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SUMMER HABITAT ECOLOGY OF NORTHERN SPOTTED OWLS IN NORTHWESTERN CALIFORNIA[1]

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Abstract. We studied the summer habitat ecology of 12 Northern Spotted Owls (*Strix occidentalis caurina*) in two areas of northwestern California. Spotted Owls used mature or old-growth conifer forests significantly more than expected relative to their availability within their home ranges. In contrast, Spotted Owls used forests of intermediate and young age significantly less than expected relative to their availability within their home ranges. Eighty four percent of 616 Spotted Owl radiotelemetry locations were recorded in mature or old-growth forests. Spotted Owls used forests of complex structure and old age. There were significant differences in habitat structure (e.g., canopy closure, shrub cover, herb cover, old-growth conifer basal area, and hardwood tree density) among habitats used for frequent foraging, infrequent foraging, and roosting. In addition, male and female owls appeared to select habitats with different structure for foraging. Male owls which are smaller than female owls foraged in habitats which had higher tree density than female owls. The mean summer home-range size was 413 ha (SD = ±196 ha) with males having smaller mean home-range size than females (338 ha and 538 ha, respectively).

Key words: Northern Spotted Owl; Strix occidentalis caurina; *Strigiformes; old-growth forest; home-range size; northwestern California.*

INTRODUCTION

The Northern Spotted Owl (*Strix occidentalis caurina*) is one of the most intensively studied birds in North America because of its close association with the old-growth conifer forests of the Pacific Northwest (Forsman et al. 1984, Gutiérrez 1985, Carey et al. 1990). These forests contain timber of high commercial value which is important to regional economies (Dixon and Juelson 1987). Thus, the owl is at the center of a national controversy on old-growth logging (Dawson et al. 1987, Simberloff 1987). Yet, despite the bird's clear association with these forests, the nature of the Spotted Owl's habitat is not well understood (Forsman 1976, Forsman et al. 1984, Gutiérrez 1985).

To better understand the relationship between Spotted Owls and old-growth forests, we studied this owl's habitat use. Our primary objectives were to estimate Spotted Owl selection of available habitat and to quantify the structure of their habitat. A secondary objective was to estimate owl home-range size during part of the breeding season.

STUDY AREA

We selected three sites within the Six Rivers National Forest for extensive observations. These sites were typical of northwestern California and were characterized by steep (15–110% slope), mountainous terrain with hot, dry summers and cold, wet winters (Sawyer et al. 1977).

The vegetation was primarily a mixed evergreen forest dominated by Douglas-fir (*Pseudotsuga menziesii*) in the overstory and a variety of hardwoods in the understory (e.g., tanoak, *Lithocarpus densiflorus*; Pacific madrone, *Arbutus menziesii*; chinquapin, *Castanopsis chrysophylla*; and several oaks, *Quercus* spp.). Coastal montane forests dominated by white fir (*Abies concolor*) were found above 1,271 m. Sawyer et al. (1977) provided more complete descriptions of the vegetation. The area was ideal for studies of habitat use because fire, edaphic, and topographic diversity combined with logging has produced a mosaic of habitat types with differing structure.

METHODS

HABITAT USE

Spotted Owls were observed directly at roost sites or indirectly using radiotelemetry. Owls were captured with mist nets (Forsman 1983). Each bird was sexed prior to capture by the pitch of

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its call (Forsman et al. 1984) and aged (adult or subadult) by the presence or absence of white downy tips on the rectrices (Forsman 1981). All captured birds were banded with U.S. Fish and Wildlife Service metal leg bands and outfitted with radiotelemetry transmitters. Transmitters were manufactured by AVM Instrument Company, Champaign, Illinois (1981 field season) and Telonics, Mesa, Arizona (1982 field season) and mounted as a backpack. Transmitters averaged 24 g (approximately 4.1% and 3.6% of the average mass of male and female Spotted Owls, respectively, in the Willow Creek area; Blakesley et al., in press). Telonics TR-2 receivers and hand-held two-element, directional Yagi antennas were used to detect radio signals.

Radio-marked Spotted Owls were selected at random each night for monitoring. An observer then tracked an individual owl for half the night before monitoring another owl the rest of the night. In this procedure all owls were monitored in all segments of the night during the course of the study. Owls were located by radio triangulation using the loudest signal method (Springer 1979). A rigorous protocol for radio monitoring and data recording was followed throughout the study to minimize observer bias and sampling error (Solis 1983, p. 9–11). Telemetry locations were plotted on 1:24,000 topographic maps in the field as they were taken. We recorded a minimum of three compass bearings on the transmitter signal for each owl location within 5–10 min. We rejected all error polygons (i.e., the area described by the intersection of three or more compass bearings) that exceeded 1 ha on our topographic maps. Error polygons exceeding 1 ha indicated that either the owl had moved while bearings were recorded or that we had a poor estimate for one or more compass bearings. Each location was then categorized by habitat type using U.S. Forest Service timber type maps. All timber type maps were verified for accuracy in the field prior to analysis of habitat use. A random distribution of habitat locations equal to the total number of radio locations was generated to compare owl habitat use and availability. We only used telemetry observations that were unambiguously located within a habitat (e.g., had a <1 ha error polygon or the error polygon was clearly within one habitat type) in these analyses (Solis 1983). We treated all nighttime observations as foraging locations and all daytime observations as roosting locations.

HABITAT ANALYSIS

We conducted a pilot study between 15 June and 30 September 1980 during which we tested and refined our telemetry and habitat sampling techniques. From habitat data gathered during the pilot study we estimated that we would need to measure habitat characteristics within 496 habitat plots in order to estimate the mean of every habitat variable with 95% confidence (Snedecor 1950). Each habitat plot was a 0.04-ha circle within which we measured 230 variables (179 tree, 40 shrub, 6 ground cover, and 5 physiographic; see Solis 1983 for a complete description). These habitat features were recorded to assess the full complement of plant species and physiographic features of Spotted Owl habitat in northwestern California (Solis 1983). However, only variables of tree density, tree basal area, vegetation cover, and physiography (less than 20 variables) were used in the analyses of habitat structure. With the exception of ocular estimates of herbaceous cover within 0.25-m^2 square plots, all variables were measured in an objective fashion using standard forestry measuring tools (Solis 1983).

Four hundred ninety-six radiotelemetry locations were randomly selected as sites for habitat plots. Three subsets of habitat plots were categorized according to owl use. The first subset was selected from areas frequently used for foraging (greater than five owl locations per hectare). The second subset was selected from infrequently used foraging sites (less than five owl locations per hectare); about 10% (n = 48 of 496) of all habitat plots were in this category. The third subset was selected from roost sites. The number of sample plots from the first category was in proportion to their occurrence within the total set of radio locations. However, infrequently used foraging sites and roost sites were selected equally among birds because we had far fewer locations for these two use categories than we did for frequently used sites (Solis 1983). For example, infrequently used foraging sites were uncommon (<15 per bird) and usually represented locations on the periphery of a home range (Solis 1983).

STATISTICAL ANALYSIS

Macrohabitat use. Chi-square analysis was used to compare differences between the observed and expected distribution of owl locations within habitat types. Three habitat types, which we defined by the size of overstory trees, occurred in each owl home range. These habitats were stands of: (1) mature/old-growth timber (>52.5 cm diameter at breast height, dbh); (2) pole/medium timber (12.5–52.4 cm dbh); and (3) brush/seedling/sapling trees (<12.5 cm dbh). Therefore, each habitat type was available to each owl for use as foraging and roosting habitat. However, macrohabitat selection analyses for owls was based only on two habitat types (pole/medium timber and mature/old-growth timber). To avoid violations of assumptions and sample-size requirements for chi-square analysis, the brush/seedling/sapling tree habitat type was excluded from macrohabitat analyses because most owls did not use this habitat type (Cochran 1954, Neu et al. 1974, Zar 1974).

Microhabitat use. Simple descriptive statistics were computed for each habitat variable. One-way analysis of variance (ANOVA) and *t*-tests were applied to parametric data. The Least Significant Difference (LSD) procedure was used to estimate where differences existed among means. Arcsine transformations were used where applicable (Zar 1974).

Principal component and factor analyses were used primarily as data reduction tools (Nie et al. 1975). Stepwise discriminant analysis was used to make inferences that differential habitat use was correlated with habitat structure and physiography; and to assess differences in habitat used by male and female owls (Nie et al. 1975).

Highly correlated ($r \geq 0.65$) variables (one of each pair) were removed from discriminant analysis, whereas variables with the greatest univariate F values were retained. Variables with the greatest among-group variation or ecological interpretation were retained if high correlations resulted after initial analyses. Group sizes were approximately equal for each analysis. Discriminant functions were interpreted by using correlations between values of original variables and discriminant functions. Classification equations developed from the discriminant models were used to predict group membership. Classification procedures correctly classifying a large percentage of habitat plots to their original groups, based on discriminant scores alone, were considered successful (Nie et al. 1975).

RESULTS

HOME-RANGE ANALYSIS

We observed 12 Northern Spotted Owls between 9 July 1980 and 24 August 1981. Ten birds (five adult males, two adult females, one subadult male, and two subadult females) were radio-marked and monitored for periods ranging from 10 to 241 days (Solis 1983, p. 23). An adult male was observed for 2 days in 1980 and then was never seen again. An adult female (AF-SL) was observed, but not radio-marked, over a period of 96 days; she nested successfully in 1981 with AM-SL (see Table 1 for owl codes). The average monitoring period in 1980 was only 29.4 (SD = ±20.2) days for the four marked birds because of transmitter failures. We used Telonics transmitters in 1981 with an average summer observation period of 113.6 (SD = ±49.6) days for eight birds. We used 1,371 telemetry locations for our home-range estimates.

Among the 12 birds that we observed, there were five radio-marked individuals from three

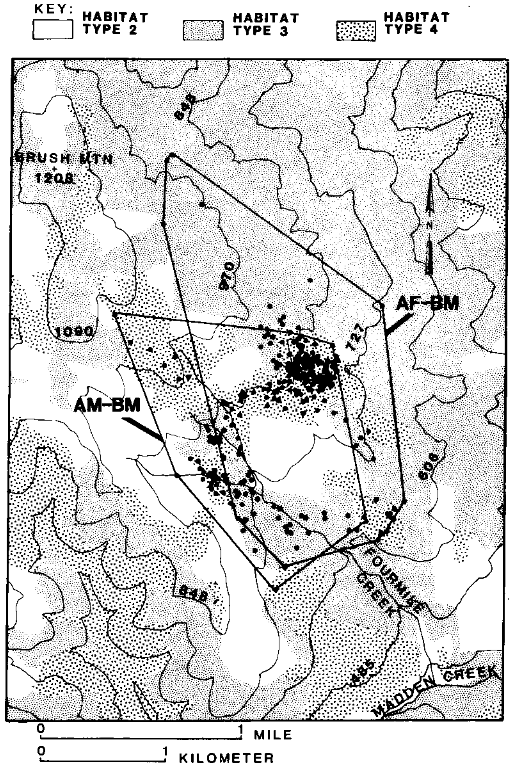

FIGURE 1. Home ranges of Spotted Owls at Fourmile Creek, northwestern California, 1980–1981. Habitat type: 2 = brush/seedling/sapling tree; 3 = pole/medium tree; 4 = mature/old-growth (Marcot 1979). Douglas-fir (*Pseudotsuga menziesii*) is the dominant vegetation type in all areas. Contour intervals are in meters. Larger solid, black dots represent radiotelemetry locations.

TABLE 1. Habitat composition and home-range size of radio-tagged Northern Spotted Owls during the summer in northwestern California, 1980–1981.

Owl code[a]	Area (ha) in habitat type[b]			Total home range (ha)
	Early	Mid	Late	
Individual home range:				
AM-LC	115.2 (16.9%)[c]	169.6 (24.9%)	396.0 (58.2%)	680.8
AM-BM	77.2 (28.4%)	78.0 (28.6%)	117.2 (43.0%)	272.4
AF-BM	62.8 (16.3%)	237.2 (61.8%)	84.0 (21.9%)	384.0
AM-SL	75.2 (39.6%)	21.2 (11.1%)	93.6 (49.3%)	190.0
AM-MC	40.8 (17.0%)	61.2 (25.5%)	138.0 (57.5%)	240.0
SF-SL	226.0 (40.3%)	112.0 (20.0%)	222.4 (39.7%)	560.4
AM-AR	71.2 (23.3%)	77.6 (25.4%)	156.8 (51.3%)	305.6
AF-AR	158.8 (23.7%)	162.0 (24.2%)	349.2 (52.1%)	670.0
Pair home range:				
Brush Mountain	88.8 (17.6%)	267.6 (53.2%)	146.8 (29.2%)	503.2
Ammon Ridge	166.0 (19.5%)	191.2 (22.5%)	493.2 (58.0%)	850.4

[a] Owl codes: First two letters represent age (A = adult; S = subadult) and sex (M = male; F = female); last two letters represent study area (LC = Leary Creek; BM = Brush Mountain; SL = Sugarloaf Mountain; MC = Mosquito Creek; AR = Ammon Ridge).
[b] Habitat types: Early = brush/seedling/sapling tree stage; mid = pole/medium tree stage; late = mature/old-growth tree stage.
[c] Percentage of home range in habitat type is in parentheses.

pairs. One pair at Fourmile Creek (AM-BM) and AF-BM) did not attempt to nest (Fig. 1). A second pair at Ammon Ridge (AM-AR and AF-AR) attempted to nest but failed prior to radio marking (Fig. 2). A third pair at Sugarloaf Mountain nested successfully; only the male (AM-SL) of this pair was radio-marked (Fig. 2). All pairs were comprised of adult birds. One adult male died during the study; his death coincided with movements away from his usual foraging and roosting area. The cause of death was not determined. One subadult male dispersed from the study area and wandered widely. Consequently, this owl was not used in the home-range analysis because it would have exaggerated home-range estimations. Two subadult owls were included in the analysis because they appeared to have stable home ranges.

Home-range size. Summer home-range size was estimated for eight owls for which we had sufficient (>30) telemetry observations. Summer home ranges averaged 412.9 ± 196.9 ha with males having smaller home ranges than females (337.6 ± 196.4 ha and 538.0 ± 144.2 ha, respectively). However, there was a great deal of variation among individual owls (Table 1).

Most Spotted Owls that we observed shared some portion of their home range with other Spotted Owls (Figs. 1, 2). On the average, adjacent males and females shared 52.1% of their home ranges (SD = ±31.4%; range = 2.0–98.9%; eight comparisons). In contrast, adjacent females only shared 10.4% of their home ranges (SD = ±1.3%; range = 9.4–11.3%; two comparisons); males were even more discrete ($\bar{x}$ = 2.3 ± 0.4%; range = 2.0–2.5%; two comparisons). As expected, overlap between members of a pair was greatest ($\bar{x}$ = 62.4 ± 21.4%; range = 40.9–89.7%).

An adult male (AM-MC) residing in Mosquito Creek was excluded from some estimates of home-range overlap because some of the range overlaps did not occur until after his death. For example, the home range of an adult female (AF-AR) paired with another male (AM-AR) at Ammon Ridge encompassed approximately 88% of AM-MC's home range. However, prior to AM-MC's death, AF-AR's foraging and roosting activities were confined to an area north and outside of AM-MC's home range. AF-AR began using AM-MC's primary use area within 5 days of his death.

MACROHABITAT ANALYSIS

Habitat use. A total of 616 of 1,371 telemetry locations were unambiguously located in a habitat type and these were used for analyzing owl habitat use. Owl habitat locations were not pooled among owls because an analysis of heterogeneity indicated that habitat use differed significantly (χ^2 = 14.067; df = 7; $P < 0.001$) among the owls. However, foraging and roosting locations used by individuals were pooled because analyses of heterogeneity indicated that the number of foraging and roosting locations within each habitat

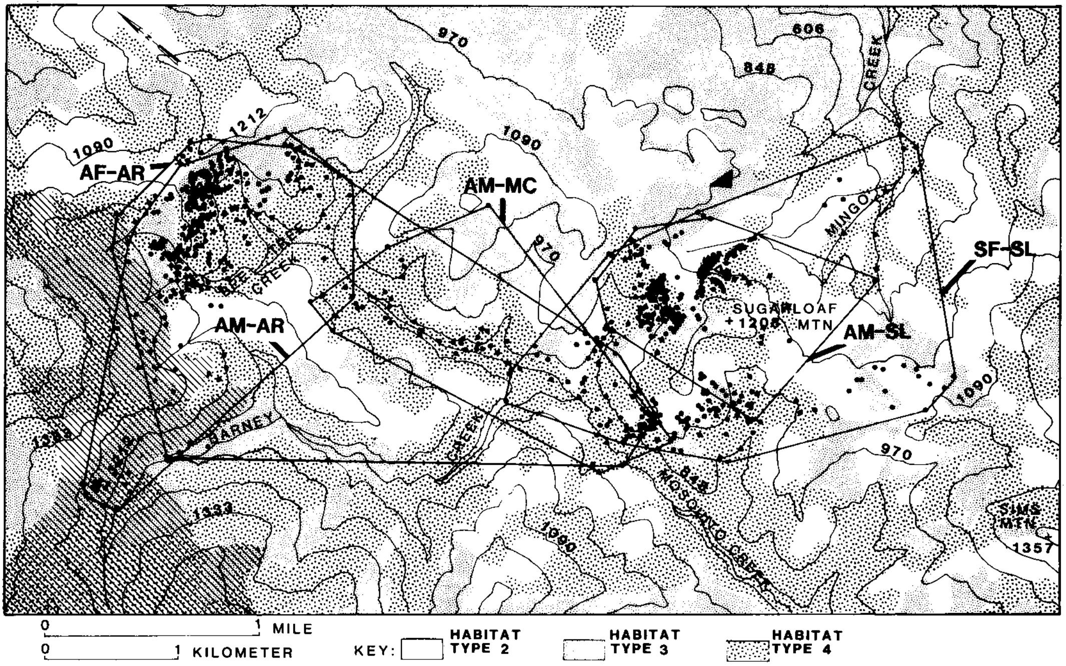

FIGURE 2. Home ranges of Spotted Owls at Mosquito Creek, northwestern California, 1980–1981. Habitat type: 2 = brush/seedling/sapling tree; 3 = pole/medium tree; 4 = mature/old-growth (Marcot 1979). Douglas-fir (*Pseudotsuga menziesii*) is the dominant vegetation type in all areas except the striped area which indicates forest dominated by white fir (*Abies concolor*). Contour intervals are in meters. Larger solid, black dots represent radiotelemetry locations.

type did not differ significantly ($\chi^2 = 1.783$; df = 1; $P < 0.05$) within individual owls (Table 2).

All owls foraged and roosted in mature/old-growth timber more often than expected ($P \leq 0.005$) based on its availability (Table 2). Approximately 70% ($n = 266$ of 378) of all foraging locations and 89% ($n = 211$ of 238) of all roosting locations were found in this habitat. Owls foraged and roosted in pole/medium timber less often than expected ($P \leq 0.05$) based on habitat availability. Approximately 27% ($n = 103$ of 378) and 11% ($n = 27$ of 238) of all foraging and

TABLE 2. Habitat selection by seven Northern Spotted Owls in northwestern California, 1980–1981.

Habitat type	Proportion of locations in habitat type $\bar{x} \pm$ SD (Range)	Proportion of home range in habitat type $\bar{x} \pm$ SD (Range)	No. of owls[a] Less	No diff.	Greater
Late[b]	0.84 ± 0.10 (0.71–1.00)	0.45 ± 0.12 (0.22–0.58)	0	0	7
Mid	0.14 ± 0.11 (0.00–0.29)	0.28 ± 0.16 (0.11–0.62)	7	0	0
Early	0.00 ± 0.00 (0.00–0.11)	0.27 ± 0.10 (0.16–0.40)	7[c]	0	0

[a] Number of owls using habitat significantly less ($P < 0.05$), not significantly different ($P \geq 0.05$), or significantly greater ($P < 0.05$) compared to its proportion within the home range.
[b] Habitat types: Late = mature/old-growth tree stage; Mid = pole/medium tree stage; Early = brush/seedling/sapling stage.
[c] We concluded that all seven owls used the brush/seedling/sapling habitat type for foraging or roosting less than expected, because only 2.3% ($n = 9$) of all foraging locations and no roosts were found in this habitat. Inclusion of this habitat type in analysis of habitat use would have violated assumptions and sample-size requirements of habitat use and chi-square analyses (Cochran 1954, Neu et al. 1974, Zar 1974).

roosting locations, respectively, were found in this habitat. Owls rarely (2.3%; $n = 9$ of 378 locations) foraged and were never observed roosting in the brush/seeding/sapling tree habitat.

MICROHABITAT ANALYSIS

Habitat structure. We estimated habitat characteristics within the home ranges of 10 Spotted Owls from a sample of 496 foraging and roosting habitat plots measured within their home ranges (Table 3). We used one-way ANOVAs to test for equality among mean values of habitat features within habitats used by each sex for foraging and roosting (Table 3).

We observed three general trends in Spotted Owl habitat structure. First, owls used forests in which hardwood and conifer trees formed multilayered (two or more layers) stands with a high (>85%) canopy closure (Solis 1983; Table 3). Canopy closure was highest in roost habitats and lowest in habitats infrequently used for foraging (Table 3). Large (>90.0 cm dbh) conifers (37.5 m^2/ha), primarily Douglas-fir, and small (<27.3 cm dbh) understory hardwoods (208.3 trees/ha) contributed most to total stand basal area (70.4 m^2/ha) and stem density (461.8 trees/ha) based on all habitats, respectively. Large conifer basal area and hardwood density were highest in habitats used for roosting, intermediate in habitats frequently used for foraging, and lowest in habitats infrequently used for foraging (Table 3). Shrub and herb cover were highest in habitats used infrequently for foraging (Table 3). There was a gradient of older stand conditions (i.e., the presence of snags, trees of declining vigor, broken-top trees, and the presence of conks) from habitats used infrequently for foraging to those used for roosting. We used a relative measure to estimate stand condition (Solis 1983). On the basis of this categorical assessment of stand condition, 37.5% of infrequently used habitats, 48.5% of frequently used habitats, and 58.0% of the roost habitats were characterized as having stand conditions typical of old-growth forests (Franklin et al. 1981).

Second, habitats used by female owls for frequent foraging or roosting had higher canopy closures than those used by males (Table 3). Hardwood tree density was higher in habitats used by foraging male owls compared to female owls (Table 3).

Third, aspect and elevation were significantly different among owl habitat-use categories. Owls primarily foraged (50.8% of foraging observations) and roosted (56.0% of roost observations) on north-facing slopes. Within a drainage, roosts occurred at lower elevations than did foraging sites (Table 3). In addition, owls roosted an average of 142.1 m ($n = 389$) from water which was significantly different ($t = 2.672$; df = 487; $P < 0.01$) from the distance computed for a random set of locations ($\bar{x} = 226.3$ m; $n = 100$).

Discriminant analysis. All variables used in discriminant analyses approached normality. Box's M-test (Klecka 1975) indicated that variance-covariance matrices were significantly different ($P \leq 0.001$).

We analyzed habitat structure used by male and female owls as well as differences in structure among habitats used by all Spotted Owls. First we assessed differences in habitat structure used by male and female owls. There was a significant difference ($P = 0.001$; $t = 9.667$; df = 450) between habitat structure used by male and female Spotted Owls (Fig. 3). We randomly selected 20 subsets of these data (i.e., habitat plots) for classification. Approximately 78% of all male and female plots were correctly classified ($n = 20$ analyses; range = 75–100%) to their respective group which exceeded the a priori probability of 50%.

Next, since there was a difference in structure of habitats used by male and female owls, we explored differences in habitat structure among the habitats used by either male or female owls. Two discriminant functions (DF-I, DF-II) explained 81.8% of the total variation in use of foraging and roosting habitats by females (Fig. 4). We observed the following significant differences in structure of habitats used by female Spotted Owls. Along DF-I, roosts were significantly different ($P = 0.001$; $t = 3.27$; df = 39) from infrequently used foraging habitat; and frequently used foraging habitat structure was significantly different ($P = 0.005$; $t = 3.20$; df = 34) from infrequently used foraging habitats. Along DF-II, roosting habitat structure was significantly different ($P = 0.001$; $t = 4.76$; df = 29) from habitat structure frequently used for foraging; and structure of habitats used frequently were significantly different ($P = 0.001$; $t = 7.49$; df = 34) from structure of habitats used infrequently for foraging. Female Spotted Owls roosted and hunted in areas that had high canopy closure, low herb cover, high Douglas-fir basal

TABLE 3. Foraging and roosting habitat characteristics of Northern Spotted Owls in northwestern California, 1980–1981. Multiple comparisons of mean values are based on the Least Significant Difference (LSD) procedure.

Variable	Habitat use[a] Infrequent forage $\bar{x}$	Infrequent forage SE	Frequent forage $\bar{x}$	Frequent forage SE	Roost $\bar{x}$	Roost SE	ANOVA F	ANOVA df	ANOVA P	LSD multiple comparison of means[b] Result	LSD P
Canopy closure (%):							7.189	495	<0.0001	d, g < f, c, e, b	≤0.05
Male habitat	75.0	4.9	87.0	1.3	92.5	1.1					
Female habitat	69.1	8.1	88.5	1.0	93.2	0.8					
All habitats	72.8	4.4	87.8	0.8	92.8	0.7					
Shrub cover (%):							2.656	495	<0.05	b, c, f < g	≤0.05
Male habitat	15.0	2.8	8.1	0.9	12.0	4.0					
Female habitat	10.2	3.7	6.6	0.8	6.2	2.3					
All habitats	13.2	2.2	7.3	0.6	9.3	2.4					
Herb cover (%):							2.866	495	<0.05	e, b, c, f < d	≤0.05
										e < d	≤0.01
Male habitat	9.9	2.3	9.2	1.2	4.7	1.9					
Female habitat	16.6	5.7	6.0	0.8	5.0	2.6					
All habitats	12.4	2.6	7.5	0.7	4.9	1.6					
Conifer (>90 cm dbh) basal area (m^2/ha):							5.394	495	<0.001	g < c, b, e	≤0.05
										g < e	≤0.01
Male habitat	16.7	4.9	29.7	3.1	49.5	8.0					
Female habitat	26.6	8.6	46.2	3.1	46.9	8.0					
All habitats	20.4	4.5	38.3	2.2	48.3	5.9					
Hardwood (<27.3 cm dbh) density (stems/ha)							2.692	495	<0.05	g < b	≤0.05
Male habitat	149.3	28.3	158.3	13.8	193.5	27.3					
Female habitat	104.3	30.3	154.5	11.3	228.3	37.5					
All habitats	132.3	32.0	156.5	8.8	209.5	22.5					
Elevation (m):							7.731	495	<0.001	b, d, e < c < f	≤0.05
										b < f	≤0.01
Male habitat	929.6	32.2	1,008.1	13.8	879.7	27.0					
Female habitat	872.2	27.2	957.2	11.5	831.2	30.5					
All habitats	908.1	22.6	981.6	9.0	857.4	20.3					

[a] Sample sizes: Males (n = 6): number of habitat plots measured—infrequently used for foraging (n = 30), habitat frequently used for foraging (n = 191), and roost (n = 27); females (n = 4): number of habitat plots measured—infrequently used for foraging (n = 18), habitat frequently used for foraging (n = 207), and roost (n = 23).

[b] Group means: b = habitat used by females for roosting; c = habitat intensively used by females for foraging; d = habitat infrequently used by females for foraging; e = habitat used by males for roosting; f = habitat intensively used by males for foraging; g = habitat infrequently used by males for foraging.

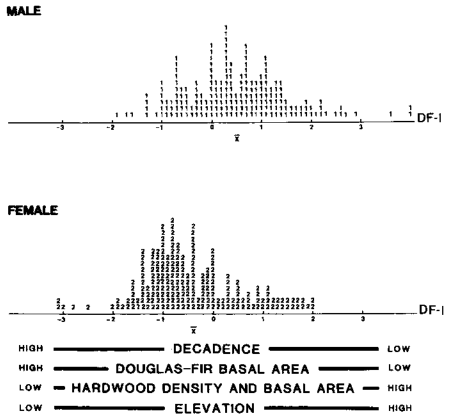

FIGURE 3. Ordination of habitat used for foraging and roosting by male and female Northern Spotted Owls in northwestern California, 1980–1981.

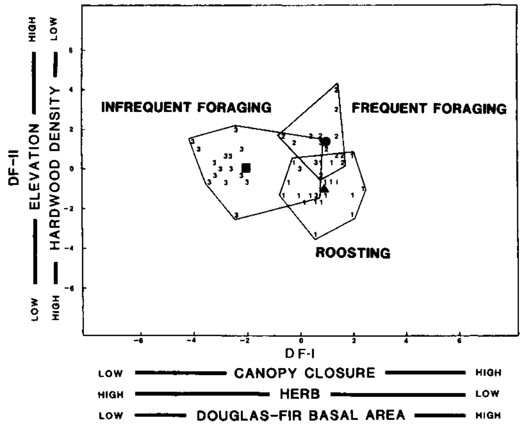

FIGURE 4. Two-dimensional ordination of habitat used by female Northern Spotted Owls in northwestern California, 1980–1981.

area, and high hardwood tree density (Fig. 4; Table 3). An average of 84% ($n = 20$ analyses; range = 73.0–94.7%) of these plots were correctly classified to their respective groups which exceeded the a priori chance probability of 33%.

Two discriminant functions explained 82.9% of the total variation in use of foraging and roosting habitat structure used by male owls (Fig. 5). Along DF-I, roosting habitat structure used by male owls was significantly different ($P = 0.02$, $t = 2.27$, df = 55 and $P = 0.001$, $t = 4.39$, df = 56) from habitat structure they used frequently and infrequently for foraging. In addition, there was a significant difference ($P = 0.001$, $t = 3.19$, df = 58), with respect to DF-I, between habitat structure used frequently or infrequently by males for foraging. Along DF-II, significant differences also occurred between roosting and frequently used habitats ($P = 0.01$, $t = 4.99$, df = 55) and between frequently used and infrequently used foraging habitats ($P = 0.001$, $t = 4.70$, df = 58). An average of 82.9% ($n = 20$ analyses; range = 74.7–92.8%) of these plots were correctly classified to their respective group which exceeded the a priori chance probability of 33%.

DISCUSSION

Our estimates of home range for Spotted Owls in northwestern California were smaller than estimates reported by Forsman et al. (1984) and Allen and Brewer (1985) for Spotted Owls in Oregon and Washington, respectively. However, we probably underestimated home-range size for two reasons. First, our observation periods were relatively short (less than 6 months). Second, Spotted Owls generally have their most restricted ranges in the summer. Spotted Owls usually expand their home ranges in winter (Forsman et al. 1984, Sisco 1990).

Our estimates of overlap between any two owls with adjacent home ranges and between members of a pair were greater than reported by Forsman (1980). A greater overlap in home ranges could be attributed to a patchier distribution of suitable habitat or to a relatively greater density of Spotted Owls in our study areas compared to other areas (Franklin et al. 1990).

Spotted Owls also consistently used large areas of mature/old-growth forests for foraging and roosting which supports the observations of other workers (Forsman et al. 1984, Allen and Brewer 1985, Carey et al. 1990). Gutiérrez (1985) summarized several hypotheses which may explain the apparent association of Spotted Owls with large areas of mature/old-growth forest, including protection from predators, availability of suitable nesting, foraging, and roosting sites, favorable microclimate, and the diversity, abundance, and accessibility of prey. Whitcomb et al. (1977) studied the response of avifauna to logging of mature-forest ecosystems and noted that wide-ranging raptors, such as the Barred Owl (*Strix varia*) were residents of small forest tracts only if these areas were part of a larger forest system containing an area sufficient for their "territorial" requirements.

Although we studied the habitat characteristics of only 10 Northern Spotted Owls, we sampled

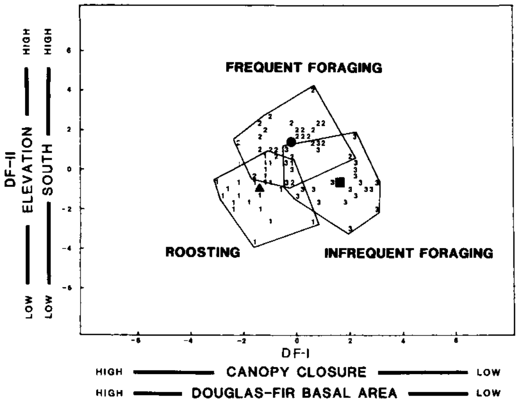

FIGURE 5. Two-dimensional ordination of habitat used by male Northern Spotted Owls in northwestern California, 1980–1981.

their habitat intensively to account for the high habitat heterogeneity within their large home ranges. Therefore, our observations reflect environmental conditions under which these owls existed on managed public lands in northwestern California. Spotted Owls in our areas used complex, structured forests that had a dominant canopy of large (>52.5 cm dbh) conifer trees for roosting and foraging. Our use of infrequently visited habitat by the owls was a conservative estimate of the availability of habitat since over 40% of the study area has been clear-cut (Franklin et al. 1990). Except for one owl, clear-cuts (i.e., habitats dominated by brush, seedling, or sapling trees) were not used by owls in our study.

The structural and physiographic characteristics of forest stands apparently differ among Spotted Owl habitats. We noted significant structural and physiographic differences among habitats used frequently for foraging, used infrequently for foraging, and those used for day roosting. We also recognize that we are observing a correlation between specific habitat structural features and owl occurrence. We are not inferring that owls are selecting old-growth habitats because of the features that we found important in describing their habitat. For example, elevation is an important distinguishing feature of Spotted Owl roosting habitat; however, Spotted Owls roost near streams which are located at the lowest point within their respective drainage. Therefore, elevation probably is a spurious correlation with respect to its importance in owl habitat selection.

Our analyses also suggest that males, which are smaller in body size than females (Blakesley et al., in press), forage in forests with higher tree density than do females. Thus, we infer that there may be ecological segregation of the sexes by differential use of foraging habitat. Because our sample of owls was small, these differences could be an artifact of small sample size. Although members of a pair often roosted and foraged within close proximity of each other, we would expect some differences in the structural characteristics of habitats they used to be due to the heterogeneity of forest stands in northwestern California. However, it should be noted that our study areas differed in vegetation structure (e.g., there was a higher density of hardwood trees at Leary Creek), yet the same patterns in habitat structure differences between the sexes were observed in all study areas. In addition, this pattern of differential habitat use continues into the winter (Sisco 1990).

Earhart and Johnson (1970) described the extent of size dimorphism in North American owls and concluded that female owls had greater wing loading and, therefore, might be less maneuverable than males. Selander (1966) and Earhart and Johnson (1970) postulated that difference in size between the sexes of raptors would permit differential use of habitats. Differential use of habitat by male and female Spotted Owls is probably the result rather than the cause of reversed sexual dimorphism (Mueller 1986).

Our descriptions of the structure and characteristics of frequently used owl habitat were consistent with descriptions by other researchers for old-growth Douglas-fir forests in general (Sawyer et al. 1977, Franklin et al. 1981, Old-Growth Definition Task Group 1986). Thus, we have demonstrated a consistent trend for use of old-growth conifer forest habitat in the southern end of the Northern Spotted Owl's range. Our descriptions of these forests now provides a quantitative basis for the experimental management of this owl's habitat. If Spotted Owls are old-growth dependent, we predict that future studies of Spotted Owls in managed forests will show their use of habitats that structurally resemble "old-growth" forests.

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