

FORAGING HABITAT AND HOME-RANGE CHARACTERISTICS OF CALIFORNIA SPOTTED OWLS IN THE SIERRA NEVADA¹

D. R. CALL² AND R. J. GUTIÉRREZ

Department of Wildlife, Humboldt State University, Arcata, CA 95521

JARED VERNER

USDA Forest Service, Pacific Southwest Forest and Range Experiment Station,
2081 E. Sierra Ave., Fresno, CA 93710

Abstract. We examined habitat use patterns at two spatial scales among six radio-tagged California Spotted Owls (*Strix occidentalis occidentalis*) in the Sierra Nevada. Foraging owls selected macrohabitats composed of larger trees (> 52 cm dbh) with canopy closures of 40% and greater. Owls used forests composed of medium trees (28–52 cm dbh) and habitats with less than 40% canopy closure, which is less frequently than expected. Fewer than 2% of telemetry locations occurred in clearcut/shrub/plantation habitat which represented 30% of available habitat. Foraging owls used microhabitats that were characterized by multiple vegetative strata, large tree size classes, high tree basal areas and woody debris. The median 100% minimum convex polygon home-range was 1,439 ha ($n = 5$, June to December, 1987). Telemetry locations were statistically independent when separated by five days. Estimates of minimum convex polygon and modified minimum convex polygon size based on statistically independent telemetry data were significantly smaller than estimates based on continuous and single-observation monitoring.

Key words: California Spotted Owl; *Strix occidentalis occidentalis*; Sierra Nevada; home-range size; habitat selection; foraging.

INTRODUCTION

The Northern Spotted Owl (*Strix occidentalis caurina*) has been studied intensively in an effort to understand its ecology and its relationship to commercially valuable forests of the Pacific Northwest (Forsman 1976, Forsman et al. 1984, Gutiérrez 1985, Carey et al. 1990, Franklin et al. 1990, Solis and Gutiérrez 1990). Because of extensive loss of habitat, the Northern Spotted Owl has been declared a threatened species (USDI 1990).

California Spotted Owls (*S. o. occidentalis*) also occur in late-successional forests in the Sierra Nevada (Laymon 1988, Bias and Gutiérrez 1992). However, their habitat needs are poorly understood. Therefore, we studied this subspecies in an intensively managed forest in the Sierra Nevada. Our objectives were: (1) to quantify habitat attributes, (2) to compare foraging sites with random sites, and (3) to estimate home-range size.

STUDY AREA AND METHODS

The study area was located in the Tahoe National Forest, Sierra County, California. The area was

approximately 110 km², ranging from 670 m to 1,585 m in elevation. The climate was typical of the western Sierra Nevada with dry, hot summers and wet, cold winters (Elford 1975). The area was bounded to the north by the North Yuba River and to the south by a prominent ridge (Pliocene Ridge). The east and west boundaries were prominent stream courses and Highway 49, respectively. Two-thirds of the area was composed of habitat having 0–39% canopy closure resulting primarily from fire and logging. Twenty-one percent of the area was composed of less affected (e.g., firewood and selective cut) and unmanaged forests while approximately 12% was composed of large trees with high canopy closure. The study area included an extensive network of logging access roads that we used for radio-tracking.

Lower-elevation, north-facing slopes were dominated by Douglas-fir (*Pseudotsuga menziesii*), while Ponderosa pine (*Pinus ponderosa*) was dominant on xeric sites. Higher elevation areas were dominated by white fir (*Abies concolor*) (Rundel et al. 1988). Subdominant species were sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), and black oak (*Quercus kelloggii*). The understory was predomi-

¹ Received 10 February 1992. Accepted 15 May 1992.

² Present address: Department of Zoology, Washington State University, Pullman, WA 99164.

nantly tan-oak (*Lithocarpus densiflorus*), Pacific dogwood (*Cornus* sp.) and chinquapin (*Castanopsis chrysophylla*). Portions of the study area were being clearcut logged during the course of this study.

RADIO-TELEMETRY

We located three adjacent owl territories on the Downieville Ranger District, following methods of Forsman (1983) and Franklin et al. (1990). Sex and age of the owls were determined by voice (Forsman 1976) and plumage characteristics (Forsman 1981), respectively. We captured owls using a noose pole (Forsman 1983). Each bird was banded with a U.S. Fish and Wildlife Service leg band and outfitted with a radio transmitter (Telonics, Mesa, Arizona, MOD 070 configuration). Transmitters were attached using a backpack harness made of tubular, teflon ribbon; the total package weighed 26 grams (4% of average body mass). Signals were monitored using Telonics hand-held receivers and "H" antennae. Signal bearings were measured with a hand-held compass.

We used the strongest signal method (Springer 1979) to estimate three or more bearings to a radio-tagged owl. Bearings were immediately plotted on 1:24,000-scale topographic maps, with the resulting polygon describing the intersection of the three bearings; the center of the polygon was the estimated location of the owl. If the polygon exceeded 1 ha, it was rejected and additional bearings were taken until a more precise location was estimated (Solis and Gutiérrez 1990). We did not quantify telemetry accuracy. However, because of the many access roads we were always less than 0.5 km from the owls and frequently <200 m from the birds. Each night we randomly selected the order in which the owls would be monitored. Once an owl was located, we monitored its movements continuously for approximately three hours beginning one-half hour before sunset. Then the next randomly selected owl was monitored for three hours, and so on until approximately one-half hour after sunrise. Movements were inferred from a noticeable drop in transmitter signal strength and pulse frequency (Solis 1983, Ganey and Balda 1989). We scheduled monitoring sessions for ten days sequentially followed by a four day break. We considered 1 February to 1 October the breeding season and the remainder of the year the non-breeding season (following Solis 1983).

MACROHABITAT ANALYSIS

We delineated macrohabitat polygons (i.e., habitat patches) based on the diameter at breast height (dbh; Dilworth 1981) and crown closure of dominant trees. Where possible we visually verified habitat types and boundaries. Tree size categories included: (1) clearcut-shrub-plantation (C/S/P, 0-12.6 cm dbh), (2) small trees (12.7-27.7 cm dbh), (3) medium trees (27.8-53.1 cm dbh), and (4) large trees (53.2+ cm dbh). Crown closure categories included (1) 0-39%, (2) 40-69%, and (3) 70% or more (unpubl. data, USDA Forest Service timber type maps).

We used the methods of Neu et al. (1974) to test the hypothesis that Spotted Owls used macrohabitat types in proportion to their availability. Only one randomly selected point per night for each owl was used in this analysis. Nighttime locations were considered foraging sites and included only those locations greater than 100 m from a habitat polygon boundary to account for telemetry error (Solis 1983). We then quantified all available habitat that was greater than 100 m from any habitat polygon boundaries within the study area and also within each home-range. Thus, we could compare the proportion of observed habitat use with the proportion of available habitat within each home-range (100% minimum convex polygon, MCP) and within a broader landscape (defined by the study area boundary). We also compared the distribution of available habitat within the study area as well as within all of the owl home-ranges (MCP) using a Chi-square test. The amount of time (minutes) owls spent in different habitat types was compared using a one-way Kruskal-Wallis nonparametric Analysis of Variance (Steel and Torrie 1980:544). We used times from continuous monitoring data and conducted separate analyses for habitat classified by tree-size, canopy closure and by season.

MICROHABITAT ANALYSIS

We measured 0.04 ha and variable circular vegetation plots at both foraging and random locations to estimate 54 habitat variables. Foraging locations were randomly selected from the telemetry data (approximately 40 locations from each owl; one location per owl per night). Random plots were selected from the set of Universal Transverse Mercator coordinates within the study area. Each plot was marked on 1:24,000-scale topographic maps and located using a compass

and altimeter. We used a line intercept transect (Mueller-Dombois and Ellenberg 1974) to estimate coverage of woody debris, shrubs and small trees (<10-cm dbh). We used a 20-factor basal area prism to estimate basal area of conifers, hardwoods, and snags (Dilworth 1981). We measured diameter at breast height (dbh), average height and the condition of all trees (i.e., state of vigor) that were tallied using the prism. Sampling protocol followed Solis (1983), LaHaye (1988) and Bias and Gutiérrez (1989). Call (1990) presented a complete description of our variables and measurement techniques.

We assessed normality of habitat variables using skewness, kurtosis and probability plots and we used logarithmic, arcsine and square root transformations (Sokal and Rohlf 1987:218) to normalize variables. Because inclusion of many variables, particularly those that are correlated, can decrease the interpretability of the DFA (Stevens 1986; Williams 1982, 1983) and can reduce the ability to correctly classify plots (Ludwig and Reynolds 1988), we reduced the number of variables in our analysis as follows. We compared vegetation variables between foraging and random sites using Mann-Whitney *U* tests and retained only variables that were significantly different ($P < 0.001$). We then examined correlated variables ($r = 0.6$) and retained those that would be simplest to measure using remote sensing or in the field. We used a stepwise discriminant function analysis (DFA, Dixon et al. 1990:339) to distinguish between owl foraging and random plots during the breeding, nonbreeding and pooled seasons. Equality of group covariance matrices was tested using Box's *M* statistic (Nie et al. 1975:460). We used cross-validation to evaluate model stability by withholding a randomly selected 25% subsample of plots for reclassification and repeating this 20 times (Capen et al. 1986). We examined frequency of variable loading and mean structure coefficients (Williams 1983) to predict the relative importance of each variable. Percent correct classifications were calculated for the data used to formulate the DFA equation and the 25% subsample (independent plots) (Capen et al. 1986, LaHaye 1988). Significance of classification rates was tested using Cohen's Kappa statistic (Titus et al. 1984).

HOME-RANGE ANALYSIS

We estimated Spotted Owl home-range size with the minimum convex polygon (MCP; Hayne

1949), modified minimum convex polygon (MMCP; Harvey and Barbour 1965), and 95% adaptive kernel (AK; Worton 1989; J. Baldwin, pers. comm, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA). We estimated combined home-ranges for owl pairs by computing separate MCPs for each member and subtracting overlap between home-ranges.

Continuous monitoring data included all locations from every night. We also simulated less intensive monitoring efforts by randomly selecting subsets of locations. We separated the first subset of observations by a minimum of one night and the second subset by two nights. This progression was continued until the seventh subset, which had seven nights between observations. The first subset (one night between observations) was defined as single-observation monitoring. We then estimated the number of days needed between observations for the telemetry data to be statistically independent by calculating Schoener's t^2/r^2 index for each of these data sets (Schoener 1981; Swihart and Slade 1985a, 1985b; Carey et al. 1989). We defined the minimum time to statistical independence as the number of nights needed between observations for a majority of the data sets to have nonsignificant t^2/r^2 values (Carey et al. 1989). Additionally, we estimated the minimum time needed between locations to meet the assumptions of bivariate uniform and bivariate normal distributions (Cramer-von Mises goodness-of-fit test, Samuel and Garton 1985). Home-range size estimates were compared between models and sampling intensities using a Kruskal-Wallis ANOVA.

Adaptive kernel estimates were generated using program Home Range (J. Baldwin, unpubl. software). The program Home Range (Ackerman et al. 1989) was used to calculate MCPs and to conduct tests for independence. We manually identified vertices for MMCP home-ranges before calculating area within the polygons.

RESULTS

RADIO-TELEMETRY

We radio-marked both adult members of two pairs; one of which produced one fledgling. We also marked two additional unpaired females (one subadult, one adult). One of these latter transmitters was damaged by the bird and we did not

TABLE 1. Habitat selection by six California Spotted Owls in the Sierra Nevada, 1987. Selection evaluated using Chi-square test with Bonferroni inequalities (Neu et al. 1974).

Owl/Habitat type	Available habitat sampled from individual MCP			Available habitat sampled from study area		
	Breed ^a	Nonbreed	Pooled	Breed	Nonbreed	Pooled
Williamson male (<i>n</i> = 69)						
Medium trees ^b	-1 ^c	-1	-1	-1	-1	-1
Large trees	+1	+1	+1	+1	+1	+1
Williamson female (<i>n</i> = 55)						
Medium trees	0	-1	-1	0	-1	0
Large trees	0	+1	+1	0	+1	0
Humbug male (<i>n</i> = 64)						
Medium trees	0	+1	+1	-1	+1	+1
Large trees	0	-1	-1	+1	-1	-1
Humbug female (<i>n</i> = 61)						
Medium trees	-1	-1	-1	-1	-1	-1
Large trees	+1	+1	+1	+1	+1	+1
Grant 27 (<i>n</i> = 28)						
Medium trees	0			-1		
Large trees	0			+1		
Grant 30 (<i>n</i> = 26)						
Medium trees	0			0		
Large trees	0			0		
All owls (<i>n</i> = 303)						
Medium trees				-1	-1	-1
Large trees				+1	+1	+1
All owls (<i>n</i> = 170)						
Canopy closure 40-69%				0	+1	0
Canopy closure 70+%				0	-1	0
All owls (<i>n</i> = 214)						
Canopy closure 0-39%				-1	-1	-1
Canopy closure 40-69%				+1	+1	+1
Canopy closure 70+%				+1	+1	+1

^a Breed = breeding season (1 Feb-1 Oct); Nonbreed = nonbreeding season (1 Oct-1 Feb); Pooled = data from both seasons.

^b Medium trees = 27.8-53.1 cm dbh; large trees = 53.2+ cm dbh.

^c 0 = use of habitat equal to expected; -1 = use of habitat less than expected; +1 = use of habitat greater than expected.

use data from it in our home-range analysis because the erratic signal resulted in intermittent locations. We estimated 1,317 radio locations (104-321 locations per owl) over a period of 154 days (14 June-9 December) involving 938 hours of continuous monitoring.

MACROHABITAT USE

Two percent of telemetry locations occurred in clearcut-shrub-plantation (C/S/P) habitat, 41% in habitats characterized by medium-sized trees, and 57% in habitat with large-sized trees. Twenty-two percent, 54% and 24% of telemetry locations occurred in habitats with 0-39%, 40-69%, and 70% or more canopy closure, respectively. We did not include small-sized trees or C/S/P in

any analyses of habitat selection because observed frequencies were too small for Chi-square tests. In addition, we had an insufficient sample size to test canopy closure selection for individual owls.

Owl habitat use within the study area was not random. Owls used forests with large trees more than expected (Table 1, $\chi^2 = 22.61$, $df = 1$, $P < 0.005$). Owls used forests having 40-69% and 70% or more canopy closure more than expected, while they used forests with 0-39% closure less than expected ($\chi^2 = 212.49$, $df = 2$, $P < 0.005$). Owl home-ranges had less C/S/P and more medium trees than expected while the quantity of large trees was equal to availability ($\chi^2 = 53.6$, $df = 2$, $P < 0.001$). The home-ranges also en-

TABLE 2. Characteristics of California Spotted Owl habitat used by six radio-tagged owls in the Sierra Nevada, California, 1987. Only variables that were used in the discriminant function analysis are reported.

Plot variable	Breeding (<i>n</i> = 157)		Nonbreeding (<i>n</i> = 100)		Pooled (<i>n</i> = 257)		Random plots (<i>n</i> = 359)	
	Mean	SD ^a	Mean	SD	Mean	SD	Mean	SD
Conifer BA	40.7*	20.4	30.3	15.4	36.4	19.2	22.6	17.6
Hardwood basal area (BA) ^b	6.7*	9.3	2.9	5.7	5.2	8.3	3.3	7.3
Mature tree BA	18.4*	12.4	13.0	10.3	16.1	11.8	7.9	10.2
Mature tree condition	1.4*	1.0	1.1	0.7	1.3	0.9	0.7	0.9
Mature tree dbh	62.6	21.5	61.2	23.8	62.2	22.3	61.2	50.7
Medium tree BA	13.3	10.2	9.7	8.8	11.8	9.7	8.2	10.0
Medium tree condition	1.5*	1.1	1.1	0.9	1.3	1.0	0.8	1.0
Number vegetative strata ^c	3.7	0.1	3.7	0.5	3.7	0.5	3.0	0.9
Old-growth trees BA ^d	8.2	8.3	8.1	8.3	7.5	7.8	3.1	5.9
Old-growth tree condition ^e	1.4*	1.5	0.8	0.9	1.2	1.4	0.5	1.0
Old-growth tree dbh	79.6	54.9	74.2	57.4	77.4	56.0	38.8	55.2
Percent canopy closure ^f	95.1*	7.5	86.8	14.3	91.9	11.5	69.6	33.0
Percent herbaceous ground cover ^g	4.5*	7.0	2.0	5.0	3.6	6.5	7.6	13.6
Percent large woody debris	2.6	3.4	4.1	8.3	3.2	5.9	1.6	3.0
Percent small woody debris ^h	4.8*	3.6	7.2	5.8	5.7	4.7	4.5	4.7
Percent tree <10-cm dbh ⁱ	20.8	22.2	26.7	20.1	23.1	21.6	17.4	20.5
Snag BA	4.4	6.4	2.9	4.5	3.8	5.7	1.7	3.4

^a Standard deviation.

^b Basal areas estimated with 20-factor basal area prism and converted to m²/ha.

^c Number of distinct vegetative strata.

^d Diameter classes: old-growth (≥ 90.0 cm dbh), mature (52.5–89.9 cm dbh), medium (27.5–52.4 cm dbh), and small (12.5–27.3 cm dbh). Height measured with clinometer.

^e Condition classes based on Maser et al. (1979:80). Stand condition was average condition of all live trees and snags. Lower values represent higher tree vigor.

^f Estimated with concave densitometer.

^g Estimated with 10 65-cm² quadrats along line-intercept.

^h Small woody debris ≥ 30.0 -cm diameter at large end and greater than 2.5 cm at small end. Large woody debris > 30.0 cm at small end.

ⁱ Line-intercept variables measured with 23-m fiberglass tape and expressed as a percentage of cover.

* Variable significantly different between seasons ($P < 0.001$).

closed more forest with 70% or more canopy closure, while the amount of habitat with 0–39% and 40–69% canopy closure was equivalent to what was available within the study area ($\chi^2 = 8.78$, $df = 2$, $P < 0.02$).

The average time (minutes) that the owls spent in a foraging location was not influenced by tree size ($H = 1.8$, $df = 1$, $n = 465$, $P = 0.18$) or canopy closure ($H = 1.2$, $df = 1$, $n = 281$, $P = 0.54$). However, during the nonbreeding season owls spent more time ($\bar{x} = 55.6$ min, $SD = 70.1$) at foraging locations compared to foraging time during the breeding season ($\bar{x} = 40.6$, $SD = 42.9$, $H = 12.8$, $df = 1$, $n = 758$, $P = 0.0004$).

MICROHABITAT CHARACTERISTICS

We measured 359 random and 257 foraging plots (areas used by six owls), which provided an estimate within 95% of the mean for most variables with 85% and 90% confidence, respectively. Most variables were not normally distributed and transformations failed to normalize them. Of the 54 initial variables, 29 were significantly different between foraging and random plots ($P < 0.001$).

We selected 14 of these variables ($r < 0.6$; Table 2) for separate discriminant function analyses (DFA) for the breeding season and pooled seasons data. We found fewer differences between random and foraging plots during the nonbreeding season, so we limited this DFA to six variables.

We inferred from the univariate tests that owls were selecting habitats with complex stand characteristics relative to random sites (Table 2). Breeding season habitat had greater canopy closure, higher conifer and hardwood basal areas and lower tree vigor compared to nonbreeding season habitat (Table 2).

The DFA analysis indicated that the number of vegetative strata, large-tree basal areas, and canopy closure were the most important variables for discriminating foraging and random plots (Table 3). These variables loaded most often and had high structure coefficients. The percent correct classification rate for plot types based on the DFAs was greater than expected by chance for jackknife and independent estimates (Table 4).

TABLE 3. Variable loading frequency for 60 stepwise discriminant function analyses comparing foraging and random vegetation plots for six radio-tagged California Spotted Owls in the central Sierra Nevada, California, 1987.

Variable	Frequency ^a			Mean structure coefficient ^c
	Breeding ^b	Nonbreeding	Pooled	
Number of vegetative strata	20		18	0.8209
Mature tree BA	20		19	0.6795
Old-growth tree BA	7		17	0.5865
Old-growth tree condition	7		9	0.5368
Percent large woody debris	6			0.3803
Old-growth tree dbh		18		0.7364
Mature tree dbh		16		0.7598
Snag BA		8		0.5058
Percent canopy closure			18	0.7818
Percent small woody debris			6	0.2867

^a Number of times the variable entered the stepwise procedure (F to enter/remove = 4.0/3.99). Only includes variables that loaded five or more times.

^b Breeding season ($n = 385$ plots), nonbreeding season ($n = 224$ plots), pooled seasons ($n = 609$ plots).

^c Correlation between plot variable and discriminant score.

HOME-RANGE ESTIMATION

Estimates of Spotted Owl home-range size were significantly different between home-range models (Table 5; $H = 10.11$, $df = 2$, $P = 0.006$). Median values for minimum convex polygon (MCP), modified minimum convex polygon (MMCP) and adaptive kernel (AK) across all data sets were 1,180 ha, 782 ha, and 1,272 ha, respectively. Estimates based on different sampling intensities were not significantly different overall ($H = 4.51$, $df = 2$, $P = 0.105$) though the statistically independent estimates were smaller for the two polygon models ($H = 7.1$, $df = 2$, $P = 0.029$). The combined home-range size estimates (MCP) for the two owl pairs were 1,985 ha and 3,061 ha. Overlap between members of a pair ranged between 47% and 63%.

Most telemetry data sets were statistically independent when locations were separated by five days. This subsampling of the data produced sample sizes of 27 to 30 observations for each

owl. As we increased the daily separation between observations the data appeared more normally distributed. Observations separated by two days were bivariate normal for both weighted and normal tests ($P < 0.05$). Observations separated by four days were uniformly distributed ($P < 0.05$).

DISCUSSION

California spotted owls in our study selected foraging macrohabitats with larger trees and greater canopy closure than would be expected by chance. These results generally agree with findings for the Northern Spotted Owl (Forsman et al. 1984, Carey et al. 1990, Solis and Gutiérrez 1990). However, these birds did use habitat that was partially logged in the past which may indicate they will use a broader range of habitats for foraging compared to the Northern Spotted Owl. The reasons for this difference, if any, may include factors such as prey availability.

The patterns of habitat selection for medium

TABLE 4. Percent correct classifications for stepwise discriminant function analyses comparing foraging and random sites for six radio-tagged California Spotted Owls in the Sierra Nevada, 1987.

Season	Jackknife ^a		Independent ^b	
	Correct	Kappa ^c	Correct	Kappa
Breeding	79.2 (2.93) ^d	0.59**	73.8 (2.88)	0.42*
Nonbreeding	67.2 (3.9)	0.33**	63.6 (4.07)	0.24*
Pooled	72.4 (1.74)	0.45**	67.4 (2.7)	0.31**

^a Classification function based on jackknife algorithm.

^b Correct classification for plots not used to formulate discriminant equation.

^c Proportion of plots correctly classified over the number of correct classifications expected by chance.

^d () standard deviation.

** $P < 0.05$, * $P < 0.001$.

TABLE 5. Home-range size estimates (ha) for five radio-tagged California Spotted Owls in the Sierra Nevada, California, 1987.

	Num ^a	100% MCP			100% modified MCP			95% adaptive kernel			Unique dates ^e
		Cont ^b	Single ^c	Uncor ^d	Cont	Single	Uncor	Cont	Single	Uncor	
F ^f	244	1,439	1,222	737	1,037	895	317	1,319	1,038	1,007	111
F	250	2,228	2,197	2,040	1,376	1,007	782	1,597	1,869	2,217	101
F	104	1,070	941	687	447	435	78	600	957	1,141	46
M	242	1,719	1,646	1,180	1,514	1,213	537	1,628	1,511	1,592	100
M	321	1,142	922	558	968	534	150	941	1,037	626	115
Mean		1,520	1,386	1,040	1,068	817	373	1,217	1,282	1,317	

^a Total number of estimated telemetry locations.

^b Estimated from continuous monitoring data.

^c Estimated from a single observation per night.

^d Estimated from statistically uncorrelated data (five days between observations).

^e Number of nights each owl was located.

^f (F)emale, (M)ale.

and large-sized trees were nearly identical when available habitats were sampled from the entire study area (second-order selection, Johnson 1980) and from within individual home-ranges (third-order selection). However, the owls clearly demonstrated a strong second-order selection by using young successional stages less than expected.

The apparent lack of habitat selection indicated by the amount of time (minutes) spent in each habitat type may have been an artifact of our sampling methods. On average we were only able to monitor owls for 43 min per location which may have been an insufficient period of time to detect differences reflected by the other analyses. Alternatively, Spotted Owls may have a fixed search time independent of habitat use after which point the owls choose to move to a new location if no prey has been captured. Owls also moved less frequently during the nonbreeding season which may reflect conservation of energy during periods of decreased temperature and increased precipitation. This also may indicate changes in search times when there are seasonal changes in prey availability.

Our discriminant function analyses (DFA) were consistent with observations that Spotted Owls select forests with complex structure (LaHaye 1988, Solis and Gutiérrez 1990, Bias and Gutiérrez 1992). Our DFA indicated that the number of vegetative strata, high old-growth and mature tree basal area, and high canopy closure were the most important distinguishing characteristics of forest stands used by the owls. Franklin et al. (1981) showed that these features were characteristic of late-successional conifer forests.

The Spotted Owls that we studied appeared to have selected habitats with different character-

istics during the breeding and nonbreeding season. This observation was supported by a change in habitat selection at the macro-level by two owls, and the differences found using both univariate and multivariate methods. Seasonal shifts in home-range size have been reported for Spotted Owls (Forsman et al. 1984, Laymon 1988, Sisco 1990) and may represent seasonal changes in habitat requirements. Seasonal habitat selection may be due to changing prey availability, predation vulnerability, and thermoregulation needs (Barrows and Barrows 1978, Forsman et al. 1984).

California Spotted Owls monitored in our study have home-ranges similar in size to those of Northern Spotted Owls (Forsman et al. 1984, $1,545 \pm 270$ ha, $n = 12$; Carey et al. 1990, $1,580 \pm 285$ ha, $n = 9$) and larger home-ranges than the Mexican Spotted Owl (*S. o. lucida*, Ganey and Balda 1989, 648 ± 89 ha, $n = 8$). These large home-ranges relative to other *Strix* owls (Southern 1970, Nicholls and Warner 1972, Nero 1980) present a challenge to forest wildlife managers developing habitat conservation plans (Thomas et al. 1990).

We estimated that radio-telemetry locations should be separated by a minimum of five days to be statistically independent and to meet assumptions of univariate and bivariate normality. Carey et al. (1989) presented similar results for Northern Spotted Owls. We found that the MMCP model produced smaller home-range estimates which was expected given the amount of area that can be excluded using this model (Harvey and Barbour 1965). Our original analysis of sampling intensity indicated no significant difference between estimates from continuous, sin-

gle-observation and uncorrelated data. However, statistical home-range models, such as the adaptive kernel (AK), tend to produce larger estimates with smaller sample sizes (Worton 1989). Therefore, inclusion of this model in the analysis obscured obvious differences between home-range estimates for continuous and non-correlated data when we used the two polygon models. Collecting statistically independent data during short duration studies will probably lead to underestimating home-range size with nonstatistical models because of the reduced sample size inherent in this kind of sampling method (Bekoff and Mech 1984).

The data used in the DFAs were not normally distributed and had heterogeneous variance/covariance matrices. The heterogeneity is particularly important because it can distort the discriminant transformations and render classification functions invalid (Williams 1982). However, we limited our analysis to ranking the relative importance of variables known through univariate analysis to be different between groups—rather than to produce predictive models of owl habitat. Thus, we do not believe that the failure to meet this assumption affected our conclusion. We emphasize that the variables used in the analysis were correlated with owl foraging habitat and were not expected, necessarily, to be the actual features that the owls selected.

A more problematic assumption for all of the analyses was that observations were independent both in terms of replication and temporal separation (Steel and Torrie 1980, Stevens 1986). We evaluated habitat data from six owls with sampling once every night. Our analysis of time to statistical independence suggested that five days were needed between observations. However, this statistical index is based on relative spatial position (Schoener 1981) and may not reflect biological independence. We chose to include more data (sampled every day) with the caveat that our results do not reflect a population estimate. Thus, our results should not be used to develop strict habitat management guidelines or be extrapolated to a regional scale. We also emphasize that management guidelines should include effects of various landscape configurations on population demography, which we did not address here. However, our data do suggest that the owls we studied have ecological requirements similar to those of Northern Spotted Owls. This information should be incorporated with work by oth-

er investigators to develop habitat-management guidelines for the Sierra Nevada population.

ACKNOWLEDGMENTS

We thank C. Clifton, J. Holyan, W. Piercy and J. Pritchard for their dedicated field assistance. M. Chapel, C. Fowler, W. Hair, S. Kluge, T. Petit, K. Remely, S. Underwood and G. Steger provided logistical support. G. Allen, J. Baldwin, L. Fox, R. Garrott and K. Norgaard reviewed earlier drafts of this manuscript and we received helpful comments from two anonymous reviewers. Funding was provided by USDA Forest Service Cooperative Agreements PSW-87-0009CA and PSW-88-0004CA.

LITERATURE CITED

- ACKERMAN, B. B., F. A. LEBAN, E. O. GARTON, AND M. D. SAMUEL. 1989. User's manual for program Home Range. Tech. Rept. 15 (draft copy), Forestry, Wildlife and Range Experiment Station, Univ. Idaho, Moscow, ID.
- BARROWS, C., AND K. BARROWS. 1978. Roost characteristics and behavioral thermoregulation in the Spotted Owl. *Western Birds* 9:1-8.
- BEKOFF, M., AND L. D. MECH. 1984. Simulation analyses of space use: home range estimates, variability, and sample size. *Behav. Res. Methods Instrum. & Comput.* 16:32-37.
- BIAS, M. A., AND R. J. GUTIÉRREZ. 1992. Habitat associations of California Spotted Owls in the central Sierra Nevada. *J. Wildl. Manage.* 56:584-596.
- CALL, D. R. 1990. Home-range and habitat use by California Spotted Owls in the central Sierra Nevada. M.Sc. thesis, Humboldt State Univ., Arcata, CA.
- CAPEN, D. E., J. W. FENWICK, D. B. INKLEY, AND A. C. BOYNTON. 1986. Multivariate models of songbird habitat in New England Forests, p. 171-176. *In* J. Verner, M. L. Morrison, and C. J. Ralph [eds.], *Wildlife 2000*. Univ. Wisconsin Press, Madison, WI.
- CAREY, A. B., S. P. HORTON, AND J. A. REID. 1989. Optimal sampling for radio telemetry studies of Spotted Owl habitat and home-range. Res. Paper PNW-RP-416, USDA Forest Service, Portland.
- CAREY, A. B., J. A. REID, AND S. P. HORTON. 1990. Spotted Owl home-range and habitat use in southern Oregon coast ranges. *J. Wildl. Manage.* 54:11-17.
- DILWORTH, T. 1981. Log scaling and timber cruising. Oregon State Univ. Press, Corvallis, OR.
- DIXON, W. J., M. B. BROWN, L. ENGELMAN, AND R. I. JENNICH. 1990. BMDP statistical software manual. Univ. of California Press, Berkeley, CA.
- ELFORD, R. 1975. Climate, p. 96-98. *In* Soil survey of Nevada County area. USDA Soil Conservation Service and Forest Service, Washington, DC.
- FORSMAN, E. D. 1976. A preliminary investigation of the Spotted Owl in Oregon. M.Sc. thesis, Oregon State Univ., Corvallis, OR.
- 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. Gen. Tech. Rept. PNW-12, USDA Forest Service, Portland, OR.
- FORSMAN, E. D., E. C. MESLOW, AND H. M. WRIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Mong.* 87.
- FRANKLIN, A. B., J. P. WARD, R. J. GUTIÉRREZ, AND J. I. GOULD, JR. 1990. Density of Northern Spotted Owls in Northwestern California. *J. Wildl. Manage.* 54:1-10.
- FRANKLIN, J. F., K. CROMACK, JR., W. DENISON, A. MCKEE, C. MASER, J. SEDELL, F. SWANSON, AND G. JUDAY. 1981. Ecological characteristics of old-growth Douglas-fir forests. Gen. Tech. Rept. PNW-118, USDA Forest Service, Portland, OR.
- GANEY, J. L., AND R. P. BALDA. 1989. Home-range characteristics of Spotted Owls in Northern Arizona. *J. Wildl. Manage.* 53:1159-1165.
- GUTIÉRREZ, R. J. 1985. An overview of recent research on the Spotted Owl, p. 39-49. *In* R. J. Gutiérrez and A. B. Carey [eds.], *Ecology and management of the Spotted Owl in the Pacific Northwest*. Gen. Tech. Rept. PNW-185, USDA Forest Service, Portland, OR.
- HARVEY, M. J., AND R. W. BARBOUR. 1965. Home range of *Microtus ochrogaster* as described by a modified minimum area method. *J. Mammal.* 46:398-402.
- HAYNE, D. W. 1949. Calculation of size of home-range. *J. Mammal.* 30:1-18.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- LAHAYE, W. S. 1988. Nest site selection and nesting habitat of the Northern Spotted Owl (*S. o. caurina*) in northwestern California. M.Sc.thesis, Humboldt State Univ., Arcata, CA.
- LAYMON, S. A. 1988. Ecology of the Spotted Owl in the central Sierra Nevada, California. Ph.D.diss. Univ. of California, Berkeley, CA.
- LUDWIG, J. A., AND J. F. REYNOLDS. 1988. Statistical ecology. John Wiley and Sons, New York.
- MASER, C., R. G. ANDERSON, K. CROMACK, JR., J. T. WILLIAMS, AND R. E. MARTIN. 1979. Dead and down woody material, p. 78-95. *In* W. J. Thomas [ed.], *Wildlife habitats in managed forests*. Handbook 553, USDA Forest Service, Portland, OR.
- MUELLER-DOMBOIS, D., AND J. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.
- NERO, R. W. 1980. The great gray owl phantom of the Northern forests. Smithsonian Institution Press, Washington, DC.
- NEU, C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38:541-545.
- NICHOLLS, T. H., AND D. W. WARNER. 1972. Barred owl habitat use as determined by radiotelemetry. *J. Wildl. Manage.* 36:213-224.
- NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences. McGraw Hill, New York.
- RUNDEL P. W., D. J. PARSONS, AND D. T. GORDON. 1988. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges, p. 559-599. *In* M. G. Barbour and J. Major [eds.], *Terrestrial vegetation of California*. California Native Plant Society, Sacramento, CA.
- SAMUEL, M. D., AND E. O. GARTON. 1985. Home-range: a weighted normal estimate and tests of underlying assumptions. *J. Wildl. Manage.* 49:513-519.
- SCHOENER, T. W. 1981. An empirically based estimate of home-range. *Theor. Pop. Biol.* 20:281-325.
- SISCO, C. 1990. Seasonal home-range and habitat ecology of Spotted Owls in northwestern California. M.Sc.thesis, Humboldt State Univ., Arcata, CA.
- SOKAL, R. R., AND F. J. ROHLF. 1987. Introduction to biostatistics. W. H. Freeman, New York.
- SOLIS, D. M., JR. 1983. Summer habitat ecology of Spotted Owls in northwestern California. M.Sc.thesis, Humboldt State Univ., Arcata, CA.
- SOLIS, D. M., JR., AND R. J. GUTIÉRREZ. 1990. Summer habitat ecology of Northern Spotted Owls in northwestern California. *Condor* 92:739-748.
- SOUTHERN, H. N. 1970. The natural control of a population of Tawny owls (*Strix aluco*). *J. Zool., Lond.* 162:197-285.
- SPRINGER, J. T. 1979. Some sources of bias and sampling error in radio triangulation. *J. Wildl. Manage.* 43:926-935.
- STEEL, R.G.D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. McGraw Hill, New York.
- STEVENS, J. 1986. Applied multivariate statistics for the social sciences. Lawrence Erlbaum Assoc., Hillsdale, NJ.
- SWIHART, R. K., AND N. A. SLADE. 1985a. Influence of sampling interval on estimates of home-range size. *J. Wildl. Manage.* 49:1019-1025.
- SWIHART, R. K., AND N. A. SLADE. 1985b. Testing for independence of observations in animal movements. *Ecology* 66:1176-1184.
- THOMAS, J. W., E. D. FORSMAN, J. B. LINT, E. C. MESLOW, B. R. NOON, AND J. VERNER. 1990. A conservation strategy for the Northern Spotted Owl. USDA Forest Service, Portland, OR.
- TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *Am. Midl. Nat.* 107:1-7.
- USDI. 1990. Endangered and threatened wildlife and plants; Determination of threatened status for the Northern Spotted Owl: final rule. *Federal Register* 55:26114-26194.
- WILLIAMS, B. K. 1982. A simple demonstration of the relationship between classification and canonical variates analysis. *Am. Statist.* 36:363-365.
- WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology* 64:1283-1291.
- WORTON, P. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 7:164-168.