

FORAGING ECOLOGY OF NUTTALL'S WOODPECKER

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ABSTRACT.—I studied relative abundances, foraging behavior, and foraging habitats of Nuttall's Woodpeckers (*Picoides nuttallii*) at three California locations. Population sizes at two areas in the foothills of the Sierra Nevada were larger than the population in the Tehachapi Mountains. These differences were attributed to habitat and weather differences. The two areas in the Sierra foothills had milder winters and contained large interior live oaks (*Quercus wislizenii*) and gray pines (*Pinus sabiniana*), species used extensively by woodpeckers outside of the breeding season. The Tehachapi area contained few large interior live oaks and no gray pines. All areas contained blue oak (*Q. douglasii*), used extensively during breeding. Trees actually used for foraging at all locations and during all seasons were larger, on average, than those generally available. Birds foraged by lightly pecking, probing, and gleaning prey from branches <30 cm in diameter, although the exact methods and substrates varied by study area, season, and year. I found little intersexual variation in either foraging behavior or foraging habitat. Received 10 May 1990, accepted 10 October 1990.

NUTTALL'S Woodpecker (*Picoides nuttallii*) is mostly restricted to California oak (*Quercus* spp.) woodlands and riparian areas of cottonwoods (*Populus* spp.) and sycamore (*Platanus racemosa*) from Baja California to southern Oregon (Dawson 1923, Grinnell and Miller 1944, Short 1965). Miller and Bock (1972) provided general natural history information from Carmel Valley, California, where Jenkins (1979) later observed intersexual differences in foraging during a postbreeding season. Short (1971) reported the behavior of Nuttall's Woodpeckers from southeastern Kern County, California. The lack of additional information precludes generalizations concerning its ecology.

Historically, lands within the range of Nuttall's Woodpecker have been used as commercial rangelands and, occasionally, as a source of firewood. Presently, commercial and residential developments are replacing oak woodlands at an unprecedented rate (Doak et al. 1987). The loss of this potential habitat is compounded by an apparent lack of regeneration by some white

oak species (Bartolome et al. 1987). The exact effects of these changes on Nuttall's Woodpeckers are difficult to determine without a thorough understanding of its ecology. In particular, understanding resource use at different locations and during different seasons is necessary to determine the factors that underlie the distribution of Nuttall's Woodpeckers. Such descriptions might elucidate seasonal and spatial patterns that determine the ecological amplitude of this woodpecker. For example, seasonal differences in foraging and habitat for many *Picoides* spp. (Conner 1981, Morrison and With 1987) including Nuttall's Woodpeckers (Miller and Bock 1972) have been reported. Behavioral differences between sexes have been noted in Nuttall's Woodpeckers (Short 1971, Jenkins 1979) and in other *Picoides* species (Austin 1976, Morrison and With 1987, Grubb and Woodrey 1990). A study that examined resource-use patterns simultaneously at a number of different locations is required to determine if these patterns extend to other geographic locations. Consequently, I studied Nuttall's Woodpeckers from 1986 to 1988 (three breeding and two nonbreeding seasons) at three locations in California along a latitudinal gradient of 600 km. My objectives were to describe spatial and temporal patterns in population numbers, foraging behaviors, and

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foraging habitats among study areas and between years and seasons.

METHODS

STUDY AREAS

I studied three resident populations of *Picoides nuttallii*. All study areas were oak or oak-pine woodlands, but each differed in topography and in structure and composition of vegetation. The climate of each area is typically Mediterranean with hot, dry summers and cool, damp winters, although variations between study areas exist in the type and quantity of winter precipitation (Block 1989).

Sierra Foothill Range Field Station (SFRFS), Yuba County (39°15'N, 121°22'W), is located in the foothills of the Sierra Nevada ca. 40 km northeast of Marysville. I used the entire 2,500-ha field station with the exception of irrigated pastures and areas denuded of woody vegetation by logging. Elevation ranges from 300 to 600 m on a generally west- to northwest-facing slope. Average annual precipitation is 750 mm, mostly winter rain and fog. Blue oak (*Quercus douglasii*) and interior live oak (*Q. wislizenii*) are the most abundant trees with fewer California black oak (*Q. kelloggii*), gray pine (*Pinus sabiniana*), California buckeye (*Aesculus californicus*), and valley oak (*Q. lobata*). A patchy, woody understory consists of buckbrush (*Ceanothus cuneatus*), coffeeberry (*Rhamnus californica*), poison oak (*Toxicodendron diversiloba*), and whiteleaf manzanita (*Arctostaphylos viscida*).

San Joaquin Experimental Range (SJER), Madera County (37°37'N, 119°42'W), is also in the foothills of the Sierra Nevada ca. 40 km north of Fresno. My study encompassed the entire 1,800-ha field station. Elevation ranges from 300 to 500 m on a generally south- to southwest-facing slope. Average annual precipitation is ca. 600 mm, mostly winter rain and fog. Blue oak and interior live oak are the major species of trees with fewer gray pine and California buckeye. The woody understory was modified by cattle grazing, which left residual stands of buckbrush, chaparral whitethorn (*Ceanothus leucodermis*), coffeeberry, redberry (*Rhamnus crocea*), and Mariposa manzanita (*Arctostaphylos mariposa*).

Tejon Ranch (TR), Kern County (34°53'N, 118°46'W), is in the Tehachapi Mountains ca. 50 km south of Bakersfield. Half of TR's 100,000 ha is oak woodland. I confined my study to approx. 2,500 ha. Elevation ranges from 1,100 to 1,700 m, and aspect includes all cardinal directions. Average annual precipitation is 450 mm mostly as winter rain, snow, and fog. Tejon Ranch supports a more diverse woodland than either SFRFS or SJER. Blue oak is the most abundant tree, although valley oak, California black oak, interior live oak, and canyon live oak (*Quercus chrysolepis*) are also common. Major shrubs are buckbrush, mountain ma-

hogany (*Cercocarpus betuloides*), redberry, chamise (*Adenostoma fasciculatum*), and big berry manzanita (*Arctostaphylos glaucus*).

RELATIVE ABUNDANCE

Field methods.—To establish 100 census points at SFRFS and TR, I used a systematic-random sampling design (Cochran 1977). Points were spaced 300–400 m apart to ensure sampling independence among points (i.e. not recording the same bird at adjacent points). At SJER, I used 100 points established by J. Verner, selected from aerial photographs, and placed within oak or oak-pine woodland (Verner 1987). Although his points were not established by a strict random design, they provided a sampling of the oak-pine woodlands throughout SJER. I counted birds at TR during the 1986, 1987, and 1988 breeding seasons (April through June) and the 1986/1987 and 1987/1988 nonbreeding seasons (November through February). At SFRFS and SJER, I censused during the 1987 and 1988 breeding seasons and the 1987/1988 nonbreeding season. Birds were counted at each point 3 times during each breeding season, and 5 times during nonbreeding seasons. Five observers collected census data; all were trained to standardize data collection. At each point the observer remained still for 1–2 min to allow the observer to become sensitive to birds present. Following this waiting period, the observer recorded all birds detected by sight or sound within 100 m of the counting station during a 5-min period.

Data analysis.—I used total count/100 points as an index of relative abundance. Total counts provide indices of relative abundance regardless of numbers of detections, and thus counts are not constrained by sample-size requirements of most density estimation models (Verner and Ritter 1985, Raphael 1987). I used Kruskal-Wallis and Mann-Whitney *U*-tests (Marascuilo and McSweeney 1977) to compare total counts by study area, year, and season.

FORAGING BEHAVIOR

Field methods.—I studied foraging at each study area during the 1987 and 1988 breeding seasons and the 1986/1987 and 1987/1988 nonbreeding seasons. Eight observers collected standardized foraging data. Observers searched for Nuttall's Woodpeckers within a 100-m belt on either side of the transect lines that connected counting stations. Once an actively foraging bird was located, the observer watched the bird for 10 s but recorded no data. Presumably, this period allowed the bird to resume normal activity patterns in the presence of the observer, and also minimized the likelihood of the observer recording only conspicuous behaviors (Hejl and Verner 1990). During the second 10-s period the observer recorded the fol-

lowing: the age and sex of the bird; the species, height, diameter, and crown radius of the plant where foraging was observed; the height of the bird and its relative location from the center to the edge of the plant canopy; the foraging substrate (twig/small branch [<10 cm diameter], medium branch [10–30 cm diameter], large branch/trunk [>30 cm diameter], leaf, fruit/seed, ground); and foraging maneuver (glean, peck, probe, pluck, other). Each 10-s observation represented one sample. During each day, observations were limited to woodpeckers spaced >300 m apart to minimize the chance of obtaining multiple samples of the same bird (cf. Beal and Khamis 1990). Up to three samples were obtained per day to distribute samples within the course of a season and to avoid biasing samples towards periods when behaviors were more conspicuous.

I used the point-center quarter method (Mueller-Dombois and Ellenberg 1974) centered at each counting station to determine the relative occurrence and size of trees potentially available to birds. I recorded the species, height, and diameter of the nearest woody plant within each of the four quadrants. Although I collected data on the nearest tree or shrub, I restricted analyses to data pertaining to trees.

Data analysis.—I restricted analyses to adults or birds that no longer exhibited juvenile plumage, to minimize possible effects of age differences. I first tested for differences in foraging by sexes, and then pooled sexes to test for general species differences. For tests of intersexual differences, I pooled data from both years to ensure adequate sample sizes for statistical analyses (cf. Morrison 1984).

I used log-linear analyses to examine partial associations of plants, foraging substrates, and foraging activities by study area, year, and season (Fienberg 1980). Plants, substrates, and activities were analyzed separately to minimize the chance of having empty cells, which may bias the results, and to ease interpretation of significant interaction terms (Noon and Block 1990). If a significant difference occurred among study areas, I applied Chi-square tests of independence (Sokal and Rohlf 1969) between study areas to determine differences. I used ANOVAs (Sokal and Rohlf 1969) on continuous data to examine sources of variation in foraging between study areas, years, seasons, and their interactions. Differences between study areas were tested using Scheffé's method (Snedecor and Cochran 1980) to determine which area(s) differed from the others.

I compared use and availability of tree species across all and for each study area using Chi-square tests of independence (Sokal and Rohlf 1969). Because sample sizes of used and available groups differed greatly, I used nonparametric Mann-Whitney *U*-tests (Marscuilo and McSweeney 1977) to compare diameters and heights of trees used with those available both across and within study areas.

MACROHABITAT USE

Field methods.—At the locations of foraging observations, I measured a series of macrohabitat characteristics within a 20-m radius, circular plot (0.13-ha). I measured the diameter of each main tree stem 1.5 m from the ground (DBH) using a Biltmore stick. To record heights of all trees, I used a clinometer to measure the height of one tree within the plot and then estimated heights of other trees in the plot relative to the measured tree. To estimate tree cover, I paced the crown of the tree in two perpendicular directions and applied these measures to the general equation of an ellipse (Selby 1970). Total lengths of dead tree limbs for two size classes (10–30 cm and >30 cm) were estimated visually to the nearest meter. Shrub heights and two perpendicular crown measures were taken with a meter stick. Shrub cover was estimated using the method described above for trees.

Data analysis.—Because of floristic differences among study areas, I pooled data from both species of live oak (canyon live and interior live oaks) to form one variable, and I pooled all species of deciduous oaks (blue, valley, California black, and Brewer's oaks) to form another. For tests of intersexual differences in foraging, I pooled data from both years to ensure adequate sample sizes (cf. Block et al. 1987). Analyses of variance (Sokal and Rohlf 1969) were used to examine differences among study areas and between seasons for each macrohabitat variable. I then pooled data from both sexes to examine general species differences among study areas and between years and seasons using ANOVAs. If a significant difference occurred among study areas, I used Scheffé's method (Snedecor and Cochran 1980) to determine differences between study areas.

Multivariate analyses were done to describe general patterns of habitat use not apparent from the univariate analyses. To ensure that the sample-to-variable ratio met the criteria suggested by Williams and Titus (1988) and Williams et al. (1990), variables were screened before analysis by calculating product-moment correlation coefficients (Sokal and Rohlf 1969) between variables. If $r > 0.6$, I retained one variable from the pair that provided the greatest amount of unique ecological information. For example, basal area by both deciduous oaks and live oaks were highly correlated with total tree basal area; I retained the variables measuring basal area by live oaks and deciduous oaks because they provided additional floristic information not easily seen by the combined measure of total basal area. I then used multivariate analysis of variance (MANOVA; Green 1978) on the reduced set of structural habitat variables to examine variations in foraging between sexes by study area and season. A second MANOVA was done with sexes pooled to examine sources of variation in foraging habitat among study areas and between years and seasons. Stepwise discriminant analysis (DA; Green

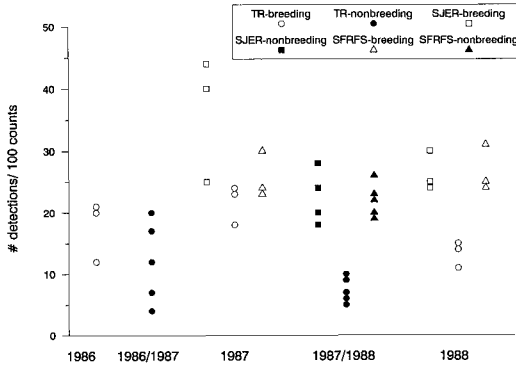


Fig. 1. Number of detections per 100 counting stations of Nuttall's Woodpeckers during the 1986, 1987, and 1988 breeding seasons (open symbols) and the 1986/1987 and 1987/1988 nonbreeding seasons (filled symbols) at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County.

1978) was used to describe general species patterns among study areas along a pair of habitat gradients.

RESULTS

RELATIVE ABUNDANCES

Total counts of Nuttall's Woodpeckers ranged from 6 (Tejon Ranch [TR] nonbreeding season 1987/1988) to 36 detections/100 counting stations (San Joaquin Experimental Range breeding 1987 breeding season; Fig. 1). Counts differed significantly between study areas and seasons. Differences among study areas reflected fewer detections at TR than at San Joaquin Experimental Range (SJER) or Sierra Foothill Range Field Station (SFRFS), but I found no difference in the numbers of birds detected at SJER and SFRFS (Fig. 1). Fewer birds were detected at TR during nonbreeding than during breeding seasons; no significant differences were found in the numbers of birds detected between seasons at SJER or SFRFS (Fig. 1). I found no significant differences in numbers of woodpeckers detected between years.

FORAGING BEHAVIOR

Tree-species use.—Observers obtained 426 samples of foraging by Nuttall's Woodpeckers across the three study areas. There were no significant differences between sexes in tree-spe-

cies use across study areas and seasons (likelihood ratio [lr] $\chi^2 = 7.1$, $P > 0.30$), or within study areas (lr $\chi^2 = 3.1$, $P > 0.99$) or seasons (lr $\chi^2 = 4.1$, $P > 0.65$). When data from sexes were pooled, Nuttall's Woodpeckers used plant species in different proportions depending on study area (lr $\chi^2 = 186.4$, $P < 0.01$) and season (lr $\chi^2 = 18.6$, $P < 0.05$; Fig. 2). Blue oak was used most frequently during all sampling periods with exception of the 1987/1988 nonbreeding season at SJER when woodpeckers used gray pine extensively (Fig. 2). At TR, birds also used valley and canyon live oaks, which were absent at SFRFS and SJER. Further, interior live oak at TR was used less than at the other two study areas ($\chi^2 = 17.8$, $P < 0.01$). This same pattern held when live-oak (interior and canyon live oaks) usage at TR was combined ($\chi^2 = 11.9$, $P < 0.01$). Use of gray pine was extensive at both SJER and SFRFS during all sampling periods but it was greater at SJER. Gray pine was absent at TR. California black oak was not used at SJER. Seasonally, blue oak was used most frequently across all areas during breeding, and gray pine was used during nonbreeding periods ($\chi^2 = 16.2$, $P < 0.01$). When examined separately, only SJER exhibited this seasonal shift ($\chi^2 = 9.8$, $P < 0.01$). No significant seasonal differences in tree-species use were noted for SFRFS ($P > 0.17$) or TR ($P > 0.76$).

Trees used by male and female Nuttall's Woodpeckers differed slightly in diameter ($F = 4.0$, $P = 0.046$), but not in height ($F = 2.2$, $P = 0.14$) or crown width ($F = 0.8$, $P = 0.36$). When sexes were pooled, heights, diameters, and crowns of trees used for foraging all differed among study areas (Table 1; see Appendix 1 for summarized data). Trees used for foraging at TR had larger diameters than those at the other two areas, and tree diameters at SJER were larger than those at SFRFS (Scheffé's test, $P < 0.05$). Heights of trees at SJER and TR were greater than at SFRFS (Scheffé's test, $P < 0.05$). Crowns of trees used during foraging were widest at SJER, and crowns of trees at TR were greater than those of SFRFS (Scheffé's test, $P < 0.05$). Seasonal differences for diameters of trees used for foraging varied by study area. For example, diameters of trees used at SFRFS were greater during breeding than during nonbreeding; the opposite held at SJER. Differences between years in the trees used for foraging occurred because trees used for foraging were taller with larger crowns the second year than the trees used dur-

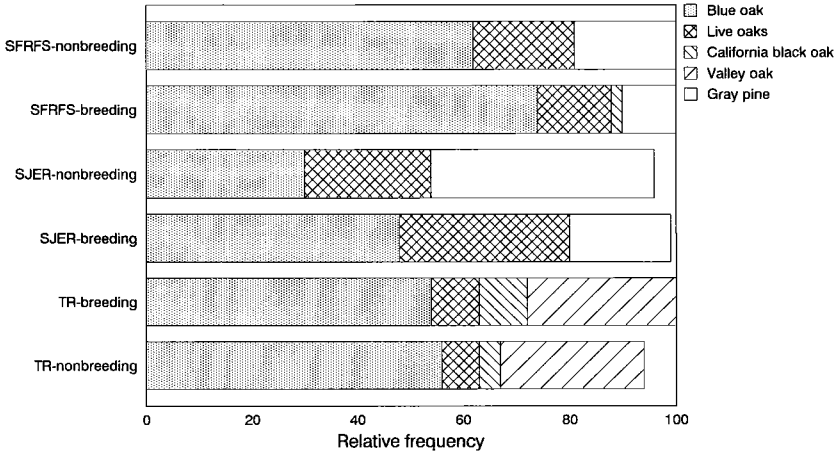


Fig. 2. Relative frequencies of tree-species use by Nuttall's Woodpeckers during the 1987 and 1988 breeding seasons and the 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County.

ing the first. Most plants (363 of 426; 85%) used for foraging appeared healthy. About 12% were live but exhibited some evidence of decline (e.g. dead large limbs, obvious infestation by an arthropod, epiphyte, or pathogen), and only 3% were snags.

Undoubtedly, differences among study areas in the relative abundances, heights, and diameters of available plants influenced plant use. Nuttall's Woodpeckers used plants across all study areas in disproportion to their occurrences ($\chi^2 = 138.3, P < 0.01$; Fig. 3). This difference was because woodpeckers used interior live oak less and gray pine more frequently than they occurred (Fig. 3). This pattern varied by study area. At SFRFS birds used blue oak and

gray pine more frequently and interior live oak and California black oak less frequently than they occurred (Fig. 3). Birds at SJER used blue oak less and gray pine more frequently than they occurred (Fig. 3). Differences between plant use and availability were not significant at TR (Fig. 3). Average diameters and heights of trees used were significantly greater than of those available (Table 2). This relationship was consistent across all and within each study area (Table 2).

Foraging location.—Approximately 97% (879 of 907) of all foraging maneuvers by Nuttall's Woodpeckers were on branches or trunks (Fig. 4). Most (ca. 53%) foraging involved twigs and small branches (<10 cm diameter). I found no

TABLE 1. Comparisons of plant characteristics and foraging locations used by Nuttall's Woodpecker during the 1987 and 1988 breeding and 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County. ANOVA results are for area (A), year (Y), season (S), area \times year (AY), and area \times season (AS). Letter indicates that *F*-ratio is significant at $P < 0.05$; letter with asterisk indicates *F*-ratio is significant at $P < 0.01$.

Variable ^a	ANOVA	Scheffé's ^b		
		TR	SJER	SFRFS
Plant diameter (cm)	A*, S*, AY, AS	B	C	D
Plant height (m)	A*, Y*, AY*, AS*	B	B	C
Plant crown (m)	A*, Y, AY*, AS*	B	C	D
Activity height (m)	A*, AS*	B	B, C	C
Relative height (%)	A	B	B	B
Canopy location (%)	Y*, S*, AS			

^a See Appendix 1 for means and standard deviations of foraging variables.
^b Study areas with the same letter are not significantly different ($P > 0.05$).

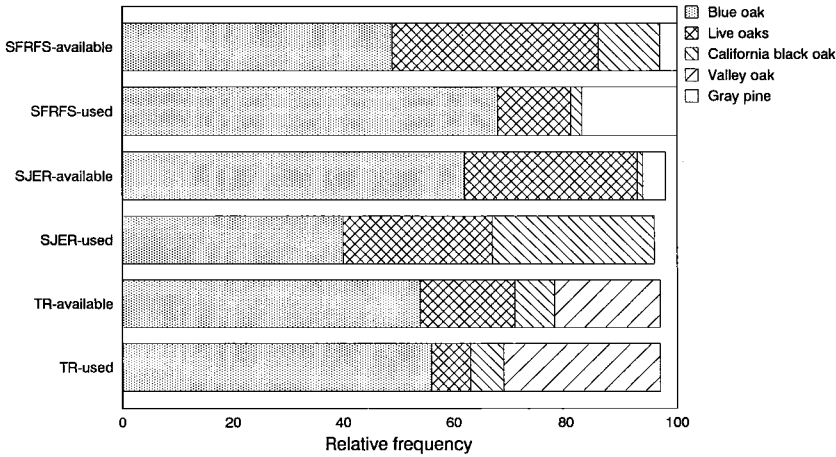


Fig. 3. Relative frequencies of trees used by and available to Nuttall's Woodpeckers during the 1987 and 1988 breeding and the 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County.

significant difference between sexes in the use of foraging substrates ($1r \chi^2 = 5.1, P > 0.16$), although differences occurred among study areas when sexes were pooled ($1r \chi^2 = 55.4, P < 0.01$). Birds at SJER foraged on medium branches (10–30 cm diameter) more frequently than birds at SFRFS or TR. Birds at SFRFS used large branches and trunks (>30 cm diameter) more often than birds at SJER or TR (Fig. 4). Birds foraged infrequently (2.4% of 907 observations) on fruits, cones, and leaves. Most commonly, seeds were plucked from cones of gray pine (17 occasions during nonbreeding seasons at SJER). Approximately 75% of all foraging was on live tree stems that exhibited no evidence of disease or decay. The remaining 25% of the substrates were of declining vigor, and 22% of all substrates were completely dead.

Although males and females foraged at the same height ($F = 4.7, P > 0.50$) and canopy location ($F = 2.9, P > 0.80$), males foraged higher than females relative to the height of the tree ($F = 6.8, P < 0.01$). Foraging height for the sexes combined differed among study areas, and birds foraged higher at TR than at SFRFS (Table 1; Scheffé's test, $P < 0.05$). When foraging heights were standardized relative to total tree height, differences between study areas were not significant (Scheffé's test, $P > 0.05$). Birds generally foraged about two-thirds up the height of trees (Table 1). Similarly, birds foraged in the same general location within the tree canopy (40–70% of the distance from the center to the edge of the tree canopy; Table 1). Thus, the relative height and position of foraging corresponded to the location of small and medium

TABLE 2. Comparison of the size of trees used by Nuttall's Woodpeckers with those occurring at three oak woodlands in California—Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County—during the 1987 and 1988 breeding and 1986/1987 and 1987/1988 nonbreeding seasons.

Study area	Tree diameter (cm)					Tree height (m)				
	Used		Available		z^a	Used		Available		z^a
	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$		<i>n</i>	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	
All areas	426	43.0 ± 21.2	1,132	27.2 ± 20.7	-14.7	426	11.3 ± 4.1	1,131	9.3 ± 4.8	-9.7
TR	92	50.5 ± 26.9	379	33.8 ± 26.6	-5.7	92	12.2 ± 3.6	378	10.7 ± 4.9	-2.6
SJER	164	43.0 ± 21.0	360	21.3 ± 15.6	-12.7	164	11.8 ± 4.2	360	8.0 ± 5.5	-10.9
SFRFS	170	37.4 ± 18.1	393	26.6 ± 15.8	-6.5	170	10.2 ± 3.7	393	9.1 ± 3.7	-3.5

^a z statistic, corrected for tied ranks, calculated from Mann-Whitney U tests. All z values are significant at $P < 0.01$.

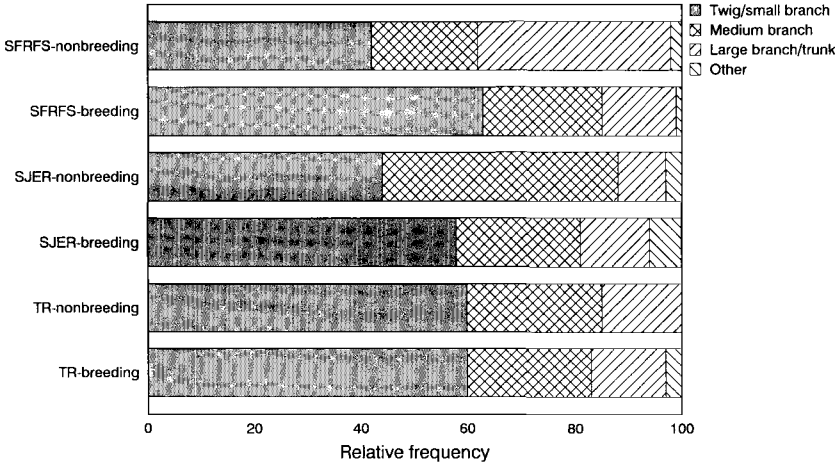


Fig. 4. Relative frequencies of substrates (twig/small branch, <10 cm diameter; medium branch, 10–30 cm diameter; large branch-trunk, >30 cm diameter; other [leaves, seeds, fruits, ground]) used by Nuttall's Woodpeckers during the 1987 and 1988 breeding seasons and the 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County.

branches, the two most frequently used substrates.

Foraging maneuvers.—Approximately 60% of all foraging involved maneuvers to obtain food; 40% consisted of searching to locate food. Gleaning, pecking, probing, and plucking food from bark comprised approximately 90% of all actual foraging maneuvers. Most foraging was by lightly pecking or tapping (see Jenkins 1979)

at bark to uncover food, although gleaning and probing were used extensively (Fig. 5). Sexes did not differ significantly in their use of foraging maneuvers ($1r \chi^2 = 7.6, P > 0.17$), although the relative use of foraging maneuvers by both sexes combined differed among study areas ($1r \chi^2 = 55.5, P < 0.01$). Birds gleaned more at TR than at SFRFS and SJER, and pecked more at SJER than at SFRFS and TR (Fig. 5). Seasonal

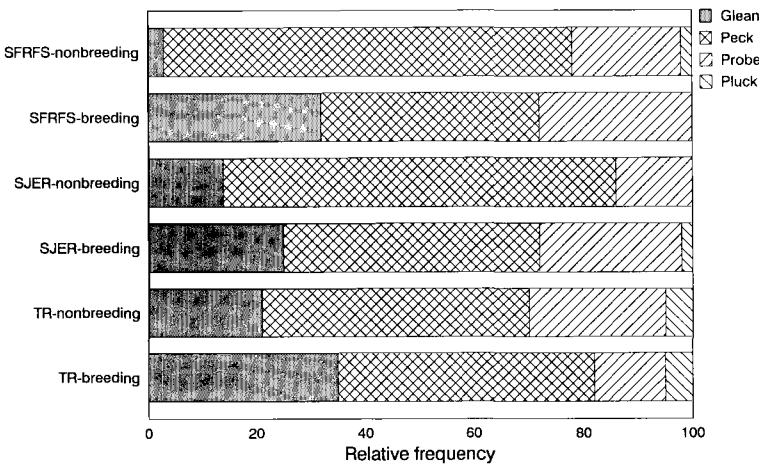


Fig. 5. Relative frequencies of foraging maneuvers used by Nuttall's Woodpeckers during the 1987 and 1988 breeding seasons and the 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County.

TABLE 3. Characteristics of Nuttall's Woodpecker foraging habitat during the 1987 and 1988 breeding and 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County. ANOVA results for area (A), year (Y), season (S), area \times year (AY), and area \times season (AS). Letter indicates that *F*-ratio is significant at $P < 0.05$; letter with asterisk indicates *F*-ratio is significant at $P < 0.01$.

Variable ^a	ANOVA	Scheffé's ^b		
		TR	SJER	SFRFS
Slope (degrees)	A*, S	B	C	D
Distance to edge (m)	A*	B	C	C
Tree species richness	AY			
Shrub species richness	A*, AY*	B	C	D
Total tree cover (%)	Y*			
Live oak cover (%)	A, Y	B	C	C
Deciduous oak cover (%)	A*, Y*	B	C	D
Shrub cover (%)	A*, Y*	B	C	C
Tree density (per ha)	A*	B	C	B
Tree height (m)	A*, AY, AS	B	B	C
Shrub height (m)	A*	B	C	C
Tree diameter (cm)	A*, AS	B	C	D
Tree basal area (m ² /ha)	A*, AY*	B	C	C
Live oak basal area (m ² /ha)				
Deciduous oak basal area (m ² /ha)	A*, AY	B	C	D
Gray pine basal area (m ² /ha)	A*, Y	B	C	D
Dead limbs, 10–30 cm diam. (m/ha)	A*, Y	B	C	D
Dead limbs, >30 cm diam. (m/ha)	A*	B, C	C, D	D
Log volume (m ³ /ha)	A*	B	B	C

^a See Appendix 2 for means and standard deviations of habitat variables.

^b Study areas with the same letter are not significantly different ($P > 0.05$).

differences in the frequency of foraging maneuvers occurred. Birds generally gleaned more but pecked and probed less during breeding than during nonbreeding seasons ($\ln \chi^2 = 43.6$, $P < 0.01$; Fig. 5).

MACROHABITAT USE

Univariate analyses.—Macrohabitat characteristics were measured at 346 of the foraging locations. Most variation in macrohabitat use occurred between study areas. Differences among study areas occurred in 15 of 18 variables. I found yearly differences for 6 variables, and only slope differed seasonally (Table 3; see Appendix 2 for summarized data). I found little variation in habitats used by sexes. Only tree diameter was significantly different ($F = 5.0$, $P = 0.026$) with trees slightly larger in habitats used by females.

Tree density was greater in the macrohabitat of woodpeckers at TR and SFRFS than at SJER. Trees were taller at TR and SJER than at SFRFS and provided greater basal area at TR than at SFRFS or SJER (Table 3; Scheffé's tests, $P < 0.05$). Habitat differences among study areas of total basal area were influenced by greater basal area

of deciduous oaks at TR than at SJER or SFRFS. Basal area of deciduous oaks at SFRFS was greater than of that at SJER (Scheffé's test, $P < 0.05$; Table 3). Basal area of gray pines was greatest in woodpecker habitat at SJER (Scheffé's test, $P < 0.05$; Table 3). Basal area of live oaks in woodpecker habitat was not significantly different among study areas, but cover by live oaks at TR was significantly less than such cover at SFRFS and SJER (Table 3). Further, woodpecker habitat at TR exhibited greater cover by deciduous oaks than at SFRFS or SJER (Table 3). Trees in habitats used by Nuttall's Woodpeckers at SJER were healthier than at SFRFS or TR with fewer dead limbs on trees and on the ground (Table 3).

Yearly differences in habitat appeared for total cover by trees and shrubs, cover by live and deciduous oaks, quantity of small (10–30 cm) dead tree limbs, and basal area by gray pine (Table 3). Total tree cover within Nuttall's Woodpecker macrohabitat was less the second year and was reflected by decreases in cover by both deciduous and live oaks (Table 3). Basal area of gray pine was greater in woodpecker habitat the second year and increased primarily during the second nonbreeding season at SJER (Table 3). Trees within habitats used by Nut-

tall's Woodpeckers had fewer dead limbs the second year than they did the first (Table 3).

Multivariate analysis.—I found no difference in the habitats used by male and female Nuttall's Woodpeckers when structural variables were combined (Wilks' lambda = 0.94, $P = 0.14$). The MANOVA when sexes were pooled revealed significant differences in habitat among study areas (Wilks' lambda = 0.31, $P < 0.01$), between years (Wilks' lambda = 0.88, $P < 0.01$), and for the interaction between study area and year (Wilks' lambda = 0.81, $P < 0.01$). The first axis (canonical correlation = 0.82) derived from the DA separated foraging habitat at TR from SFRFS and SJER by having greater basal area of deciduous oaks, greater evidence of decadence (more dead limbs and logs), less shrub cover, and no gray pine (Fig. 6). The second axis (canonical correlation = 0.31) accounted for the remaining variation and separated SFRFS from SJER and TR with smaller trees but greater tree density and tree cover (Fig. 6).

DISCUSSION

RELATIVE ABUNDANCES

Relative abundances of Nuttall's Woodpeckers differed both spatially and seasonally. Fewer birds were detected at TR than at the other areas in all sampling periods. This difference may be attributed to differences in structural and floristic habitat and in climate. Both SFRFS and SJER had gray pine, a tree absent at TR. Interior live oak, a tree used frequently at SFRFS and SJER, was considerably less abundant at TR, and the growth form of interior live oak at TR was as a scrubby tree that occurred in dense thickets. Interior live oaks at SFRFS and SJER were substantially larger and more arborescent in form (Block 1989). Climate differences also occurred. Much of the winter precipitation came at TR as snow, often as blizzards with up to 1 m of snow. Extended periods of freezing weather were common. This severe weather may have contributed to winter mortality, thus maintaining a low bird population (Raphael and White 1984). Weather may have affected food availability and induced birds to move to locations with adequate food. The absence of gray pine, the scarcity of arborescent interior live oaks, and the presence of harsher winters at TR all may contribute to the relatively low populations of Nuttall's Woodpeckers there. Although the relationship between population size and

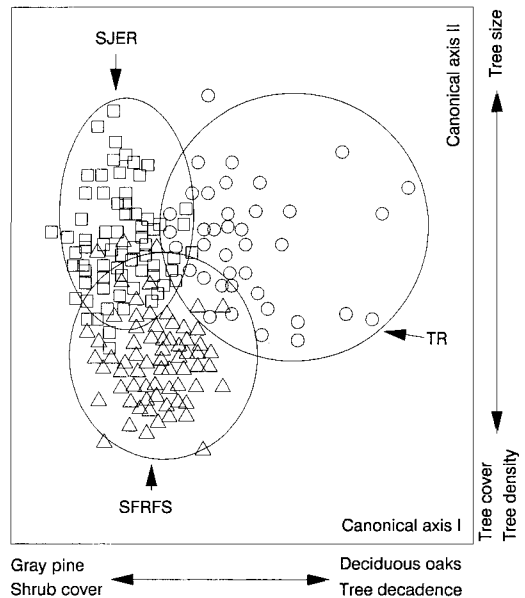


Fig. 6. Ordination by study area of macrohabitat plots of Nuttall's Woodpeckers along canonical axes derived from discriminant analysis using data collected during the 1987 and 1988 breeding and the 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County. Each circle (TR), square (SJER), and triangle (SFRFS) represents 2 habitat plots. Sample sizes were 76, 134, and 136 plots for TR, SJER, and SFRFS, respectively. Ellipses were drawn by hand to include 95% of all plots measured within each study area.

environmental conditions is only correlative, the birds numbers at TR were far less than those at the other two areas. Perhaps the mix of trees and habitat structure at SFRFS and SJER represented better quality habitat than that at TR. Estimates of reproductive success and survival rates are needed to accurately assess habitat quality (Van Horne 1983).

FORAGING ECOLOGY

In contrast to Jenkins (1979), I found little variation between sexes in foraging ecology. I showed that sexes had similar foraging behavior and used similar macrohabitats. I found that the average DBH of trees used differed between sexes, although this difference was quite small ($\bar{x} \pm SE = 3.4 \pm 4.2$ cm). Further, I observed that males foraged relatively higher in trees

than females, whereas Jenkins (1979) reported that females foraged higher in trees than males. I found no differences between sexes in substrates or maneuvers used for foraging. Various factors may have influenced the discrepancy between Jenkins' (1979) and my results. First, Jenkins grouped foraging substrates differently than I, which possibly allowed detection of finer intersexual differences than were possible with my categories. However, Jenkins' samples were probably not independent (i.e. repeated observations on the same individuals), which rendered his statistical analyses inappropriate (cf. Beal and Khamis 1990). Second, Jenkins studied during postbreeding, which overlapped my breeding observations only slightly. Factors unique to postbreeding birds (e.g. increased numbers of birds requiring food as young fledged from nests) may have induced a divergence in foraging behaviors between sexes to partition limited resources. Third, Jenkins studied at a different location, and the results may represent geographic variation in foraging in response to local environmental conditions (Block 1990).

Grubb and Woodrey (1990) reviewed intersexual foraging differences in *Picoides* woodpeckers and found no consistent pattern. For example, both male and female Downy Woodpeckers (*P. pubescens*) were reported by different studies to forage higher in trees than the other sex. Similarly, there was no consistent pattern across species as to which sex foraged on smaller substrates (Grubb and Woodrey 1990). My results indicated that male Nuttall's Woodpeckers foraged slightly higher in trees than females across all study areas, but sexes did not differ in their use of foraging substrates. This slight difference in foraging position may have allowed the sexes to partition limited resources (Selander 1966) or may have reflected behavioral dominance by one sex over the other (Grubb and Woodrey 1990).

Characteristics of the macrohabitats of Nuttall's Woodpeckers varied among study areas and between years. The birds showed no seasonal variations in macrohabitat as found in other *Picoides* woodpeckers (Conner 1981). Thus, Nuttall's Woodpeckers appear to alter patterns of foraging seasonally within a macrohabitat that varies little between seasons. Perhaps the most consistent element of Nuttall's Woodpecker foraging habitat was the dominance by oak trees. Differences occurred among study ar-

reas in the relative dominance (cover, height, diameter, and density) of different types of trees. For example, foraging habitat at TR was dominated by deciduous oaks, with few live oaks and no gray pine. Conversely, foraging habitat at SFRFS and SJER were more diverse in having deciduous oaks, live oaks, and gray pine all contribute substantially to the macrohabitat.

Only a few riparian trees were present on any of my study areas, and those were restricted to widely scattered, intermittent creeks. Miller and Bock (1972) summarized nest records of Nuttall's Woodpeckers and reported that approximately 65% (of 57 nests) appeared in riparian trees (*Salix*, *Platanus*, *Populus*, and *Alnus* spp.). Although I did not study nest sites, we found 8 nests during foraging observations, 7 in oaks and 1 in a sycamore (Block unpubl. data). Further, of 8 nests Waters (1988) reported from SJER, 7 were in interior live oaks and 1 was in a blue oak. Thus, Nuttall's Woodpeckers may nest in oaks more frequently in the absence of suitable riparian trees.

Within microhabitats, Nuttall's Woodpeckers used a wide variety of plants for foraging. Seasonal variations in foraging have been described for other *Picoides* woodpeckers as well (Stallcup 1968, Austin 1976, Travis 1977, Conner 1981, Morrison and With 1987). Miller and Bock (1972) reported seasonal shifts in plant use as Nuttall's Woodpeckers used blue oak with greatest frequency during breeding and coast live oak (*Quercus agrifolia*) during nonbreeding periods. Similarly, woodpeckers at SFRFS and SJER used primarily blue oak during breeding and then increased their use of other trees, primarily interior live oak and gray pine, during nonbreeding. Woodpeckers also used blue oak with greater frequency than other trees during the 1986 breeding season at TR (Block and Morrison 1987). At Santa Rosa Plateau Preserve, Riverside County, California, Nuttall's Woodpeckers used Englemann oak (*Quercus engelmannii*) in 19 of 23 observations during the 1987 breeding season (Block unpubl. data). The other 4 observations involved coast live oak. Blue oak does not occur at Santa Rosa Plateau, but it shares with Englemann oak a similar growth form, leaf structure, and bark rugosity. White oaks may be a better source of food during breeding, but birds may shift their use of trees during nonbreeding to find sufficient food. Data collected specifically to determine the relative abundance and availability of insects (cf. Morrison et al.

1989) to woodpeckers on different trees and during different times of the year are needed to explain this pattern.

Obviously, plant use was influenced by plant availability. However, none of the woodpeckers I studied used plants in proportion to their availability. Similarly, Miller and Bock (1972) found that Nuttall's Woodpeckers used plants disproportionately to their frequency of occurrence. At SFRFS and SJER, woodpeckers used plant species in disproportion to their occurrences, and the average size of trees used was larger than random. In contrast, birds at TR used plant species in proportion to their occurrences, but used larger than average plants. The use of larger trees may be a function of the availability of suitable substrates. Larger trees generally have a greater volume of branches that exhibit signs of decadence in the form of dead or dying branches. I agree with Miller and Bock (1972) and Jenkins (1979), who found that Nuttall's Woodpeckers generally foraged on the surface or shallow subsurface of bark. The place and methods of foraging are not surprising given that most foraging was done on small-medium branches, and prey could not be buried too deeply. Drilling and extensive excavations to uncover prey in the cambium occurred only rarely. I conclude that the use of particular tree species was influenced by the availability of food, and the use of large trees was influenced by both food availability and the presence of suitable foraging substrates.

The geographic and temporal variations in foraging by Nuttall's Woodpeckers demonstrate a behavioral plasticity to search for and locate food at different locations. Lima (1983) concluded that Downy Woodpeckers sampled the environment to locate food. Once a patch of food was located, they returned to that patch on consecutive days based on prior expectations. The observed patterns of foraging by Nuttall's Woodpeckers are generally consistent with Lima's (1983) model. At SJER and SFRFS, birds used tree species in disproportion to availability, which may have reflected a learned response to a nonrandom distribution of food. The pattern of tree-species use shifted seasonally, perhaps reflecting a shift in prey availability and foraging expectations. Conversely, birds at TR used tree species in proportion to availability. This implies that prey was distributed randomly and that birds continuously sampled different tree species for food. The fact

that Nuttall's Woodpeckers foraged on the same types of substrates using similar maneuvers at all study areas implies morphological constraints (e.g. Richardson 1942) that limited their foraging repertoire.

Nuttall's Woodpeckers are closely tied to oaks throughout the year, but they select species and tree size used during different periods. During breeding they depend upon white oaks, particularly blue and Engelmann oaks, for foraging. Unfortunately, these trees are dwindling because of natural mortality and anthropogenic factors. Replacement is well below what is being lost. During nonbreeding periods additional species of trees are used for foraging. Regardless of season, the trees used are larger than the average size of those available. Conservation of Nuttall's Woodpecker must consider habitat needs to avert potentially deleterious population effects in light of current land-use practices in California oak woodlands.

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APPENDIX 1. Characteristics ($\bar{x} \pm SD$) of plants and locations used for foraging by Nuttall's Woodpeckers during the 1987 and 1988 breeding seasons and 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County.

Variable	Breeding		Nonbreeding	
	1987	1988	1986/1987	1987/1988
Plant DBH (cm)				
TR*	53.5 ± 27.1	46.4 ± 28.3	52.0 ± 23.7	48.5 ± 27.1
SJER	44.5 ± 14.9	39.6 ± 14.3	42.6 ± 16.1	48.1 ± 23.2
SFRFS	38.6 ± 13.5	47.5 ± 20.1	32.5 ± 16.6	30.4 ± 17.9
Plant height (m)				
TR	12.0 ± 2.7	12.4 ± 5.1	12.6 ± 2.9	12.2 ± 3.5
SJER	11.2 ± 2.9	11.6 ± 4.2	11.3 ± 3.6	13.8 ± 5.7
SFRFS	10.1 ± 2.3	11.6 ± 4.4	9.4 ± 3.3	9.9 ± 4.4
Plant crown radius (m)				
TR	5.1 ± 1.6	6.3 ± 2.6	5.3 ± 1.7	4.4 ± 1.7
SJER	5.3 ± 1.4	6.3 ± 1.9	4.9 ± 1.3	7.8 ± 3.2
SFRFS	4.0 ± 1.0	5.4 ± 2.0	3.8 ± 1.5	4.3 ± 2.3
Activity height (m)				
TR	8.1 ± 2.8	7.9 ± 4.3	7.0 ± 3.4	8.0 ± 3.2
SJER	7.2 ± 3.3	6.6 ± 3.5	7.3 ± 3.6	8.8 ± 4.9
SFRFS	6.8 ± 2.6	8.0 ± 4.2	5.9 ± 2.7	6.2 ± 3.5
Relative height (%)				
TR	66.7 ± 16.8	65.3 ± 22.8	58.4 ± 18.3	67.4 ± 19.9
SJER	64.5 ± 23.5	58.4 ± 18.8	64.3 ± 23.3	60.9 ± 22.9
SFRFS	66.2 ± 19.0	68.8 ± 18.8	62.3 ± 18.4	61.2 ± 21.3
Canopy location (%)				
TR	56.0 ± 30.4	58.8 ± 29.4	48.5 ± 27.0	45.4 ± 35.4
SJER	55.3 ± 32.8	55.8 ± 23.0	53.9 ± 30.2	65.3 ± 28.3
SFRFS	56.7 ± 30.8	69.3 ± 25.8	37.1 ± 31.7	57.3 ± 33.8

* Sample sizes by period (breeding 1987, breeding 1988, nonbreeding 1986/1987, nonbreeding 1987/1988): 41, 32, 16, 22 for TR; 42, 47, 44, 29 for SJER; and 46, 34, 47, 30 for SFRFS.

APPENDIX 2. Characteristics ($\bar{x} \pm SD$) of Nuttall's Woodpecker foraging habitat during the 1987 and 1988 breeding and 1986/1987 and 1987/1988 nonbreeding seasons at 3 California oak woodlands: Tejon Ranch (TR), Kern County; San Joaquin Experimental Range (SJER), Madera County; and Sierra Foothill Range Field Station (SFRFS), Yuba County.

Variable	Breeding		Nonbreeding	
	1987	1988	1986/1987	1987/1988
Slope (degrees)				
TR	17.3 ± 9.0	19.2 ± 11.0	22.3 ± 12.2	17.3 ± 12.1
SJER	8.2 ± 4.6	9.3 ± 4.4	10.1 ± 5.1	9.7 ± 4.7
SFRFS	15.5 ± 9.3	13.0 ± 6.1	15.3 ± 5.9	17.5 ± 5.6
Distance to edge (m)				
TR	62.0 ± 28.4	51.8 ± 47.4	44.7 ± 24.8	45.5 ± 24.7
SJER	52.3 ± 28.7	46.0 ± 22.0	49.9 ± 29.7	63.0 ± 34.9
SFRFS	36.6 ± 29.6	46.6 ± 68.7	36.9 ± 23.4	39.0 ± 16.5
Tree species richness				
TR	2.1 ± 1.3	2.4 ± 1.3	1.6 ± 1.0	3.2 ± 6.3
SJER	1.8 ± 0.9	2.1 ± 1.0	2.1 ± 0.7	2.5 ± 1.0
SFRFS	2.2 ± 0.9	1.9 ± 0.9	2.4 ± 1.0	1.9 ± 0.9
Shrub species richness				
TR	1.1 ± 1.3	1.2 ± 1.0	1.0 ± 1.2	0.4 ± 1.0
SJER	2.6 ± 2.7	2.8 ± 2.1	2.7 ± 2.0	2.7 ± 2.3
SFRFS	4.0 ± 2.1	2.5 ± 1.7	4.4 ± 2.3	2.0 ± 1.7
Tree cover (%)				
TR	54.3 ± 22.2	48.1 ± 26.8	50.1 ± 22.0	44.7 ± 22.1
SJER	38.4 ± 21.4	39.2 ± 24.9	43.1 ± 22.1	48.2 ± 29.6
SFRFS	56.9 ± 32.4	29.7 ± 16.3	60.2 ± 32.6	38.5 ± 41.3
Live oak cover (%)				
TR	7.5 ± 16.2	5.8 ± 14.2	13.6 ± 23.5	1.0 ± 2.1
SJER	17.7 ± 18.7	17.3 ± 22.5	17.6 ± 19.0	13.8 ± 14.2
SFRFS	17.6 ± 24.2	8.3 ± 11.1	21.4 ± 28.3	12.8 ± 41.6
Deciduous oak cover (%)				
TR	44.1 ± 20.6	34.7 ± 24.0	35.7 ± 20.6	22.4 ± 13.5
SJER	10.6 ± 10.7	13.2 ± 10.9	11.6 ± 11.3	12.1 ± 11.8
SFRFS	32.3 ± 17.4	18.4 ± 11.9	32.8 ± 20.6	22.4 ± 13.5
Shrub cover (%)				
TR	2.4 ± 5.1	5.0 ± 9.2	3.6 ± 5.0	2.0 ± 4.2
SJER	10.5 ± 1.8	10.0 ± 12.6	13.2 ± 13.2	8.4 ± 13.4
SFRFS	1.4 ± 1.1	4.5 ± 6.2	16.8 ± 16.6	2.5 ± 4.4
Tree density (per ha)				
TR	202.4 ± 152.0	160.8 ± 124.8	174.4 ± 143.2	183.2 ± 215.2
SJER	106.4 ± 67.2	105.6 ± 77.6	115.2 ± 84.0	131.2 ± 111.2
SFRFS	198.4 ± 152.0	144.8 ± 100.8	240.0 ± 158.8	175.2 ± 100.8
Tree height (m)				
TR	9.8 ± 2.3	11.2 ± 4.5	11.2 ± 4.5	11.9 ± 3.2
SJER	10.7 ± 2.2	10.3 ± 2.3	10.6 ± 3.0	11.9 ± 3.2
SFRFS	8.9 ± 1.8	8.1 ± 2.3	8.3 ± 1.5	7.5 ± 1.8
Shrub height (m)				
TR	2.2 ± 0.8	2.1 ± 0.9	1.8 ± 1.0	2.3 ± 1.2
SJER	2.6 ± 0.9	2.5 ± 0.7	2.6 ± 0.8	2.2 ± 0.6
SFRFS	2.8 ± 0.9	2.6 ± 1.0	2.6 ± 0.9	2.6 ± 0.7
Tree diameter (cm)				
TR	34.0 ± 17.8	40.2 ± 27.1	43.9 ± 30.7	45.5 ± 26.3
SJER	28.8 ± 10.3	30.7 ± 13.3	29.2 ± 9.0	31.2 ± 10.4
SFRFS	24.8 ± 8.6	28.2 ± 9.7	22.1 ± 5.8	23.9 ± 10.4
Tree basal area (m ² /ha)				
TR	16.8 ± 7.2	13.6 ± 7.2	15.2 ± 6.4	15.2 ± 8.8
SJER	8.0 ± 4.8	8.0 ± 4.0	8.0 ± 4.0	10.4 ± 6.4
SFRFS	8.8 ± 4.8	8.8 ± 4.8	9.6 ± 4.0	7.2 ± 4.0

APPENDIX 2. Continued.

Variable	Breeding		Nonbreeding	
	1987	1988	1986/1987	1987/1988
Live oak basal area (m ² /ha)				
TR	2.1 ± 5.2	2.0 ± 5.0	3.2 ± 6.6	0.4 ± 1.0
SJER	2.9 ± 3.3	3.1 ± 4.4	2.8 ± 3.5	2.3 ± 2.7
SFRFS	2.3 ± 3.6	2.4 ± 3.2	2.9 ± 3.9	1.2 ± 1.6
Deciduous oak basal area (m ² /ha)				
TR	14.4 ± 5.5	10.9 ± 7.9	11.8 ± 7.0	13.1 ± 8.9
SJER	2.0 ± 1.9	2.9 ± 2.4	2.1 ± 1.7	2.7 ± 3.7
SFRFS	5.8 ± 3.3	5.3 ± 2.8	5.5 ± 2.9	5.6 ± 3.3
Gray pine basal area (m ² /ha)				
TR	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
SJER	2.4 ± 4.0	1.6 ± 2.4	2.4 ± 4.0	4.8 ± 5.6
SFRFS	0.8 ± 2.4	0.8 ± 2.4	0.8 ± 1.6	0.8 ± 2.4
Dead limbs 10-30 cm diam. (m/ha)				
TR	163.8 ± 166.4	108.8 ± 108.9	140.0 ± 163.2	60.8 ± 53.6
SJER	52.8 ± 60.8	45.6 ± 61.6	55.2 ± 66.4	40.8 ± 46.4
SFRFS	99.2 ± 129.6	89.6 ± 97.6	86.4 ± 135.2	57.6 ± 80.8
Dead limbs >30 cm diam. (m/ha)				
TR	23.2 ± 33.6	27.2 ± 36.8	12.0 ± 18.4	8.0 ± 18.1
SJER	8.8 ± 18.4	3.2 ± 8.0	5.7 ± 16.1	4.8 ± 12.0
SFRFS	10.4 ± 24.0	19.4 ± 46.4	10.7 ± 42.4	6.4 ± 11.2
Log volume (m ³ /ha)				
TR	14.4 ± 13.6	11.2 ± 13.6	16.8 ± 18.4	12.0 ± 17.6
SJER	3.9 ± 8.0	3.5 ± 6.2	2.6 ± 4.0	3.5 ± 6.1
SFRFS	10.4 ± 20.8	3.8 ± 6.2	3.8 ± 5.9	5.0 ± 9.5

* Sample sizes by period (breeding 1987, breeding 1988, nonbreeding 1986/1987, nonbreeding 1987/1988): 29, 19, 14, 14 for TR; 37, 34, 38, 25 for SJER; and 40, 31, 41, 24 for SFRFS.