

Chapter 6

Home-Range Size and Habitat-Use Patterns of California Spotted Owls in the Sierra Nevada

Cynthia J. Zabel, George N. Steger, Kevin S. McKelvey, Gary P. Eberlein, Barry R. Noon, and Jared Verner

Home range is an "area utilized by an individual during its normal activities such as food gathering, mating, and caring for young" (Burt 1943), as distinguished from its territory, which is typically defended against intrusion by other individuals of the same species, except a mate or a potential mate (Nice 1941). Home ranges of neighboring individuals commonly overlap, but territories are usually more exclusive. Studies of home ranges often require attachment of radio transmitters on animals, so their movements can be monitored. Many such studies have been done on spotted owls (recent review in Thomas et al. 1990, appendix I). In this chapter we report results of two radio-tracking studies in three different study areas, one in the northern and two in the central Sierra Nevada. These data provide estimates of home-range sizes of individual males and females, and of pairs, during different periods of the annual cycle. In addition, we have compared patterns of habitat use in home ranges in relation to the different habitats available to the birds. In that sense, habitat-use information given here augments that presented in Chapter 5.

A fundamental difference exists, however, between the scales of habitat use reported here and those reported in Chapter 5. Studies in Chapter 5 examined habitat selection by owls at three scales—landscape, home-range, and stand. Stand-scale studies measured habitat attributes very near the point of an owl's activity—nesting, roosting, or foraging—and compared them with similar measurements at random locations in the surrounding forests. This was a fine-grained scale of analysis that addressed habitat attributes closely associated with an activity. Studies reported in Chapter 6 were done at a scale intermediate between the home-range and stand scales. Here we examined habitat selection at the scale of a habitat polygon (stand), a patch in the overall forest landscape that was similar enough within itself to be set apart from adjoining patches. The minimum patch size we recognized was 5 acres. For example, a meadow would be one polygon type, and an adjoining patch of forest with fairly uniform canopy closure and tree size-class would be another type. But a forest polygon could still be heterogeneous—and typically it is, with smaller subgroups of trees within it having higher canopy closure and/or larger trees than the polygon as a whole. If an owl were selecting for attributes at a scale less than the polygon size, the stand-level analyses reported in Chapter 5

would be much more likely to detect that selection than would be the results reported in this chapter. We can differentiate habitat selection only at the level of the entire polygon. Consequently, evidence of habitat selection given in this chapter is likely to be less conclusive than that given in Chapter 5.

Study Areas

Results presented here came from two study areas, one in the Sierra National Forest (NF) near the southern end of the Sierra Nevada, and the other east of Lassen National Park (NP) in the Lassen NF, at the northern end of the Sierra Nevada and the extreme southern end of the Cascade Mountains. The study area in the Sierra NF had one division in mixed-conifer forest in the Huntington quadrangle (hereafter the S-CON site) and another in foothill riparian/hardwood forests and adjoining oak-pine woodlands in the Patterson quadrangle (the S-OAK site). These were situated about 45 miles northeast of Fresno, in watersheds of the San Joaquin River and the North Fork of the Kings River. Vegetation in the S-CON site was dominated by mixed-conifer forests of white fir, Jeffrey pine, ponderosa pine, sugar pine, incense-cedar, and red fir. Elevations ranged from 5,000 to 8,000 feet. Much of the area was selectively logged from 1880 to the present, with most of the old-growth conifer trees removed. Logging within the NF and on small parcels of private land within NF boundaries is now concentrated on second-growth timber and the few remaining stands of old-growth. The S-OAK site, at elevations from 1,000 to 3,000 feet, was dominated by blue oak, interior live oak, digger pine, and various chaparral species. The Lassen NF study area (the L-CON site) was dominated by red and white fir at high elevations (5,800 to 6,600 feet) and Jeffrey, ponderosa, sugar, and lodgepole pines at lower elevations (5,000 to 5,800 feet). Selective logging has been the predominant silvicultural method used there.

Methods

Field Operations

Owls were captured with noose poles, mist nets, or fish-landing nets and fitted with backpack-mounted radio tags weighing 0.6-0.8 ounces. We attached the radio tags with cross-chest harnesses (Forsman 1983). Radio tags (AVM Instrument Co., Livermore, Calif.) had 12-inch antennae and life expectancies of 12 months. Owls tracked >1 year were recaptured and fitted with new radio tags. Owls were located by radio triangulation using the loudest-signal method (Springer 1979). At least three compass bearings were taken from known points for each owl location and plotted on 1:24,000 topographic maps. Error polygons (the area enclosed by the intersection of three or more compass bearings) at L-CON were classified as <50, <20, <5, or <2.5 acres. We attempted to obtain error polygons of <2.5 acres for all observations. At S-CON and S-OAK, we obtained additional bearings on all birds until error polygons of <2.5 acres were attained. The geometric center of each error polygon was assumed to be the owl's location. We attempted to obtain one nighttime location, by radio tracking, on each of four nights per week and one daytime location per week by direct visual observation. All nighttime observations were considered foraging locations and all daytime observations were classed as roosting locations.

Vegetation Classification

Stands of relatively homogeneous vegetation were mapped at each study site and grouped into habitat types that could be cross-classified to U.S. Department of Agriculture, Forest Service (FS) timber stand types. Black-and-white aerial photos, U.S. Geologic Survey topographic maps, large-scale color aerial photos, and 1:24,000 FS black-and-white orthophotoquads were used to define vegetation boundaries. Stands were classified according to compositional (vegetation type) and structural (diameter size-class of dominant trees and canopy-closure classes) features that could be estimated from aerial photos (table 6A). Structural classes at S-OAK differed from those at S-CON and L-CON, because most trees there were oaks with relatively small diameters at breast height (d.b.h.) when compared to conifers. We assigned each stand to two canopy-closure classes: cover by all vegetation above 7 feet (total canopy closure) and cover by only the dominant trees in the canopy (dominant canopy closure). About 70 percent of the mapped stands (polygons) in each study area were field-verified for classification accuracy. Vegetation maps were subsequently digitized, stored in a Geographic Information System (GIS), and analyzed using ARC/INFO software.

Table 6A-Vegetation classifications used in Chi-square tests of habitat selection.

Classes	Characteristics
Tree size-classes	
Open grassland	No trees
Sapling	D.b.h. <5 inches ¹
Pole	D.b.h. 5-10 inches
Small sawtimber	D.b.h. 11-20 inches
Medium sawtimber	D.b.h. 21-35 inches
Large sawtimber	D.b.h. >35 inches
Canopy-closure classes	
Open	10 percent closure ²
Sparse	10-19 percent
Poor	20-39 percent
Normal	40-69 percent
Good	<69 percent
Suitability as owl habitat	
Suitable	Medium or large sawtimber, canopy closure class poor or better, and total closure >69 percent
Unsuitable	All other lands

¹ Diameter at breast height of the dominant size-class, according to basal area

² Canopy closure based on the dominant tree size-class.

Statistical Analysis

By definition, home-range estimators assume repeated use of an area, and a random flight path does not constitute a home range. For this reason, we determined whether individual owls exhibited site fidelity prior to calculating home-range size (Spencer et al. 1990). The mean-squared distance from the center of activity (MSD) (Calhoun and Casby 1958) was used to measure site fidelity. A bird displayed site fidelity if its flight path was less than the MSD for 975 of 1,000 simulated paths. (See Spencer et al. 1990 for simulation techniques.)

Home-range size was computed using two estimators, the 100-percent minimum convex polygon (MCP) (Mohr 1947 Hayne 1949) and the 95-percent adaptive kernel (AK) (Worton 1989, Baldwin pers. comm.). Because convex polygon areas are sensitive to sample size (Jennrich and Turner 1969), we used the 95-percent AK estimates for all comparisons and statistical tests. We report 100-percent MCP estimates of home-range size to allow comparisons with other studies reported in the literature and elsewhere. The correlation coefficient between AK and MCP estimates was significant ($r = 0.93$, d.f. = 52, $P < 0.0001$). Telemetry data were partitioned into a breeding period (1 March-31 August) and a nonbreeding period (1 September-28 February). Foraging (nighttime) locations were used to estimate home ranges.

The Chi-square goodness-of-fit test was used to test the hypothesis that owls used habitat types *within* their home ranges in proportion to availability (Neu et al. 1974). When this hypothesis was rejected, we used Bonferroni confidence intervals (at the $P < 0.05$ level) to determine which habitat types were used more or less than expected (Byers et al. 1984). Mapped polygons were classified by diameter size-class of the dominant

trees, total canopy closure, and dominant canopy closure. Chi-square analyses were performed for each of the three types of classification. In addition, the analyses were repeated after reclassifying polygons as suitable or unsuitable, based on current FS, Region 5 (R5), definitions of suitable spotted owl habitat. Suitable stands were those in which the diameter size-class of dominant trees was ≥ 21 inches in d.b.h., canopy closure of dominant trees was ≥ 20 percent, and total canopy closure was ≥ 70 percent.

Results

Home-Range Size

Eleven females and 10 males were radio-tracked between 26 April 1987 and 28 February 1990 at S-CON; and six females and six males were radio-tracked between 28 February 1989 and 28 February 1990 at S-OAK. Nine females and eight males were tracked between 25 May 1989 and 5 April 1990 at L-CON. Owls were monitored over periods ranging from 56 to 794 days. sampling intervals varied among owls because transmitters failed, individuals died, or owls permanently left the study areas.

Eighteen of 21 owls at S-CON, 12 of 12 at S-OAK, and 13 of 17 at L-CON passed the site-fidelity test. Owls that failed to exhibit site fidelity had few radio locations or made long movements during the breeding or nonbreeding seasons. All three birds at S-CON that failed the test were migrants that exhibited long movements (see Chapter 4).

To compare home-range sizes among sites and between seasons, we excluded owls that were tracked over a period of less than 5 months during the 6-month nonbreeding season. Our sampling frequency varied among individual owls, and 5 months was as close to complete coverage as we could achieve because of irregular sampling intervals. Estimates of home-range sizes for the nonbreeding period were calculated for 13 owls at S-CON, 5 at S-OAK, and 7 at L-CON that passed the site fidelity test and were tracked for a period of at least 150 days. The number of radio locations per season among these owls ranged from 21 to 91 ($\bar{x} = 58.6 \pm 17.0$). Home-range sizes of owls that passed the site-fidelity test and that were tracked over a period of at least 150 days were not significantly correlated with the number of radio locations. We relaxed the criteria for breeding-season estimates. Requiring a tracking period of at least 150 days, only seven owls had sufficient data to estimate a home-range size. To use a larger sample of owls, we excluded only owls with fewer than 20 radio locations within a breeding season. Fifteen of 21 owls at S-CON, 7 of 12 at S-OAK, and 9 of 15 at L-CON met this criterion. The mean number of locations among these owls as 37.6 (± 10.6) and they were tracked over an average period of 116.0 days (± 39.1 , range = 56-184 days).

Home ranges were significantly larger at S-CON than at S-OAK during both seasons (table 6B). A two-way ANOVA for these two sites indicated significant effects of study site ($F = 13.9$, d.f. = 1, 50, $P < 0.001$) and season ($F = 4.2$, d.f. = 1, 50, $P < 0.05$) on AK home-range size, with an interaction effect. The interaction effect was due to larger home ranges in the nonbreeding than in the breeding season at S-CON, but home ranges at S-OAK were larger during the breeding season. The difference in home-range size between seasons at L-CON was not significant ($t = 1.4$, d.f. = 14, $P > 0.15$), but owls at L-CON had home-range sizes about twice those at S-CON in both seasons. Home-range sizes did not differ significantly between sexes at any site during either season.

Owls at S-CON exhibited variable behavior during the winter. Individual birds either migrated, occupied nearly the same home range in winter as in summer, enlarged their home range in winter but still used most or all of the summer home range as well, or shifted their home range for the winter but still overlapped a portion of the summer home range (Chapter 4). Among 21 owls radio-tagged at this site, six were classified as year-round residents, two as enlargers, five as shifters, five as migrants, and three as unknown. Differences in nonbreeding home-range sizes among these categories of birds were significant ($F = 12.4$, d.f. = 3, 17, $P < 0.001$). Shifters had the largest home ranges ($\bar{x} = 13,254 \pm 4,984$ acres), followed by enlargers ($\bar{x} = 5,960 \pm 3,031$), and residents ($\bar{x} = 3,302 \pm 781$). Only one migrant passed the site-fidelity test, and its home range was 9,146 acres.

Annual home ranges were calculated for owls that passed the site-fidelity test both seasons, were tracked over a period of at least 150 days during the nonbreeding season, and had ≥ 20 radio locations during the breeding season (table 6B). Owls at S-CON had significantly larger annual home ranges than those at S-OAK ($t = 2.5$, d.f. = 19, $P < 0.05$). As with breeding and nonbreeding home-range sizes, annual home-range sizes at L-CON were more than twice the size of those at S-CON.

Seasonal home-range sizes of pairs were calculated only when both members of pairs passed the site-fidelity test, were tracked for at least 150 days during the nonbreeding period, and had ≥ 20 radio locations during the breeding period (table 6B). Only one pair at L-CON met these criteria, precluding further analysis of pair home-range data. A two-way ANOVA for S-CON and S-OAK indicated no significant differences between the nonbreeding and breeding periods ($F = 1.1$, d.f. = 1, 12, $P > 0.30$), but pair home ranges were larger at S-CON than at S-OAK ($F = 3.9$, d.f. = 1, 12, $P = 0.07$). The mean proportion of home-range overlap between members of pairs did not differ significantly by study site ($F = 0.3$, d.f. = 1, 12, $P > 0.60$) or by season ($F = 0.2$, d.f. = 1, 12, $P > 0.60$). At both sites in the Sierra NF, pairs had more overlap in their areas of use during the nonbreeding period ($\bar{x} = 51 \pm 18$ percent) than during the breeding period ($\bar{x} = 47 \pm 12$ percent).

Spotted owl home ranges shifted seasonally. Overlap between breeding and nonbreeding periods, using 95-percent AKs of individual home ranges, was 34 ± 18 percent at S-CON, 54 ± 5 percent at S-OAK, and 38 ± 8 percent at L-CON.

Table 6B--Means (\bar{x}) and standard deviations (SD) of home-range sizes of California spotted owls studied from 1987-1990 in the northern and central Sierra Nevada. Study sites were in conifer forest on the Lassen NF (L-CON) and in conifer forest (S-CON) and riparian/hardwood forest (S-OAK) on the Sierra NF. Estimates were determined using foraging locations and the 95-percent adaptive kernel method; 100-percent minimum convex polygon estimates of home-range sizes are in parentheses; n = number of individuals or pairs of owls.

Birds	Total home-range size (acres)					
	L-CON		S-CON		S-OAK	
	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>
Individual birds						
Breeding	7,061.2 \pm 5,992.5 (5,422.6 \pm 5,194.4)	9	2,366.8 \pm 740.0 (1,798.7 \pm 787.2)	24	985.0 \pm 745.0 (714.6 \pm 624.4)	7
Nonbreeding	11,601.0 \pm 6,664.1 (14,676.7 \pm 8,251.8)	7	6,834.5 \pm 5,138.3 (5,943.3 \pm 4,529.5)	18	661.0 \pm 510.1 (761.7 \pm 495.7)	5
Annual	12,473.5 \pm 7,305.5 (12,927.2 \pm 10,132.2)	6	5,715.1 \pm 4,289.9 (5,968.8 \pm 4,639.9)	16	874.1 \pm 644.2 (1,042.6 \pm 865.7)	5
Pairs-breeding period						
Total area	3,869.3 (3,014.4)	1	3,420.5 \pm 858.1 (2,514.8 \pm 873.6)	8	720.5 \pm 402.9 (457.4 \pm 274.4)	2
Area shared	1,869.3 (1,164.9)		1,544.5 \pm 364.8 (1,027.5 \pm 317.6)		397.9 \pm 341.6 (278.6 \pm 225.8)	
Pairs-nonbreeding period						
Total area	9,871.8 (17,292.5)	1	9,730.8 \pm 10,168.0 (7,201.0 \pm 6,901.2)	4	573.3 \pm 271.0 (818.8 \pm 251.4)	2
Area shared	1,407.9 (563.2)		4,021.2 \pm 3,929.3 (3,766.0 \pm 4,355.4)		321.3 \pm 160.1 (297.6 \pm 133.9)	
Pairs-annual						
Total area			8,253.0 \pm 7,872.6 (7,709.4 \pm 7,184.0)	4	778.0 \pm 405.8 (875.6 \pm 303.8)	2
Area shared			4,443.0 \pm 4,626.1 (4,492.2 \pm 4,945.2)		447.6 \pm 318.9 (459.9 \pm 201.3)	

Habitat Use

Habitat Composition Within Home Ranges

During the breeding season, 13 and 63 percent of the habitat types available within individual home ranges were medium and large sawtimber (≥ 21 inches in d.b.h.) at S-CON and L-CON, respectively (tables 6C-6E), and 91 percent of the habitat types available within owl home ranges at S-OAK were classified as old-growth. Percentages were similar during the nonbreeding season in all areas. The mean proportions of individual home ranges that were ≥ 40 percent dominant canopy closure varied among sites (table 6F); proportions were similar at L-CON and S-CON, but they were about two times greater at S-OAK. Proportions for ≥ 40 percent total canopy closure were similar among all sites. Mean percentages of home ranges that were "suitable" habitat using R5 definitions were 4 (S-CON), 27 (S-OAK), and 26 (L-CON) at the three sites during the breeding season.

Habitat-Use Patterns Within Home Ranges

Among all of the owls during the breeding season, 10 and 82 percent of the radio locations were in medium and large sawtimber at S-CON and L-CON, respectively, and 92 percent were in old-growth at S-OAK; 21, 70, and 99 percent of the locations were in these size classes at the three sites, respectively, during the nonbreeding season (tables 6C-6F). More use occurred in small than in medium and large sawtimber at S-CON 87 percent and 73 percent of the radio locations during the breeding and nonbreeding seasons, respectively. The proportions of radio locations that were in dominant canopy closure ≥ 40 percent were again similar at L-CON and S-CON, but nearly twice as high at S-OAK. Higher proportions of locations occurred in total canopy closure ≥ 40 percent, and results were similar among the sites. Use of R5 suitable habitat was low--means of radio locations in this habitat class were 4 percent (S-CON), 47 percent (L-CON), and 49 percent (S-OAK) during the breeding season (table 6F). Use was greater than availability for most site-season comparisons and definitions of suitable habitat (fig. 6A). Use of R5 suitable habitat at S-CON was equal

Table 6C Means (\bar{x}) and standard deviations (SD) of areas, proportions of home ranges, and proportions of foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the S-CON study site in the central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for 1987-1989 breeding and nonbreeding seasons.

Habitat type	Breeding period ¹						Nonbreeding period ¹					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Tree size-class d.b.h. in inches)												
No trees	9.1	35.8	0.003	0.01	0	0	736.3	1,828.5	0.058	0.14	0.031	0.08
<5	0	0	0	0	0	0	0	0	0	0	0	0
5 - 10	66.4	82.3	0.029	0.04	0.027	0.05	101.8	109.9	0.020	0.02	0.023	0.04
11 - 20	1,666.0	976.1	0.839	0.17	0.870	0.22	4,028.8	2,826.9	0.671	0.18	0.732	0.19
21 - 35	230.0	319.1	0.095	0.11	0.065	0.16	1,281.7	998.1	0.192	0.10	0.141	0.11
>35	59.0	143.8	0.032	0.08	0.038	0.08	477.5	684.4	0.054	0.07	0.073	0.12
Dominant canopy closure (percent)												
< 10	98.8	254.4	0.027	0.06	0.007	0.02	245.8	492.0	0.022	0.03	0.013	0.03
10 - 19	164.7	154.9	0.076	0.06	0.040	0.04	568.6	509.8	0.080	0.05	0.043	0.03
20-39	1,147.8	776.1	0.537	0.18	0.416	0.24	3,117.6	2,220.8	0.492	0.14	0.442	0.19
40 - 69	605.4	311.0	0.354	0.22	0.537	0.25	1,945.9	977.6	0.342	0.14	0.471	0.19
70 - 100	4.2	16.3	0.002	0.08	0	0	13.1	35.1	0.001	0	0	0
Total canopy closure (percent)												
<10	32.9	70.1	0.010	0.02	0.002	0.01	124.2	215.9	0.012	0.01	0.007	0.01
10 - 19	111.1	230.7	0.038	0.06	0.015	0.03	288.2	367.3	0.035	0.02	0.019	0.02
20 - 39	306.5	293.2	0.137	0.07	0.076	0.08	999.4	1,172.8	0.126	0.07	0.077	0.06
40 - 69	1,318.0	618.5	0.677	0.12	0.685	0.21	3,534.6	1,943.9	0.598	0.14	0.644	0.15
70 - 100	252.9	188.5	0.132	0.09	0.222	0.21	944.3	560.7	0.164	0.06	0.222	0.13

¹ Breeding period--*n* = 24 owls with a total of 1,583 locations; nonbreeding period--*n* = 18 owls with a total of 1,358 locations. An individual owl may contribute to *n* more than once if it was radio tracked during multiple breeding or nonbreeding seasons.

to or less than availability, but note the small amounts of this type available at S-CON

Nearly half of the owls at all three sites had significant Chi-square tests of habitat use for tree size-class, and nearly three-fourth of the owls had significant tests for use of canopy-closure classes. Differences in the proportion of owls that demonstrated habitat selection between the breeding and nonbreeding seasons were neither large nor consistent (fig. 6B). Fewer owls selected for tree size-class than for canopy-closure classes, and more selected for dominant canopy closure than for total canopy closure. Fewer owls had significant tests for habitat use when only foraging locations were used than when foraging and roosting locations were pooled. Summed across the three study areas (foraging and roosting locations pooled), 14 of 39 owls had significant tests for use of tree size-class, 26 owls for total canopy closure, and 29 owls for dominant canopy-closure classes during the breeding season. During nonbreeding season, 14 of 29 owls at the three study sites selected significantly for three size-class, 20 owls for total canopy closure, and 20 owls for dominant canopy-closure classes.

We tested whether owls used "suitable" habitat more than expected based on FS, R5, definitions (fig. 6A). Results were similar for L-CON and S-OAK: seven of eight birds at L-CON had significant tests during the breeding season, and four of six birds tested significant during the nonbreeding season. At S-OAK, six of seven birds and four of five birds had significant tests during the breeding and nonbreeding seasons, respectively. On the other hand, at S-CON, only four of 24 owls during the breeding season and six of 18 owls during the nonbreeding season had significant tests for use of suitable habitat.

Patterns of habitat use were weak and inconsistent among the subset of owls that passed the test of habitat selection (figs. 6C-6E). Most owls at all three sites used habitat types in proportion to their availability. Patterns were clearer and stronger for canopy closure than for tree size-class. More than half of the owls used poor cover classes less than expected and many used canopy closure ≥ 40 percent more than expected. Differences between dominant and total cover were minor. Patterns of selection for canopy closure did not appear to be stronger during the breeding than during the nonbreeding season. Use of tree size-class

Table 6D—Means (\bar{x}) and standard deviations (SD) of areas, proportions of home ranges, and proportions of foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the S-OAK study site in the central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for the 1989 breeding and nonbreeding seasons.

Habitat type	Breeding period ¹						Nonbreeding period ¹					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Tree size-class (d.b.h. in inches)												
No trees	6.2	10.6	0.005	0.01	0	0	0	0	0	0	0	0
<5	0	0	0	0	0	0	0	0	0	0	0	0
5-10	0	0	0	0	0	0	0	0	0	0	0	0
11 - 20	67.7	138.1	0.083	0.15	0.080	0.18	7.7	11.1	0.014	0.02	0.006	0.01
21 - 35	703.2	577.5	0.912	0.15	0.920	0.18	647.6	556.5	0.986	0.02	0.994	0.01
>35	0	0	0	0	0	0	0	0	0	0	0	0
Dominant canopy closure (percent)												
<10	26.4	55.3	0.021	0.03	0	0	52.6	76.6	0.055	0.04	0.024	0.03
10 - 19	127.9	161.3	0.132	0.14	0.081	0.09	156.6	145.7	0.210	0.16	0.108	0.09
20 - 39	102.0	167.7	0.105	0.11	0.033	0.04	125.0	244.3	0.113	0.14	0.068	0.13
40 - 69	444.8	312.7	0.542	0.23	0.494	0.36	239.6	152.2	0.391	0.10	0.378	0.17
70 - 100	69.4	32.4	0.194	0.24	0.391	0.36	81.8	39.8	0.231	0.23	0.422	0.32
Total canopy closure (percent)												
<10	26.4	55.3	0.021	0.03	0	0	52.6	76.6	0.055	0.04	0.024	0.03
10 - 19	99.0	141.5	0.093	0.09	0.069	0.08	102.8	145.7	0.112	0.08	0.060	0.06
20 - 39	76.6	80.0	0.106	0.10	0.027	0.03	113.9	86.4	0.170	0.07	0.057	0.06
40 - 69	455.0	400.4	0.501	0.27	0.416	0.30	268.5	293.9	0.347	0.11	0.385	0.23
70 - 100	114.1	49.6	0.273	0.26	0.488	0.31	117.6	43.0	0.316	0.25	0.474	0.32

¹ Breeding period-- $n = 7$ owls with a total of 498 locations; nonbreeding period-- $n = 5$ owls with a total of 548 locations.

showed stronger patterns at L-CON than at S-CON and S-OAK. More than half of the birds at L-CON used small sawtimber (<11 inches in d.b.h.) less than expected, and medium and large sawtimber more than expected, during the breeding season. These results were weaker during the nonbreeding season.

Discussion

Home-Range Size

Estimates of home-range size among California spotted owls are extremely variable. All available data indicate that they are smallest in habitats at relatively low elevations that are dominated by hardwoods, intermediate in size in conifer forests in the central Sierra Nevada, and largest in true fir forests in the northern Sierra Nevada.

Home-range sizes of owls in our studies at L-CON, S-CON, and S-OAK varied among areas and between seasons. The mean area used was about twice as large in the northern compared to

the central Sierra Nevada, and was two to 10 times larger in high-elevation conifer forests compared to low-elevation oak woodlands in the central Sierra Nevada. Median home-range estimates for pairs of northern spotted owls were 3,000 to 5,000 acres (Thomas et al. 1990)—less than half the size of pair home ranges of California spotted owls at L-CON (12,500 acres) but about the same as the pair estimates at S-CON. California spotted owls in the foothill riparian/hardwoods and oak woodlands at S-OAK used less than 900 acres, or approximately 20-30 percent of the area used by northern spotted owls.

Two pairs of owls radio tracked in the San Bernardino Mountains used home ranges averaging more than 5,300 acres (100-percent MCP-LaHaye pers. comm.) (table 6G). Home-range sizes of pairs during the breeding period averaged 4,569 acres on the Tahoe NF (100-percent MCP, $n = 2$; Call 1990, p. 21) and 4,759 acres on the Eldorado NF [100-percent MCP, $n = 4$ (excludes two pairs with relatively few radio locations); Laymon 1988, p. 187]. These estimates, with those of 3,869 acres for the Lassen NF ($n = 1$, table 6B) and 3,421 acres for the Sierra NF ($n = 8$, table 6B), give an overall estimate of about 4,200 acres (grand mean, unweighted for sample size) for home-range sizes of owl pairs during the breeding period in Sierran conifer forests.

Table 6E—Means (\bar{x}) and standard deviations (SD) of areas, proportions of home ranges, and proportions of foraging and roosting radio locations in different tree size and canopy-closure classes for owls that passed the site fidelity test at the L-CON study site in the northern Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges for breeding (1990) and nonbreeding (1989-1990) seasons.

Habitat type	Breeding period ¹						Nonbreeding period ¹					
	Area (acres)		Proportion of home range		Proportion of locations		Area (acres)		Proportion of home range		Proportion of locations	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Tree size-class (d.b.h.in inches)												
No trees	515.0	913.2	0.049	0.04	0	0	1,368.4	1,241.2	0.112	0.09	0.007	0.01
<5	9.9	17.5	0.001	0	0	0	39.3	38.8	0.003	0	0.002	0.01
5 - 10	207.7	332.5	0.023	0.01	0.011	0.02	608.9	383.8	0.046	0.02	0.029	0.04
11 - 20	2,659.2	3,724.8	0.300	0.15	0.172	0.11	3,502.0	2,340.1	0.247	0.12	0.261	0.12
21 - 35	1,394.8	962.3	0.251	0.10	0.298	0.15	2,755.5	1,490.4	0.224	0.10	0.220	0.05
> 35	2,371.9	2,287.2	0.377	0.12	0.519	0.17	4,644.8	2,164.0	0.368	0.09	0.480	0.10
Dominant canopy closure (percent)												
<10	1,296.3	1,797.4	0.160	0.04	0.072	0.08	2,198.5	1,469.6	0.165	0.06	0.064	0.04
10 - 19	1,598.6	2,003.9	0.204	0.04	0.142	0.07	2,859.0	1,329.1	0.223	0.05	0.131	0.13
20 - 39	2,043.2	2,230.9	0.303	0.10	0.329	0.21	3,266.3	1,415.1	0.255	0.03	0.318	0.14
40-69	1,607.0	1,461.7	0.251	0.11	0.350	0.17	2,436.2	1,439.3	0.187	0.06	0.318	0.12
70 - 100	532.8	614.3	0.076	0.03	0.108	0.08	1,294.3	840.3	0.094	0.03	0.165	0.11
Total canopy closure (percent)												
<10	679.5	1,191.5	0.067	0.05	0.033	0.06	1,088.0	985.8	0.079	0.06	0.006	0.01
10 - 19	300.8	403.4	0.041	0.02	0.012	0.02	666.9	618.7	0.048	0.04	0.013	0.01
20 - 39	1,595.1	1,983.9	0.211	0.06	0.105	0.06	1,983.2	1,359.0	0.145	0.05	0.117	0.04
40 - 69	2,038.2	2,369.7	0.263	0.09	0.204	0.16	3,268.1	1,630.2	0.257	0.08	0.185	0.11
70 - 100	2,464.3	2,063.7	0.411	0.09	0.647	0.15	5,048.4	2,205.2	0.396	0.05	0.675	0.11

¹ Breeding period-- $n = 8$ owls with a total of 479 locations; nonbreeding period-- $n = 6$ owls with a total of 402 locations.

The smallest estimated use areas of California spotted owls (means for pairs ranging from 98 to 243 acres) were based on known sizes of small stringers of dense riparian/hardwoods in the Cleveland, Angeles, and Los Padres NFs (table 6G). Owls in these stringers were not radio-tagged. Perhaps some of them used more than one canyon bottom, but the Forest Biologists who made these estimates reported that, in some cases, other individuals or pairs of owls occupied the riparian stringers in adjacent canyons. Most canyon sides above the riparian zones were covered by dense chaparral. We believe it is most unlikely that the owls can use the chaparral, as it is too dense for safe or effective flight.

We strongly suspect that the large differences in home-range sizes reported here are related, at least in part, to differences in the primary prey of the owls in different localities. Consistently, California spotted owls with the smallest observed home ranges prey primarily on woodrats, but those with the largest home ranges specialize on flying squirrels. Woodrat densities generally tend to be much greater than flying squirrel densities, and woodrats weigh nearly twice as much as flying squirrels (Chapter 4). Similar relations are suggested in recent studies of northern spotted owls by Carey et al. (1992).

Habitat Selection

Here we evaluate habitat quality based on use versus availability of types (Thomas et al. 1990, appendix F). We regard as suitable those habitats selected in excess of availability by most owls. Marginal habitats are seldom or never used in excess of availability, used in proportion to availability by many owls, and used less than expected by many other owls. Habitat types used less than expected by most owls are considered to be poor in quality and are classed as unsuitable habitat.

Spotted owls in this study more consistently selected for high canopy closure than for large tree size-class. Chi-square values were consistently higher for canopy closure, and more owls had significant tests for selection of high canopy closure than for tree-size class in 18 site-season comparisons. Differences between total and dominant canopy closure were minor, but because more owls exhibited significant selection for high dominant cover than for high total cover, dominant cover may be a better measure of suitable habitat for California spotted owls.

The amount of medium and large sawtimber in individual home ranges did not appear to be a good indicator of the amount of that habitat needed to sustain California spotted owls, unlike the case for northern spotted owls (see Thomas et al. 1990). Nearly half of the California spotted owls had significant tests of

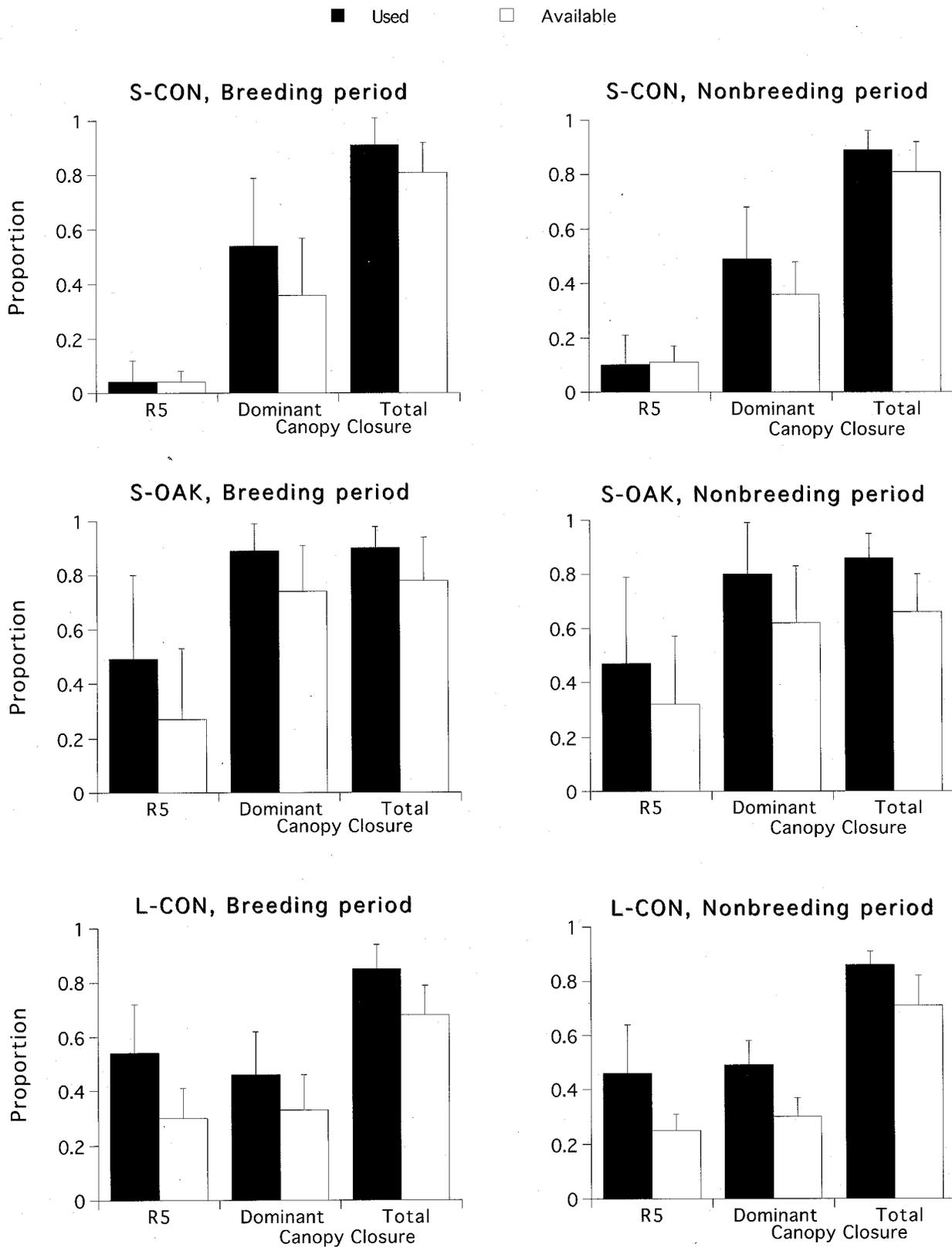


Figure 6A—Mean proportions of suitable habitat available in home ranges of California spotted owls in relation to proportions used by radio-tagged birds in different seasons and study sites. Study areas were in conifer forests of the Sierra (S-CON) and Lassen (L-CON) National Forests, and in hardwood/riparian forests of the Sierra (S-OAK) National Forest. Three categories of suitable habitat were tested: (1) R5 = Forest Service (Region 5) definition—medium or large sawtimber, dominant canopy closure poor or higher, and total closure >69 percent; (2) canopy closure of dominant trees ≥ 40 percent; and (3) total canopy closure ≥ 40 percent. Error bars are standard deviations (SD). The 95-percent adaptive kernel was used to delineate home ranges.

■ Breeding □ Nonbreeding

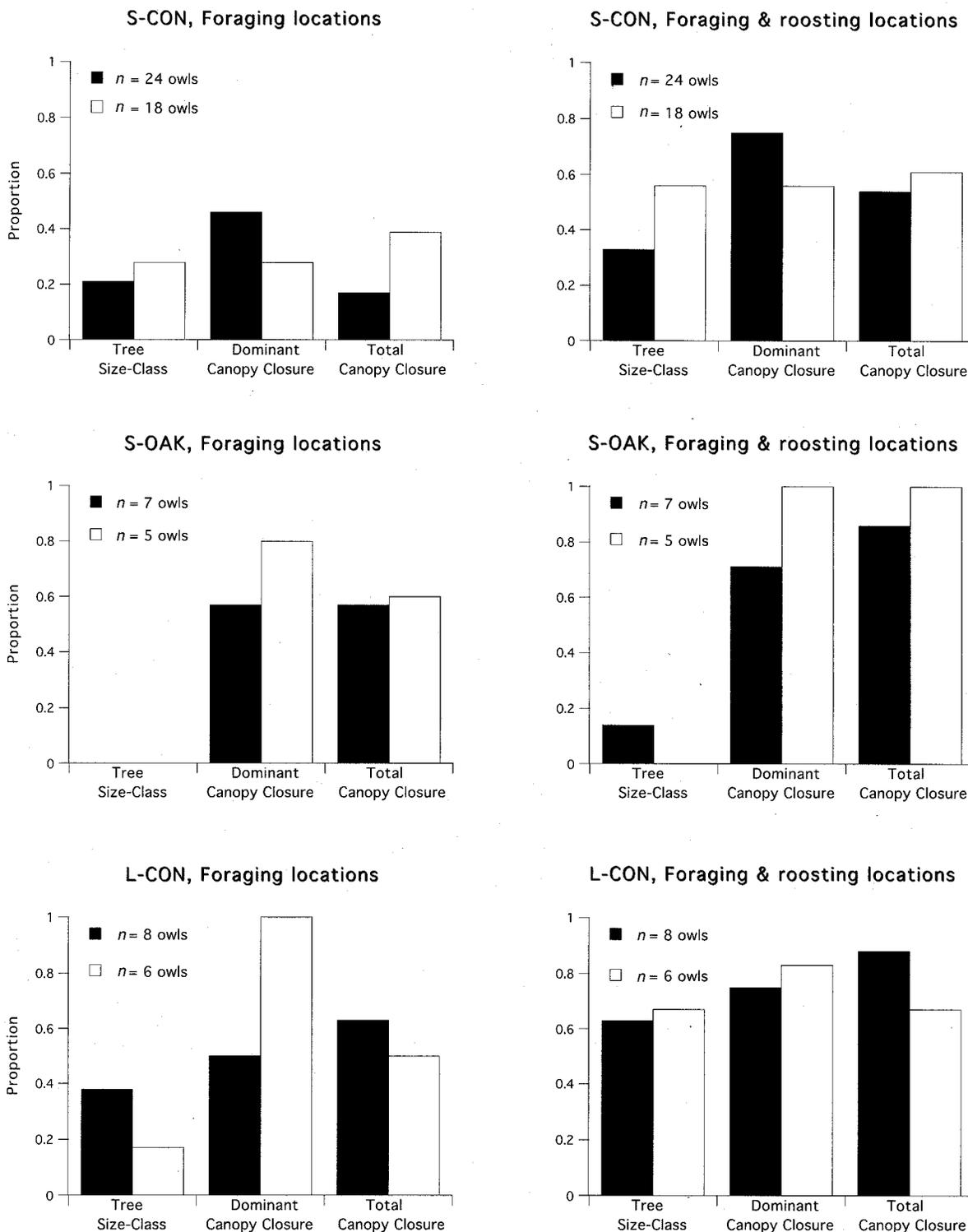


Figure 6B—The proportion of California spotted owls with significant ($P \leq 0.05$) Chi-square tests for selection of habitats based on tree size-classes, dominant canopy closure, and total canopy closure. Study areas were in conifer forests of the Sierra (S-CON) and Lassen (L-CON) National Forests, and in hardwood/riparian forests of the Sierra (S-OAK) National Forest. Tests were done separately for breeding and nonbreeding periods using foraging locations alone, and using foraging and roosting locations pooled.

selection for tree size-class, but most of them used all size classes in proportion to availability in the central Sierra Nevada. Patterns were stronger at L-CON during the breeding season, when about half of the birds used medium and large sawtimber more than expected. By contrast, old-growth was used in greater proportion than its availability, for nesting, roosting, and foraging, by most northern spotted owls in Oregon and Washington, and it was never used less than expected. Throughout their range and across all seasons, northern spotted owls consistently showed foraging and roosting patterns significantly associated with old-growth stands or mixed stands of mature and old-growth trees. Among California spotted owls, however, patterns of habitat use for tree size-class were weaker, and they were not consistent among study areas.

Canopy closure ≥ 40 percent was used by many California spotted owls greater than expected, by a few less than expected, and by many equal to its availability. Canopy closure ≤ 39 percent was used by most owls less than expected and in proportion to availability by many others. Based on these results, then, suitable habitat for California spotted owls appears to include canopy closure ≥ 40 percent, and habitat with ≤ 39 percent canopy closure is marginal to unsuitable.

The R5 definition of suitable habitat does not appear to be appropriate across the range of the California spotted owl. Most owls at L-CON (79 percent) and S-OAK (83 percent) used R5-defined suitable habitat in excess of availability. But results were quite different for owls in the conifer forest at S-CON, where this habitat type was generally not available within home ranges. At S-CON, most birds used R5-defined suitable habitat in proportion to availability, a few used it more than expected, and a few less than expected.

Habitat Selection and Population Stability

Habitat selection by owls at S-CON was generally less evident than at L-CON, even though both sites were in Sierran conifer forests. We also determined that only 13 percent of the forest in the study area at S-CON was in medium and large sawtimber, whereas the L-CON site had 63 percent of its forest in those timber size classes and several of the owls there exhibited significant selection for those timber stands. During the breeding periods of 1987, 1988, and 1989, owl crews on the Lassen and Sierra NFs monitored the occupancy status and breeding activity of owl pairs in Spotted Owl Habitat Areas (SOHAs) managed for the owls. Over that period on the Lassen NF, an absence of pairs was confirmed in 8 of 27 cases (30 percent) and breeding was confirmed in 8 of 27 cases (30 percent). During the same period on the Sierra NF, an absence of pairs in SOHAs was confirmed in 8 of 11 cases (73 percent) and breeding was confirmed in only 1 of 11 cases (9 percent). Because we lack sufficient information to determine whether California spotted owls in any part of the Sierra Nevada are reproducing at a rate that can maintain the population (Chapter 8), we cannot be certain that habitats used by owls either at L-CON or S-CON were adequate to provide for a balance between births and deaths. The data suggest, however, that the habitat available to spotted owls on the Sierra NF may be less adequate than that on the Lassen NF. Indeed, it may be that

spotted owls on the Sierra NF cannot maintain their numbers, and that perhaps they are maintained in part by immigration from populations in the neighboring NPs. Note that the Sierra NF shares its northern border with Yosemite NP and its southern border with Sequoia/Kings Canyon NPs (fig. 4B).

Power of Chi-square Tests

The power of Chi-square tests of habitat selection is influenced by classification error (telemetry and/or mapping), the resolution of habitat classification, and by the number of locations available to estimate use. These factors may reduce the likelihood of detecting habitat selection when, in fact, it is occurring (type-II error-see White and Garrott 1986). In addition, the power of a test depends on the "effect size" (Cohen 1988) or, in the case of habitat selection, the degree to which differences exist between proportions of available and used habitat types. The smaller the effect size, other things being equal (significance level, desired power), the larger the sample size needed to detect selection. The small number of locations in our data could have reduced the likelihood of detecting habitat selection when it occurred. Owls with significant Chi-square tests for selection of canopy-closure classes had a mean of 72 (± 23) radio locations, but owls with insignificant tests had a mean of only 57 (± 19) locations. The difference between these, sample sizes was significant (t test = 2.8, d.f. = 78, $P < 0.01$), indicating that small sample sizes may have been associated with our failure to detect habitat selection by radio-tagged owls. On the other hand, the difference between the number of locations between owls that passed ($\bar{x} = 69 \pm 24$) and failed ($\bar{x} = 62 \pm 21$) tests of selection for tree size-class was not significant ($t = 1.3$, d.f. = 68, $P > 0.20$).

The number of radio locations approximately doubled when we pooled foraging and roosting locations. More owls had significant Chi-square tests of habitat use for the pooled data set than was the case for the foraging locations alone. The difference in Chi-square results between these two groups was apparently due primarily to differences in habitat use by foraging and roosting owls, and less so to the increase in sample size. Roost sites were more distinct from available sites than was the case for foraging sites. For example, 18 of 18 owls at S-CON used sites that had ≥ 40 percent canopy closure more than expected for roosting during the breeding period, and 83 percent had significant tests of habitat selection. Use of sites that had ≥ 70 percent canopy closure for roosting was similar: 16 of 18 owls had significant tests of habitat selection, and 11 of 18 owls used, these stands more than expected (G. N. Steger pers. observ.). By contrast, only 7 of 24 owls at S-CON had significant tests for use of foraging sites with dense canopy during the breeding period, and only seven owls foraged more than expected in sites with ≥ 40 percent canopy closure.

Effect size increases with the size of the difference between proportions of available and used habitat types, providing a useful index to identify where habitat selection is greatest. We found higher effect sizes for canopy closure than for tree size-class, and for foraging and roosting locations combined than for foraging locations alone. These results support the conclusion that the owls had differential use patterns between daytime roosting

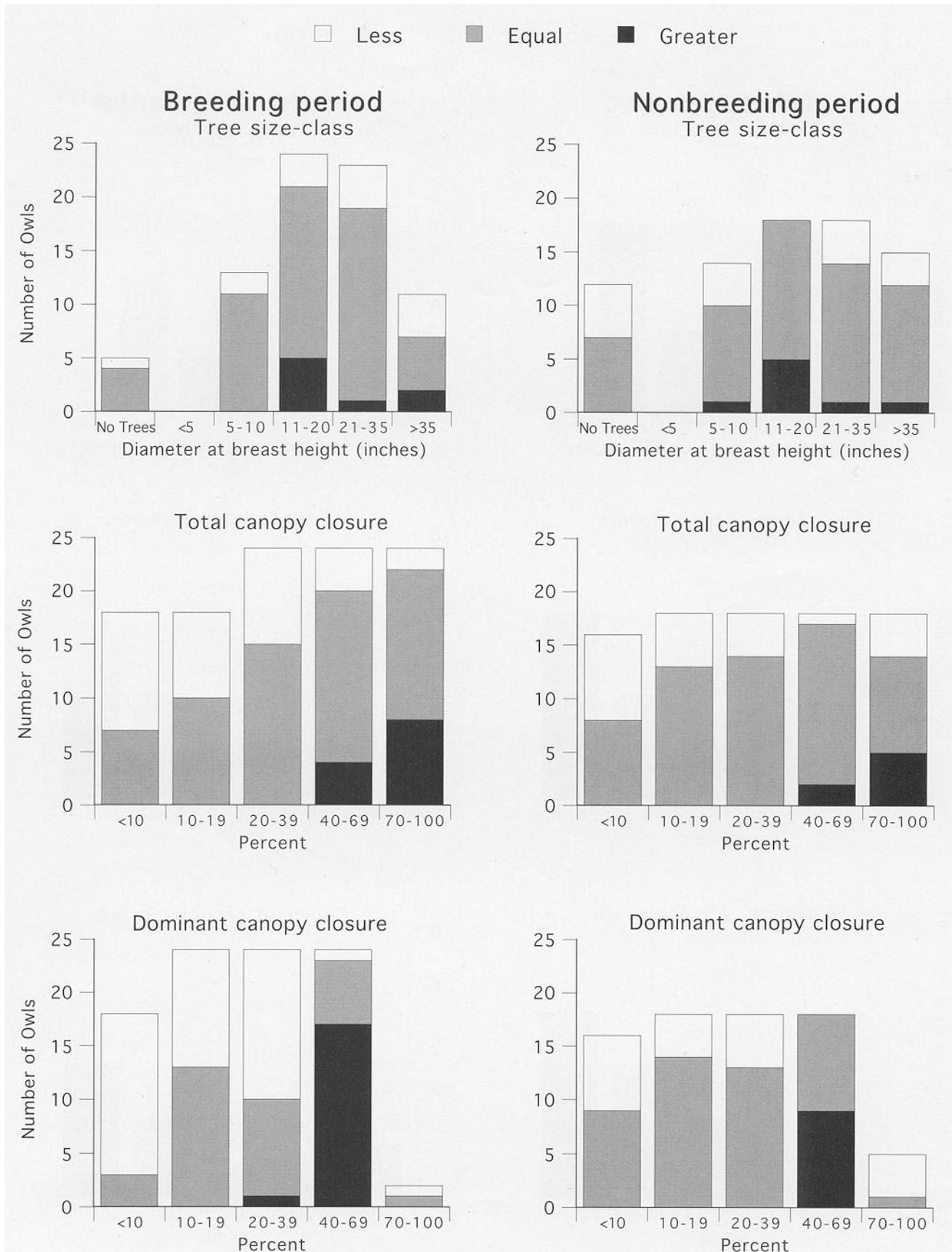


Figure 6C—The number of California spotted owls at S-CON (conifer forest study area in the Sierra National Forest) that used tree size-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

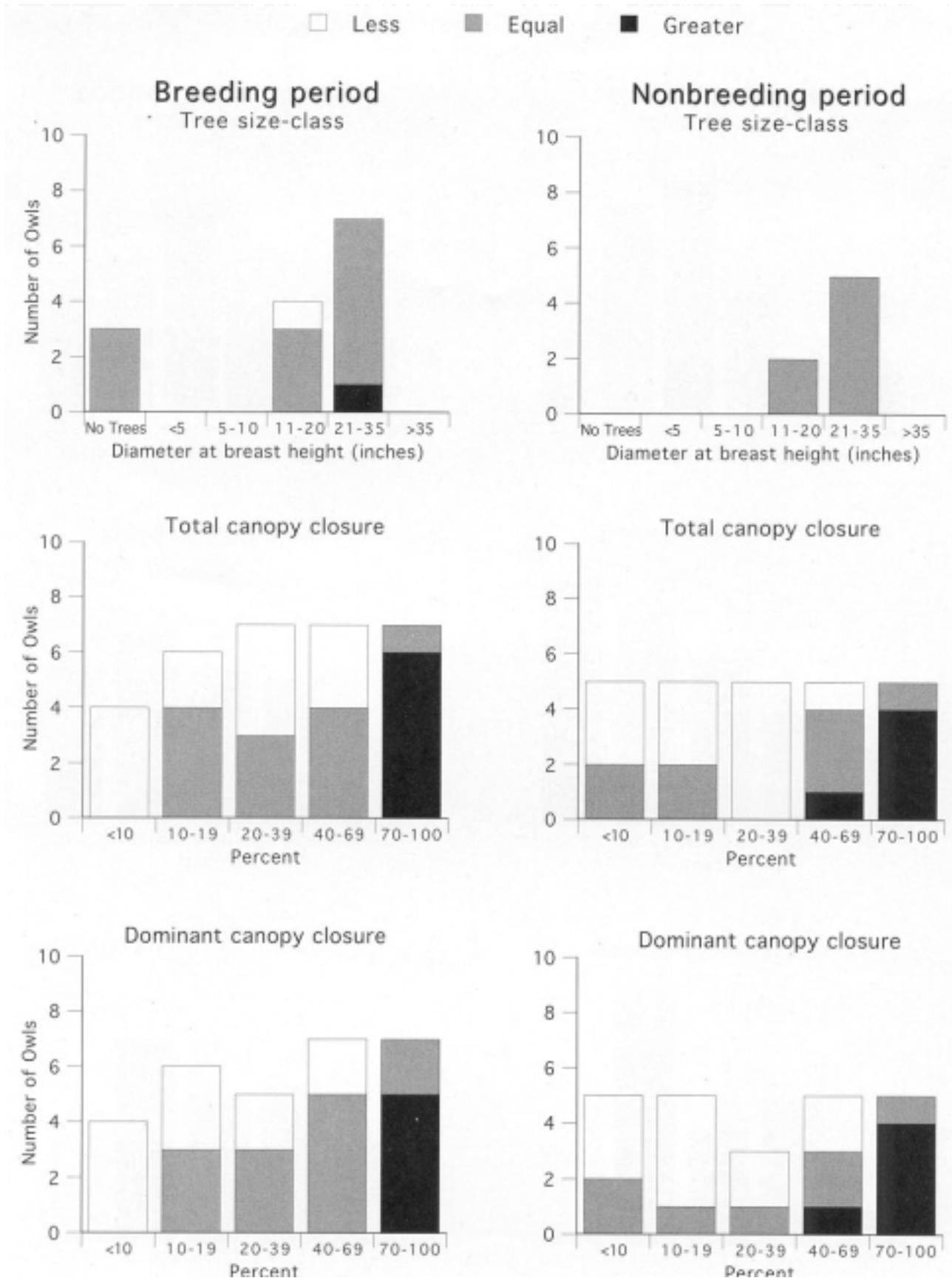


Figure 6D-The number of California spotted owls at S-OAK (riparian/hardwood forest study area in the Sierra National Forest) that used tree size-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

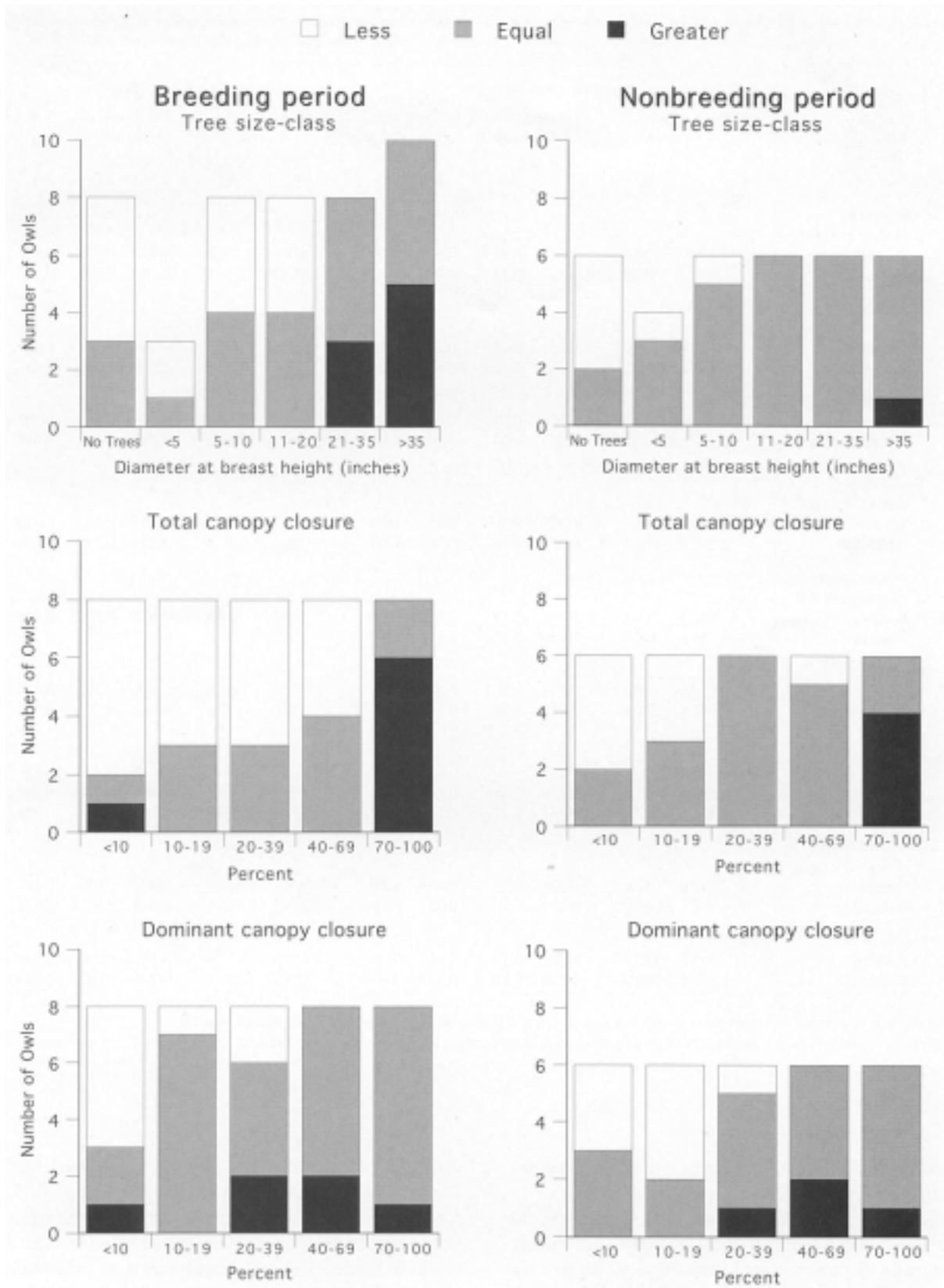


Figure 6E—The number of California spotted owls at L-CON (conifer forest study area in the Lassen National Forest) that used tree diameter-classes (diameter at breast height) and canopy-closure classes (percent) greater than, equal to, or less than expected during breeding and nonbreeding periods.

Table 6F--Means (\bar{x}) and standard deviations (SD) of total area, proportions of home ranges, and proportions of foraging and roosting radio locations in suitable and unsuitable habitat for California spotted owls that passed the site fidelity test for the 1987-1990 breeding and nonbreeding period at L-CON, S-CON, and S-OAK study sites in the northern and central Sierra Nevada. The 95-percent adaptive kernel method was used to estimate home ranges (n = number of individual owls).

Study site	Habitat type	Breeding period ¹						Nonbreeding period ¹										
		n	Area (acres)		Proportion of home range		Proportion of locations		n	Area (acres)		Proportion of home range		Proportion of locations				
			\bar{x}	SD	\bar{x}	SD	\bar{x}	SD		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD			
S-CON	Total canopy closure ≥ 40 pct	24	Suitable	1,570.7	734.1	0.813	0.11	0.907	0.10	18	Suitable	4,478.9	2,378.6	0.806	0.11	0.893	0.07	
			Unsuitable	450.5	540.9	0.187	0.11	0.093	0.10		Unsuitable	1,412.1	1,734.4	0.194	0.11	0.107	0.07	
	Dominant canopy closure ≥ 40 pct	24	Suitable	609.6	308.0	0.357	0.22	0.537	0.25	18	Suitable	1,959.0	991.5	0.361	0.12	0.487	0.19	
			Unsuitable	1,411.6	1,095.7	0.643	0.22	0.463	0.25		Unsuitable	3,932.0	3,053.7	0.639	0.12	0.513	0.19	
	Region 5 ²	24	Suitable	93.6	126.5	0.039	0.05	0.037	0.08	18	Suitable	655.8	499.9	0.105	0.06	0.105	0.11	
			Unsuitable	1,927.6	1,117.4	0.961	0.05	0.963	0.08		Unsuitable	5,256.2	3,560.3	0.895	0.06	0.895	0.11	
	S-OAK	Total canopy closure ≥ 40 pct	7	Suitable	569.1	365.8	0.779	0.16	0.904	0.08	5	Suitable	386.1	256.4	0.663	0.14	0.859	0.09
				Unsuitable	202.0	261.1	0.221	0.16	0.096	0.08		Unsuitable	269.2	299.4	0.337	0.14	0.141	0.09
		Dominant canopy closure ≥ 40 pct	7	Suitable	514.5	284.5	0.740	0.17	0.886	0.10	5	Suitable	321.3	122.0	0.623	0.21	0.799	0.19
Unsuitable				256.6	349.8	0.260	0.17	0.114	0.10	Unsuitable		334.2	439.9	0.377	0.21	0.201	0.19	
Region 5 ²		7	Suitable	113.6	49.6	0.273	0.26	0.488	0.31	5	Suitable	117.6	43.0	0.316	0.25	0.474	0.32	
			Unsuitable	657.5	599.5	0.727	0.26	0.512	0.31		Unsuitable	538.0	592.8	0.684	0.25	0.526	0.32	
L-CON	Total canopy closure ≥ 40 pct	8	Suitable	4,502.6	4,425.3	0.679	0.11	0.851	0.09	6	Suitable	8,316.5	3,739.6	0.709	0.12	0.864	0.05	
			Unsuitable	2,575.2	3,557.8	0.321	0.11	0.149	0.09		Unsuitable	3,737.9	2,750.8	0.291	0.12	0.136	0.05	
	Dominant canopy closure ≥ 40 pct	8	Suitable	2,140.0	2,059.0	0.328	0.13	0.458	0.16	6	Suitable	3,730.4	2,114.3	0.304	0.07	0.487	0.09	
			Unsuitable	4,938.0	6,005.8	0.672	0.13	0.542	0.16		Unsuitable	8,323.7	3,986.6	0.696	0.07	0.513	0.09	
	Region 5 ²	8	Suitable	1,465.5	883.5	0.262	0.10	0.468	0.13	6	Suitable	2,238.8	971.0	0.252	0.09	0.415	0.17	
			Unsuitable	5,167.5	5,269.0	0.738	0.10	0.532	0.13		Unsuitable	7,898.8	4,339.5	0.749	0.09	0.585	0.17	

¹ An individual owl may contribute to n more than once if it was radio tracked during multiple breeding or nonbreeding periods.

² Region 5 definition--suitable habitat = medium or large sawtimber, dominant canopy closure poor or higher, and total closure >69 percent; unsuitable habitat=all other types.

locations and nighttime foraging locations--they were less selective among habitats when foraging than when roosting.

The small number of radio locations among our owls did not result in low power to reject the null hypothesis for canopy closure. Estimates of power ranged from 70 to 90 percent for canopy closure. We had high likelihood of detecting habitat selection for canopy closure when it occurred. Our power to detect selection for tree size-class was lower--70 percent at L-CON, 59 percent at S-CON, and 29 percent at S-OAK. Thus, even if selection for tree size-class occurred, we had low power to detect it, especially in the oak woodlands at S-OAK. The number of radio locations for canopy closure and tree size-class

was the same; the differences in power were due to differences in effect size. To achieve 80 percent power at an 0.05 level of significance, with 4 degrees of freedom, given the effect size we observed for tree size-class (0.20 at S-OAK), 298 radio locations would be needed; if the effect size were 0.30, only 133 locations would be needed (see Cohen 1988, p. 258).

Effect size can also be strongly influenced by the definition of the available sampling frame. In general, the more widely defined the available frame, the greater the likelihood of demonstrating selection. By using the AK method to define the available sampling frame for each home range, we decreased the likelihood of demonstrating selection relative to a less restrictive

Table 6G Estimated areas of use by California spotted owls that were not radio tracked. Data are tabulated by National Forest (NF), and some Ranger Districts, as minimum breeding-season estimates. Estimated areas of use were based on the sizes of drainages occupied by owls during summer surveys.

Areas of use	Total area used (acres)		
	$\bar{x} \pm SD$	Range	<i>n</i>
Cleveland NF			
All sites	133.4 ± 70.0	38.0 - 294.0	15
Chaparral sites	159.5 ± 85.9	38.0 - 294.0	8
Oak/Pines sites	103.6 ± 29.4	70.0 - 155.0	7
Angeles NF			
All sites	225.8 ± 148.1	37.0 - 689.0	71
Saugus Ranger District	172.6 ± 156.7	48.0 - 530.0	14
Tujunga Ranger District	235.4 ± 123.3	119.0 - 405.0	8
Arroyo Seco Ranger District	304.6 ± 144.1	37.0 - 689.0	21
Mount Baldy Ranger District	185.6 ± 134.3	46.0 - 496.0	14
Valyermo Ranger District	195.3 ± 139.7	65.0 - 600.0	14
All pairs	242.5 ± 147.4	54.0 - 600.0	38
Singles	206.5 ± 148.7	65.0 - 600.0	33
Los Padres NF			
All sites	89.3 ± 52.2	25.0 - 200.0	21
All pairs	98.4 ± 50.4	25.0 - 200.0	16
Singles	60.0 ± 51.9	25.0 - 150.0	5
San Bernardino NF¹			
All pairs	5,329.0 ± 4,941.0	1,835.0 - 8,823.0	2
All individuals	3,450.1 ± 2,504.6	674.0 - 6,294.0	4

¹ Owls on the San Bernardino NF were radio tracked. Home-range estimates were determined using the 100-percent minimum convex polygon.

definition of availability based on, for example, the 100-percent MCP. This occurred because the AK algorithm tightly fits the actual distribution of points with an irregular polygon. In the limiting case with many data points, the AK could fit just the used distribution of points and exclude other habitats that truly may have been available.

Thus, failure to reject the null hypothesis (that habitat use = habitat available) in some of our tests of selection may have resulted from the effects of small samples and the use of the AK algorithm, rather than demonstrating a lack of selection. The extent to which this occurred is unknown. It is clear, however, that failure to detect habitat selection should be interpreted, for those tests with low power, in terms of a high likelihood of type-II errors. Given these limitations, it may be that confirmed selection for particular attributes (for example, canopy closure or tree size) by even a few owls should be considered strong evidence for selection in our studies. An incorrect inference would be to conclude that failure to detect significant habitat selection proves a lack of selection. For these reasons, we believe the most significant insights to spotted owl biology are provided by the habitat-use results, rather than results of tests for selection.

References

- Baldwin, James A., Statistician, USDA Forest Service, Pacific Southwest Research Station, Albany, CA. [Personal communication]. April 1986.
- Burt, William H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.
- Byers, C. Randall; Steinhorst, R. K.; Krausman, P. R. 1984. Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management* 48:1050-1053.
- Calhoun, J. B.; Casby, J. U. 1958. Calculation of home range and a density of small mammals. *United States Public Health Monograph* 55:1-24.
- Call, Douglas R. 1990. Home range and habitat use by California spotted owls in the central Sierra Nevada. Arcata, CA: Humboldt State Univ.; 83 p. Thesis.
- Carey, Andrew B.; Horton, Scott P.; Biswell, Brian L. 1992. Northern spotted owls: influence of prey base and landscape character. *Ecological Monographs* 65:223-250.
- Cohen, Jacob. 1988. *Statistical power analysis for the behavioral sciences*. Hillsdale, NJ: Lawrence Erlbaum Associates, Publishers; 567 p.
- Forsman, Eric D. 1983. *Methods and materials for locating and studying spotted owls*. Gen. Tech. Rep. PNW-162. Portland, OR: Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 8 p.
- Hayne, Don W. 1949. Calculation of size of home range. *Journal of Mammalogy* 30:1-18.
- Jenrich, R. I.; Turner, F. B. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology* 22:227-237.
- LaHaye, William S., Research Associate, Wildlife Department, Humboldt State Univ., Arcata, CA. [Personal communication]. January 1992.
- Laymon, Stephen A. 1988. *Ecology of the spotted owl in the central Sierra Nevada, California*. Berkeley, CA: Univ. of California; 285 p. Dissertation.
- Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223-249.
- Neu, Clyde W.; Byers, C. Randall; Peek, James M. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38:541-545.
- Nice, Margaret Morse. 1941. The role of territory in bird life. *American Midland Naturalist* 26:441-487.
- Spencer, Stephen R.; Cameron, Guy N.; Swihart, Robert K. 1990. Operationally defining home range: temporal dependence exhibited by hispid cotton rats. *Ecology* 71:1817-1822.
- Springer, Joseph T. 1979. Some sources of bias and sampling error in radio triangulation. *Journal of Wildlife Management* 43:926-935.
- Thomas, Jack Ward; Forsman, Eric D.; Lint, Joseph B.; Meslow, E. Charles; Noon, Barry R.; Verner, Jared. 1990. *A conservation strategy for the northern spotted owl*. Washington, DC; U.S. Government Printing Office; 427 p.
- White, Gary C.; Garrott, Robert A. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. *Journal of Wildlife Management* 50:509-513.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70:164-168.