 161 sites and the same sites we classified using the orthophotographs.

We created a suite of a priori candidate models based on our alternative hypotheses (Table 1). To examine these models, we calculated the following habitat metrics: proportion of vegetation class (PROP), patches per area (PPA), average elevation (AVGELEV), standard deviation of elevation (STDEVELEV), average slope (AVGSLP), amount of edge per area (EDGE) for each owl home range, and the core area (CORE) for each owl's traditional roost using our vegetation map. Our sampling unit was the individual owl. Our response variable was total home-range size. Our independent variables included the habitat metrics described above. We divided categorical variables as follows: 7 vegetation classes (described above, except we excluded water to avoid trivial comparisons), sex, and pair status (paired or unpaired to account for the potential lack of independence between members of a pair). We then used Akaike's Information Criterion adjusted for small sample size to evaluate model likelihood (AIC_c; Burnham and Anderson 2002). We verified model assumptions by inspecting residual plots using the GRAPHICS package in Program R (R Version 2.9.1, www.r-project.org, accessed 01 Jul 2009). We tested for outliers or other influential data points using the STATS package in Program R.

Habitat Selection

We examined habitat selection by comparing used habitat to available habitat at 2 spatial scales (second- and third-order selection; Johnson [1980]). These scales corresponded to habitat associations within entire home ranges and habitats associated with individual telemetry locations.

We examined home-range (second-order) habitat selection using habitat selection ratios (Manly et al. 2002) combined with Bonferroni simultaneous confidence intervals to assess whether owl home ranges contained a disproportionate amount of certain resources (i.e., vegetation classes) relative to their availability within the study area. We defined used resources as the proportion of each vegetation class in each owl's home range. We estimated available resources by selecting 2,161 random locations within the study area and then mapping all vegetation contiguous to the random location to represent the proportional composition of our entire study area (see Correlates of Home Range Size above). We then compared the proportion of vegetation classes used by each owl (i.e., the proportion of each vegetation class within each owl's home range) to the proportion of available vegetation categories within the study area (design 2 analysis from Thomas and Tayler [1990]; sampling protocol A from Manly et al. [2002]; Table 2). We calculated the resource selection function (RSF), variance of the RSF, and simultaneous confidence intervals using the ADEHABITAT package in Program R.

We examined foraging site (third-order) resource selection by comparing used habitat resources (telemetry locations) to random locations within the home range (available locations)

Table 2. Estimated Manly selection ratios for different vegetation classes used by individual California spotted owls in the central Sierra Nevada, California, June–October 2006. Table modified from Manly et al. 2002:69).

Vegetation class	1	2	3	4	5	6	7	8
Available sample (proportion)	0.08	0.28	0.04	0.10	0.44	0.01	0.03	0.02
Used sample (owl identification, sex, proportion)								
BALDM F	0.00	0.09	0.10	0.13	0.62	0.00	0.06	0.00
CANYC M	0.01	0.20	0.11	0.26	0.37	0.00	0.06	0.00
DIXQM F	0.23	0.40	0.02	0.09	0.18	0.05	0.03	0.00
DOLLY F	0.00	0.03	0.03	0.19	0.22	0.07	0.46	0.00
ED028 F	0.00	0.10	0.16	0.12	0.52	0.02	0.09	0.00
ED028 M	0.00	0.11	0.16	0.23	0.31	0.01	0.18	0.00
ED121 F	0.00	0.10	0.03	0.20	0.58	0.03	0.06	0.00
ED124 F	0.00	0.09	0.11	0.27	0.39	0.01	0.14	0.00
ED124 M	0.00	0.07	0.10	0.33	0.27	0.02	0.22	0.00
ED200 F	0.00	0.03	0.00	0.11	0.74	0.00	0.13	0.00
ROBPK M	0.00	0.15	0.18	0.45	0.19	0.03	0.01	0.00
SUGAR M	0.21	0.02	0.14	0.08	0.17	0.04	0.33	0.00
BALDM M[a]	0.00	0.10	0.10	0.10	0.61	0.00	0.10	0.00
BALDM M[b]	0.05	0.09	0.06	0.30	0.46	0.00	0.03	0.00
Selection ratio								
w_i'	0.44	0.42	1.71	1.98	1.06	2.98	3.68	0.00
SE								
se(w_i')	1.51	0.67	8.80	6.10	1.20	40.12	21.28	0.01
Bonferroni confidence limit								
IC lower[c]	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
IC upper	4.21	2.10	23.70	17.21	4.05	103.19	56.82	0.04

[a] Data collected prior to 5 Aug 2006 (date of the death of presumed mate).
[b] Data collected after 5 Aug 2006.
[c] We set negative lower confidence limits to zero.

to assess if owls used certain resources within their home range disproportionately to availability. We estimated available resources by randomly sampling 3 times as many locations within each owl's home range as we had locations used (telemetry) by each owl (sampling protocol A from Manly et al. [2002]). We used the multiplier of 3 because it provided the best estimate of available habitat without introducing a contamination rate (i.e., areas selected as both used and available sites) that would bias parameter estimates (contamination rate was <25% for all parameters; Johnson et al. 2006). We examined owl use of edges by calculating the distance of used sites to the nearest edge and random sites to nearest edge and then compared their distributions using a Kolmogorov–Smirnov test for each vegetation class.

We examined the correlation between habitat metrics and owl foraging sites using model selection based on models developed a priori to the analysis (Table 3). We included a null (intercept-only) model (model 1). We hypothesized that

Table 3. Model selection results for models predicting foraging locations (third-order selection) of California spotted owls in the central Sierra Nevada, California, June–October 2006, based on likelihood estimation.

Model no.	Model[a]	$-2\log_e(\mathcal{L})$[b]	K[c]	ΔAIC[d]	w_i[e]
15	VEGTYPE + PATCHSIZE + VEGTYPE × PATCHSIZE	177.32	14	0	1
11	ELEV + PATCHSIZE + ELEV × PATCHSIZE	196.16	4	18.84	0
13	VEGTYPE + PATCHSIZE + DISTROAD + DISTWATER + ELEV + SLOPE + ASPECT	203.46	13	22.13	0
12	VEGTYPE + PATCHSIZE + DISTROAD + DISTWATER + ELEV	231.24	11	43.92	0
14	VEGTYPE + PATCHSIZE	272.56	8	79.23	0
6	PATCHSIZE	281.19	2	83.87	0
8	DISTWATER + ELEV + DISTWATER × ELEV	296.37	4	105.05	0
7	DISTWATER	328.4	2	135.08	0
2	VEGTYPE	321.09	7	143.77	0
4	TREESIZE	337.52	3	144.2	0
5	CANOPY	338.05	3	148.72	0
1	NULL	349.31	1	151.98	0
3	POTENTIAL	350.01	2	152.68	0
9	DISTROAD	353.59	2	156.27	0
10	DISTROAD + ELEV + DISTROAD × ELEV	356.51	4	157.18	0

[a] AREA = vegetation patch area; PERIM = vegetation patch perimeter; VEGCLASS = vegetation class of the vegetation patch; ELEV, SLOPE, and ASPECT = elevation, slope, and aspect, respectively, at the sample point within the vegetation patch; DISTWATER = distance from the sample point to the nearest permanent water body; DISTROAD = distance from the sample point to the nearest road.
[b] $-2 \times \log_e$(likelihood).
[c] No. of parameters in the model.
[d] Difference between model Akaike's Information Criterion (AIC) and AIC value of the best model.
[e] AIC wt.

certain vegetation classes would be selected as foraging sites over others (model 2) because different vegetation classes may provide different foraging opportunities (e.g., prey availability, forest structure). Of the different vegetation classes, we hypothesized that owls would select medium- and mature-sized coniferous forest with medium to high canopy cover more frequently than other classes because these vegetation classes have been shown to be selected by California spotted owls (model 3; Gutiérrez et al. 1992). Because spotted owls are associated with old growth and mature-sized tree classes (Gutiérrez et al. 1995), we hypothesized that owls would select vegetation classes having larger trees more often than vegetation classes having smaller trees (model 4). Owls in our area selected sites with higher canopy cover, so we included a model representing this hypothesis (model 5; Call et al. 1992). We hypothesized that owls would select sites in large vegetation patches because larger vegetation patches result in less fragmented or heterogeneous landscapes, which may enhance foraging efficiency (model 6). We hypothesized owls would select sites at higher elevations and shorter distances to water because both water and high elevation are associated with cooler microclimates, which we hypothesized were beneficial to owls between June and October (models 7 and 8, respectively; Gutiérrez et al. 1995). In model 8 we included an interaction because the effect of selecting cooler microclimates associated with water may be dependent on elevation (i.e., owls may not select areas near water at higher elevation because of cooler microclimates at higher elevations). Wasser et al. (1997) suggested traffic may stress owls near roads. Therefore, we hypothesized owls would select areas farther from roads (model 9). It was also plausible that roads at higher elevations would have less traffic and, thus, would have less effect on owls than roads at lower elevations so we included an interaction between roads and elevation (model 10). As with correlates of home-range size (see model 12, Table 1), we also hypothesized that at this scale owls that prey primarily on woodrats used edge habitats whereas owls that prey on flying squirrels used interior forests. Therefore, owls at lower elevations would select smaller patches than would owls at higher elevations because of the change in prey base (model 11). We hypothesized that vegetation class, patch size, distance to roads and water, and elevation may all be associated with habitat selection by owls (model 12). Further, we considered all of the variables of model 12 plus 2 additional topographical variables, aspect and slope, because they may be correlated with habitat selection (model 13). Models 12 and 13 were compositions of several models above, and we included them because we thought each of the variables included in the models might contribute to habitat selection by owls. We hypothesized owls would select large areas of certain vegetation classes (model 14; Verner et al. 1992) or that the selection of certain vegetation classes depended on the size of that vegetation class, thus, we included an interaction between vegetation class and patch size (model 15).

We created statistical hypotheses (Table 3) from our alternative models and analyzed the data using logistic regression. We ranked each of the logistic regression models using AIC and evaluated each model's likelihood using Akaike weights (w_i; Burnham and Anderson 2002; Table 3). We estimated RSF model parameters β_0, $\beta_1, \ldots, \beta_{n-1}$ from the weighted mean of coefficient estimates from the generalized linear logistic regression model applied to each owl with weight = 1/variance of each parameter estimate (Murtaugh 2007). We assessed the goodness-of-fit of the top model by calculating the area under the receiver operating characteristic (ROC) curve with the pROC package in Program R. We assessed goodness-of-fit for 2 sets of parameter estimates. First, we used the weighted mean of the coefficient estimates from the 14 samples to assess the goodness-of-fit for our final model to our sample. Second, we fit the top model to each owl, estimated model coefficients for each owl, and used those estimates to assess the area under the ROC curve for individual owls.

RESULTS

Sample Selection and Telemetry Monitoring Results

We radio-marked 14 adult California spotted owls during 2006 (4 pairs, 4 single F, and 2 single M). These owls were distributed across a 271,320-ha area. Tracking periods among owls averaged 99.9 days (SE = 8.7 days) but varied greatly (45–136 days, median = 77 days). We removed 1 female from the analysis because she disappeared from her territory shortly after her capture. We found her remains on 11 July 2007 on private property approximately 18 km from her capture site. Another female was killed in her territory by a vehicle around 5 August 2006, but we had obtained 52 telemetry locations prior to her death, which was sufficient to estimate a home-range size, so we included data from this bird in our analyses. Shortly after this female's death, her mate dispersed and established a new home range 4.5 km from his previous activity center. Therefore, we treated this owl as 2 separate samples (pre- and post-5 Aug) because the 2 home ranges were in completely different areas, the 2 areas had different management regimes (the first on public land and the second on private land), his pair status changed, and he represented a breeding dispersal (Blakesley et al. 2006). A male we captured on 1 June 2006 disappeared sometime after 10 August 2006. We were unable to relocate him despite conducting extensive ground and air searches. However, we obtained 41 telemetry locations over 71 days so we included him in our analysis. Therefore, our sample size for analysis was 14 data sets from 13 owls. We collected 1,337 usable (i.e., error ellipse <5 ha) telemetry locations from 8 June to 27 October 2006, ranging from 41 to 209 ($\bar{x} = 95.5$, SE = 13.4) locations per owl. We also obtained daytime roost locations for owls because we visually monitored their reaction to radios.

Home Range

Mean home-range sizes varied from 508 ha to 946 ha, depending on the home-range estimator we used. Generally, the MCP produced the largest estimates and the fixed-kernel density estimator produced the smallest. However, the adaptive-kernel or the fixed-kernel were always the most parsimonious estimators of owl home range (adaptive $n = 5$, fixed $n = 9$). Mean home-range size of the most parsimonious home-range models was 554.9 ha (SE = 99.9 ha). All home-range models appeared to meet model assumptions (linear relationship between predictors and response, constant variance, and normally distributed), with the exception that paired owls may not have been independent, which is why we included pair status as a model covariate (model 7, Table 1). Patch heterogeneity (PPA) was most correlated with differences in home range sizes of owls (model 5). The relative likelihood of this model ($w = 0.615$) was 3.60 times more likely than the second-ranked model ($w = 0.171$) and 51.25 times more likely than the no-effect (null) model ($w = 0.012$; Table 1). The parameter estimate for heterogeneity ($\beta = 55.17$, SE = 14.38; 95% CI = 23.86–87.40; Fig. 1) indicated that home-range size increased as heterogeneity increased.

Male and female mean home-range sizes averaged 378.7 ha and 722.0 ha, respectively, suggesting that females had larger home ranges. However, the model that included only sex (model 6) had little support from the data ($w = 0.014$; Table 1), and the confidence interval for the parameter estimate overlapped zero ($\beta = -352.3$, SE = 181.5; 95% CI = −747.68, 43.08). The parameter estimate was heavily influenced by one female (ED200) who made large erratic movements (perhaps a floater, sensu Franklin 1992). We estimated the influence of this owl on model parameters by calculating the DFBETAS value for each parameter using the STATS package in Program R. The DFBETAS value for the slope of the variable sex was 0.72, which exceeded the sample-size corrected cut-off value ($2/\sqrt{n} = 0.53$) that indicates influential observations (Belsley et al. 1980). After excluding this owl from the analysis, male and female mean home-range sizes were 378.7 ha and 622.0 ha, respectively ($\beta = -243.3$, SE = 157.7; 95% CI = −552.68, 65.79). Therefore, these data were not sufficiently precise to detect a difference in male and female home-range sizes, if a difference was present.

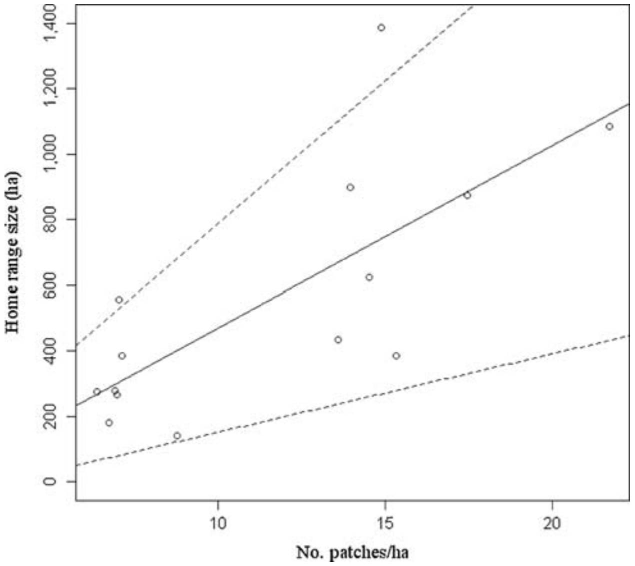

Figure 1. California spotted owl home-range sizes as a function of the relative patchiness within owl home ranges (TOT_HR = 55.17 × PPA [an index of relative patchiness of each owl's home range] − 86.12) in the central Sierra Nevada, California, June–October 2006. We estimated patchiness by dividing the number of different vegetation patches by the home-range size for each owl. The 95% confidence intervals for the slope did not overlap zero (CI = 29.64, 81.62).

Habitat Selection

Of 2,161 random vegetation patches classified throughout the study area, the percent cover of available vegetation categories were: hardwood forest = 8%, areas with low canopy cover = 28%, pole-sized conifer forest (medium to high canopy cover) = 4%, medium-sized conifer forest with medium canopy cover = 10%, medium-sized conifer forest with high canopy cover = 44%, mature conifer forest with medium canopy cover = 1%, mature conifer forest with high canopy cover = 3%, and water = 2%. Vegetation-patch size ranged from 0.5 ha to 5,049.1 ha ($\bar{x} = 70.0$ ha). User and producer mapping accuracy of all vegetation classes were >80%, except producer accuracy of mature conifer forest with medium canopy cover (50%) and user and producer accuracy of mature conifer forest with high canopy cover (71% and 67%, respectively). The proportions of vegetation classes within home ranges (used home-range habitat) varied widely among owls (Table 2), but on average consisted of: hardwood forest = 3.5%, areas with low canopy cover = 11.8%, pole-sized conifer forest (medium to high canopy cover) = 6.3%, medium-sized conifer forest with medium canopy cover = 19.0%, medium-sized conifer forest with high canopy cover = 47.1%, mature conifer forest with medium canopy cover = 1.6%, mature conifer forest with high canopy cover = 10.7%, and water = 0.0%. Mature forests with medium canopy cover and mature forest with high canopy cover were selected most often relative to their availability (i.e., had the highest selection ratios; selection ratios = 2.98 and 3.68, respectively; Table 2). However, due to variability among owls all vegetation classes had a selection ratio with a 90% Bonferroni confidence interval that overlapped one.

Foraging habitat selection within the home range was most correlated with vegetation class, patch size, and their interaction (model 15, Table 3, $n = 14$). There were no competing models ($\Delta \mathrm{AIC} < 2$; Burnham and Anderson 2002). Therefore, we used this top model to make inferences about owl foraging-habitat selection. The effect of increasing patch size varied among vegetation classes (Fig. 2). In general, the relative probability that hardwood forests and pole-sized conifer forests were used increased as patch size increased, whereas probability of use of areas with low canopy cover, medium-sized conifer forests with either medium or high canopy cover, and mature forests with either medium or high canopy cover decreased as patch size increased (Fig. 2). In relation to patch size, relative probability of using mature forests with medium canopy cover and pole-sized conifer forests decreased and increased the most dramatically, respectively (Fig. 2). The substantial decrease in relative probability of using mature forests with medium canopy cover may be due to the scarcity of that vegetation class in patch sizes >38.13 ha ($\bar{x} = 8.48$ ha). For all patch sizes

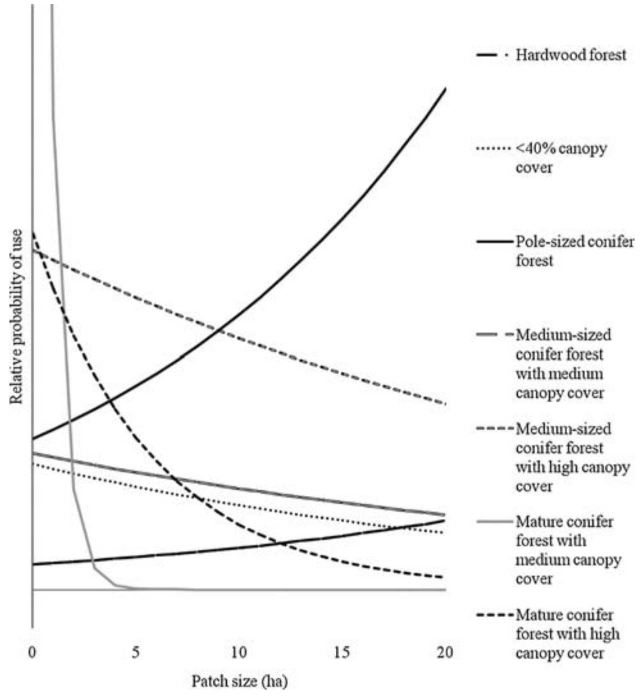

Figure 2. Relative probability of use by California spotted owls of 7 vegetation types in relation to vegetation patch size in the central Sierra Nevada, California from June to October 2006. We estimated relative probability of use using exponentiation of the parameter estimates of the most parsimonious model for our data [resource selection function = w_i = exp(β_1 vegetation type$_i$ + β_2 vegetation type$_i$ × patch size)]. Vegetation size classes were: pole (15–28 cm dbh), medium (28–68 cm dbh), and mature (>60 cm dbh). Canopy cover classes were: medium (40–70%) and high (>70%).

>10 ha, pole-sized coniferous forests had the highest relative probability of use; for all patch sizes <1 ha mature forests with medium canopy cover had the highest relative probability of use (Fig. 2). The goodness-of-fit tests (area under the ROC curve) indicated that our final model (in which we calculated the parameter estimates using the weighted mean of the parameter estimates from all owls in our sample) only fit the data moderately well (area under the ROC = 0.66). However, mean area under the ROC curve when we fit the model to individual owls was 0.88 (range = 0.69–0.98). Kolmogorov–Smirnov tests on the distance-to-edge distributions of used sites versus random sites were statistically significant ($P < 0.05$) for hardwood forests, medium-sized conifer forests with medium canopy cover, medium-sized conifer forests with high canopy cover, and mature forest with high canopy cover. However, differences in mean values of distance-to-edge between used and random locations were <10 m and unlikely to be biologically significant, except for mature forests with high canopy cover. Owls using this type of forest on average used areas 30.5 m closer to edges than random areas ($P < 0.001$).

DISCUSSION

Home-Range Estimation

The fixed- and adaptive-kernel density estimators were always the most parsimonious of home-range estimators of California spotted owls, likely due to the flexibility of nonparametric estimation in modeling complex patterns (Worton 1989). Previous studies of California spotted owl home ranges used the MCP as their primary estimator. Although this estimator is biased, we estimated it for comparative purposes. Our MCP estimate ($\bar{x} = 946$ ha) was similar to the mean MCP estimate from 3 previous home-range studies of the California spotted owl in the central Sierra Nevada (combined weighted [by sample size] $\bar{x} = 862$ ha; Laymon 1988, $\bar{x} = 856$ ha, $n = 12$; Call et al. 1992, $\bar{x} = 1{,}520$ ha, $n = 5$; Zabel et al. 1992, $\bar{x} = 728$ ha, $n = 24$). However, our median estimate (547.1 ha) was smaller than previous studies (Laymon 1988, median = 1,005 ha; Call et al. 1992, median = 1,439 ha; Zabel et al. 1992, median not reported).

We did not find support for our hypothesis that owls having the highest proportion of mature vegetation within their home range would have the smallest home range despite many studies linking spotted owls to old growth or mature forests (Forsman et al. 1984, Carey et al. 1990, Gutiérrez et al. 1995). Home-range size variation was most correlated with the number of patches within home ranges (i.e., habitat heterogeneity). There were alternative explanations for this result: owls may have been occupying patchy landscapes that enhanced their foraging opportunities or fitness (Franklin et al. 2000); the patterns may simply have reflected the nature of habitat distribution in the central Sierra Nevada because most areas we studied did not contain large contiguous areas of old forest; or it may have meant that owls in heterogeneous areas have to travel longer distances to forage, which would have been reflected as a larger home-range size.

Habitat Selection

None of the selection ratios for any particular vegetation class was different from 1 given the 90% Bonferroni confidence intervals. Thus, we could not distinguish whether owls selected vegetation classes in proportion to their availability, or alternatively, that estimates of selection ratios were not sufficiently precise to detect selection or avoidance for any particular vegetation class. However, mature forests with medium and high canopy cover had the highest selection ratios, whereas water, hardwoods, and areas with low canopy cover had the lowest selection ratios, which was consistent with other studies of home-range habitat selection by spotted owls (Gutiérrez et al. 1995).

The goodness-of-fit tests for our final model suggested that vegetation type, patch size, and their interaction were good predictors of owl habitat use within a home range (area under ROC for this model fit to each owl = 0.69–0.98, $\bar{x} = 0.88$). However, because foraging habitat selection varied among owls, the model with coefficients estimated from all of the owls in our sample did not predict data as well as covariates we estimated from individual owls. This variation in habitat selection suggests that vegetation type, patch size, and their interaction were correlated with spotted owl habitat selection but that there was considerable variation in selection among owls. In general, foraging sites having mature forests with medium (40–70%) canopy cover (vegetation class 6) had a high relative probability of selection for patches <1 ha. However, due to limited availability of patches of this vegetation class >30 ha, and its low mapping accuracy (50% and 83% for user and producer accuracy, respectively), this probability of selection result was inconclusive. Mature forests with high (>70%) canopy cover did not have a high relative probability of selection at this scale. Owls using this class foraged more closely to edges than random points, which was consistent with the findings by Franklin et al. (2000), who reported that annual survival and reproductive output were positively correlated with the amount of edge between mature and old-growth forests and other vegetation classes. There was also the possibility that the size of very small patches were incorrectly identified to foraging location because the size of acceptable confidence ellipses was larger than these small patches. Pole-sized conifer forests had the highest probability of selection in all patches >10 ha. Although owls showed selection for this vegetation class for habitat within home-ranges (second-order selection; Table 2), the selection ratio was not as high as it was for medium- to large-sized conifer forests. Selection probability of hardwood forests was also high in large patch sizes. Laymon (1988) reported similar results for spotted owls in the central Sierra Nevada.

Our results were also consistent with Franklin et al. (2000) who suggested that a mosaic of older forest interspersed with other vegetation types was correlated with high fitness in northern spotted owls (*S. o. caurina*). California spotted owls in the central Sierra Nevada 1) had home-range sizes that correlated with landscape habitat heterogeneity, 2) had home ranges with high proportions of mature forests, and 3) selected large areas of pole-sized coniferous forests. Although pole-sized coniferous forests had a higher selection probability than mature forests for foraging areas, mature forests were also related to home-range selection; thus, both forest types were related to owl home-range selection. Folliard et al. (2000) also reported that owls did not use landscapes dominated by young forests for nesting if they lacked patches of older forest. It was possible that small patches of mature forests were embedded within the larger patches of pole-sized stands that owls were using for foraging, but our mapping techniques were not sufficiently precise to detect these areas. In addition, some habitats we classified as pole stands might actually have been stands of younger forest that had residual trees. Residual trees were uncommon outside of mature or old growth stands but their presence within stands seems to facilitate owl use (e.g., Moen and Gutiérrez 1997). These residual trees were less likely to be detected by our habitat delineation techniques than if we had used an advanced mapping technology such as light detection and ranging (LIDAR).

We conducted our study during a year when owls failed to reproduce and, thus, our study may not be indicative of the habitat required by spotted owls when raising offspring because foraging areas may change when owls have dependent young. Further, the subset of habitat metrics we examined probably did not incorporate all habitat components important to owls selecting foraging habitat (e.g., differences in vegetation structure between stands used and not used for foraging) and probably did not reflect habitat required to meet other needs (e.g., nest sites). However, we believe our results represented an unbiased estimate of general foraging habitat use of central Sierra Nevada spotted owls during a year of poor reproduction. Studies of selection patterns over time would be more likely to reveal the influence of patterns on owl fitness or population growth.

MANAGEMENT IMPLICATIONS

Management of California spotted owls in the central Sierra Nevada has relied on protecting 121 ha of the best habitat (i.e., vegetation classes 4, 5, 6, and 7) around owl nest or roost sites (Protected Activity Centers [PACs]; U. S. Forest Service 2004). There are numerous studies that suggest owls in our study area center their territories in areas that have greater amounts of these vegetation classes than are available to them (Verner et al. 1992, Chatfield 2005). Although forests dominated by medium-sized trees with >40% canopy cover (vegetation classes 4 and 5) are common in our study area, the distribution of large stands of mature forests (vegetation classes 6 and 7) outside of PACs is sparse. Because our results suggest that owls select home ranges with high proportions of mature forest, of which little remains in the central Sierra Nevada, we recommend that mature forest continue to receive protection.

We found that home-range size was positively correlated with heterogeneous landscapes. This finding was somewhat confounded by the different landscape compositions among owl home ranges. Moreover, our results were observational and because of this, we did not infer either cause and effect relationships or that heterogeneous landscapes were better or worse for owls. However, our study did provide a framework for thinking about forest or fire management strategies in the future. If landscape heterogeneity (i.e., disjunct patches of foraging habitat) requires owls to expend greater energy to move between hunting patches, then the landscape habitat heterogeneity we observed associated with home-range selection would be disadvantageous to foraging owls. It would imply that what we observed were landscapes owls used because they had no other alternatives, which was also supported by the sparseness of mature forest in our study area. Alternatively, if owl fitness in the central Sierra Nevada was associated with landscape heterogeneity (e.g., older forests interspersed with other vegetation types as in Franklin et al.'s [2000] study), then it suggests owls might be selecting heterogeneous landscapes and management of some level of heterogeneity may be desirable.

Although our results suggest owls were selecting pole-sized conifer forests for foraging locations, we do not recommend simply managing for this type of forest without further examining the relationship between these forests, owl foraging, and owl fitness. We recommend that management for pole-sized conifer forest proceed with caution and under an adaptive management framework to monitor owl population response to management. Nevertheless, our study supports the hypothesis that owls will use a much broader array of forests for foraging than they will for nesting.

ACKNOWLEDGMENTS

We thank D. Andersen, J. Fieberg, C. Phillips, M. Bechard, and 2 anonymous reviewers for providing valuable comments on earlier drafts of the paper. C. Binschus, A. Hover, R. Hundt, T. Lavictoire, D. Wilcox, and J. Wright assisted in field data collection. M. Seamans and D. Tempel also provided valuable suggestions. M. Bond conducted an accuracy assessment of USFS vegetation maps. W. Berigan provided GIS and technical support. The University of California, Berkeley's Blodgett Forest Research Station and their staff, S. Rambeau, R. Heald, R. York, and F. Schurr, provided much assistance and cooperation during the study. Funding was provided by the USFS (contract no. 53-91S8-5-ECO54 to RJG).

LITERATURE CITED

Belsley, D. A., E. Kuh, and R. E. Welsch. 1980. Regression diagnostics: identifying influential data and sources of collinearity. John Wiley and Sons, New York, New York, USA.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools>. Accessed 1 Jan 2007.

Bias, M. A., and R. J. Gutiérrez. 1992. Habitat associations of California spotted owls in the central Sierra Nevada. Journal of Wildlife Management 56:584–595.

Blakesley, J. A., D. R. Anderson, and B. R. Noon. 2006. Breeding dispersal in the California spotted owl. Condor 108:71–81.

Bond, M. L., M. E. Seamans, and R. J. Gutiérrez. 2004. Modeling nesting habitat selection of California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada using standard forest inventory metrics. Forest Science 50:773–780.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burt, W. H. 1943. Territoriality and home-range as applied to mammals. Journal of Mammalogy 24:346–352.

Call, D. R., R. J. Gutiérrez, and J. Verner. 1992. Foraging habitat and home-range characteristics of California spotted owls in the Sierra Nevada. Condor 94:880–888.

Carey, A. B., and K. C. Peeler. 1995. Spotted owls: resource and space use in mosaic landscapes. Journal of Raptor Research 29:223–239.

Carey, A. B., J. A. Reid, and S. P. Horton. 1990. Spotted owl home-range and habitat use in southern Oregon Coast Ranges. Journal of Wildlife Management 54:11–17.

Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. Ecological Monographs 62:223–250.

Chatfield, A. H. 2005. Habitat selection by a California Spotted Owl population: a landscape scale analysis using resource selection functions. Thesis, University of Minnesota. St. Paul, USA.

Folliard, L. B., K. P. Reese, and L. V. Diller. 2000. Landscape characteristics of northern spotted owl nest sites in managed forests of northwestern California. Journal of Raptor Research 34:75–84.

Forsman, E. D. 1981. Molt of the spotted owl. Auk 98:735–742.

Forsman, E. D. 1983. Methods and materials for locating and studying spotted owls. U.S. Forest Service General Technical Report PNW-162. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs 87.

Franklin, A. B. 1992. Population regulation in northern spotted owls: theoretical implications for management. Pages 815–827 *in* D. R. McCullough, and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Sciences, London, United Kingdom.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. F. Wagner. 1996. Methods for collecting and analyzing demographic data on the northern spotted owl. Studies in Avian Biology 17:12–20.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539–590.

Gutiérrez, R. J., J. Verner, K. S. McKelvey, B. R. Noon, G. S. Steger, D. R. Call, W. S. LaHaye, B. B. Bingham, and J. S. Senser. 1992. Habitat relations of the California spotted owl. Pages 79–147 *in* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck, Jr., technical coordinators. The California spotted owl: a technical assessment of its current status. General Technical Report PSW-GTR-133. U.S. Forest Service, Albany, California, USA.

Gutiérrez, R. J., A. B. Franklin, and W. S. LaHaye. 1995. Spotted owl (*Strix occidentalis*). *in* A. Poole, and F. Gill, editors. The birds of North America number 179: life histories for the 21st century. The Philadelphia Academy of Sciences and The American Ornithologists' Union, Washington, D.C., USA.

Horne, J. S., and E. O. Garton. 2006a. Selecting the best home range model: an Information Theoretic approach. Ecology 87:1146–1152.

Horne, J. S., and E. O. Garton. 2006b. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. Journal of Wildlife Management 70:641–648.

Horne, J. S., and E. O. Garton. 2007. Animal space use 1.2. Available at: <http://www.cnr.uidaho.edu/population_ecology/animal_space_use.htm>. Accessed 15 Sep 2008.

Irwin, L. L., T. L. Fleming, and J. Beebe. 2004. Are spotted owl populations sustainable in fire prone forests? Journal of Sustainable Forestry 18:1–28.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Küchler, A. W. 1977. Appendix: the map of the natural vegetation of California. Pages 909–938 *in* M. G. Barbour, and J. Major, editors. Terrestrial vegetation of California. John Wiley and Sons, New York, New York, USA.

LaHaye, W. S., R. J. Gutiérrez, and D. R. Call. 1997. Nest-site selection and reproductive success of California spotted owls. Wilson Bulletin 109:42–51.

Laver, P. N., and M. J. Kelly. 2008. A critical review of home-range studies. Journal of Wildlife Management 72:290–298.

Laymon, S. A. 1988. Ecology of the spotted owl in the central Sierra Nevada, California. Dissertation, University of California, Berkeley, USA.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, Dordecht, The Netherlands.

Mayer, K. E., and W. F. Laudenslayer, Jr. 1988. A guide to the wildlife habitats of California. California Department of Forestry and Fire Protection, Sacramento, USA.

McNab, B. K. 1963. Bioenergetics and the determination of home-range size. American Naturalist 97:133–140.

Moen, C. A., and R. J. Gutiérrez. 1997. California spotted owl habitat selection in the central Sierra Nevada. Journal of Wildlife Management 61:1281–1287.

Murtaugh, P. A. 2007. Simplicity and complexity in ecological data analysis. Ecology 88:56–62.

Skinner, C. N., and C. Chang. 1996. Fire regimes, past and present. Pages 1041–1069 *in* Sierra Nevada ecosystem project, final report to congress. Volume 2. Assessments and scientific basis for management options. Centers for Water and Wildland Resources, University of California, Davis, USA.

Solis, D. M. 1983. Summer habitat ecology of spotted owls in northwestern California. Thesis, Humboldt State University, Arcata, California, USA.

Story, M., and R. G. Congalton. 1986. Accuracy assessment: a user's perspective. Photogrammetric Engineering and Remote Sensing 52:397–399.

Thomas, D., and E. Tayler. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322–330.

U.S. Forest Service. 2004. Framework. Sierra Nevada forest plan amendment: final supplemental environmental impact statement. Region 5, U.S. Forest Service, Vallejo, California, USA.

U.S. Department of Agriculture National Agricultural Imagery Program. 2005. Available at: <http://datagateway.nrcs.usda.gov>. Accessed 15 Jul 2006.

Verner, J., K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, Jr., and T. W. Beck, technical coordinators. 1992. The California spotted owl: a technical assessment of its current status. General technical report PSW-GTR-133. U.S. Forest Service, Albany, California, USA.

Wasser, S. K., K. Bevis, G. King, and E. Hanson. 1997. Noninvasive physiological measures of disturbance in the northern spotted owl. Conservation Biology 11:1019–1022.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Zabel, C. J., G. N. Steger, K. S. McKelvey, G. P. Eberlein, B. R. Noon, and J. Verner. 1992. Home-range size and habitat-use patterns of California spotted owls in the Sierra Nevada. Pages 149–163 *in* J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérrez, G. I. Gould, and T. W. Beck, Jr., technical coordinators. The California spotted owl: a technical assessment of its current status. General technical report PSW-GTR-133. U.S. Forest Service, Albany, California, USA.

Zabel, C. J., K. S. McKelvey, and J. P. Ward, Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). Canadian Journal of Zoology 73:433–439.

Zimmerman, G. S., and R. J. Gutiérrez. 2001. Breeding season home ranges of spotted owls in the San Bernardino Mountains, California. Western Birds 32:83–87.

Associate Editor: Marc Bechard.