FORAGING AND HABITAT RELATIONSHIPS OF INSECT-GLEANING BIRDS IN A SIERRA NEVADA MIXED-CONIFER FOREST

DANIEL A. AIROLA

AND

REGINALD H. BARRETT

ABSTRACT.—Foraging habits and relative abundances of 12 birds comprising the insect-gleaning guild in a Sierran mixed-conifer forest were studied during two breeding seasons to determine: (1) foraging habitat preferences, (2) the extent to which species differ in their use of various components of the foraging niche, (3) patterns of relative abundance vs. niche breadth, and (4) differences between resident and migrant species. Comparisons of proportional availability and bird use of foliage height classes and tree species showed that tree species and, to a lesser extent, heights were used selectively by the guild. Incense-cedar (*Calocedrus decurrens*) was consistently avoided by all species; other tree species were generally used in a complementary manner by different birds. Of four measured components of foraging niche, the use of foraging site (consisting of air or tree part) showed the greatest difference between species, followed by tree species, foraging techniques, and foraging height. We found no correlation between niche breadth and species abundance for all guild members; however, a significant positive correlation existed for the five resident species. Resident and migrant species groups showed few fundamental differences in foraging patterns, except that migrants tended to use a greater proportion of deciduous foliage than residents. Our results suggest that to provide for this guild, land managers should maintain natural levels of tree species diversity in the mixed-conifer forest type.

Many studies have shown that syntopic insectivorous birds differ in their methods of foraging. In forested habitats, birds tend to use different foraging techniques, foraging sites, tree species, and heights. The relative importance of these foraging niche components in distinguishing species has received less attention. Differences in importance of niche components reported in previous studies may reflect either real differences that exist in different habitats and geographic areas (Balda 1969), or incomplete analysis of all potentially relevant factors (Holmes and Robinson 1981). In particular, the importance of differential plant species use has not been fully appreciated (Holmes and Robinson 1981). Additional information is needed before sound generalizations can be made regarding patterns of differentiation among insect-gleaning birds.

In managed forests, plant species composition and vegetation structure may be altered by logging, other silvicultural activities, and disruption of natural fire regimes (Kilgore 1971, Franzreb and Ohmart 1978, Szaro and Balda 1979). Identification of habitat preferences of forest birds can suggest recommendations to mitigate impacts of manipulation.

The mixed-conifer forest of the Sierra Nevada, California, supports a large number of arboreal insectivorous birds (Verner and Boss 1980). We studied foraging substrate preferences, foraging behaviors and relative abundances of the 12 most common members of an insect-gleaning guild. We sought to: (1) compare the guild's use of tree species and vertical foliage layers with the availabilities of these habitat components; (2) describe and compare foraging sites and techniques used by each species; (3) evaluate the relative importances of foraging heights, tree species use, foraging sites, and foraging techniques in differentiating species ecologically; (4) determine if resident and migrant species differed in their foraging and abundance patterns; and (5) suggest management recommendations to mitigate the effects of habitat manipulation on members of the insect-gleaning guild.

METHODS

STUDY AREA

We worked at Blodgett Forest Research Station, a 1,186-ha mixed conifer-oak forest located at 1,350- to 1,450-m elevation in the central Sierra Nevada, El Dorado County, California. The Forest contains five conifer tree species that are typical of the mixed-conifer forest type (Rundel et al. 1977:563, Verner and Boss 1980:4), and a substantial amount of California black oak (see Fig. 1 for scientific names
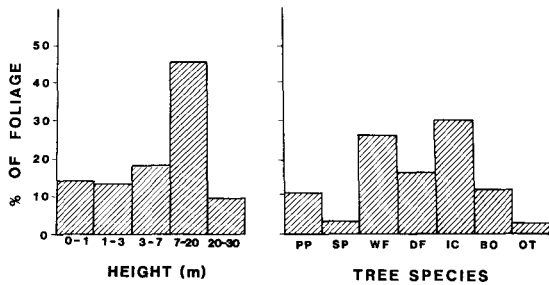
FIGURE 1. Proportions of foliage: (a) in height classes, and (b) contributed by various tree species, at Blodgett Forest. Tree species codes and scientific names are PP = ponderosa pine (*Pinus ponderosa*), SP = sugar pine (*P. lambertiana*), WF = white fir (*Abies concolor*), DF = Douglas-fir (*Pseudotsuga menziesii*), IC = incense-cedar (*Calocedrus decurrens*), BO = California black oak (*Quercus kelloggii*), and OT = other tree species.

of tree species). Dominant vegetation consists of an overstory of older trees left from the original logging of the area in 1900–1913, and an understory of trees and brush that subsequently regenerated (Fig. 1). All tree species are present in all vertical layers. In some areas, trees that grew following logging have grown rapidly owing to high soil fertility, and now form an overstory nearly as tall as residual trees. Various small (0.5–10 ha) experimental treatments (clearcutting, selective logging, planting, brush control) have been performed over the last 15 years, demonstrating many of the management practices that occur in mixed-conifer forests of the Sierra Nevada.

We defined the forest insect-gleaning guild as the group of birds that gleaned from forest trees either from a stationary perch or while hovering during >50% of observations. We did not subdivide this group into foliage- and bark-gleaners because of the high degree of overlap in use of bark, branches, twigs, and foliage by most guild members. Excluded from the group are species that gleaned insects predominantly from successional and riparian shrubs (cf. Airola and Barrett 1981).

DATA COLLECTION

We sampled vegetation, bird species abundance, and foraging activities on a set of 0.28-ha plots located throughout the Forest. In 1977, we randomly selected 41 sample plots from a set of 70 plots that had been previously established. The original plots were randomly selected from a set of coordinates within each of 70 5–15-ha management compartments at the Forest. In 1978, data were collected on 80 plots which were systematically located 100 m apart within five of the 70 compartments.

Vegetation sampling. Vegetation was measured on 20 circular 10-m² subplots laid out in a 10-m grid pattern on each sample plot

(Dedon and Barrett 1982). Species composition was determined by visually estimating percent canopy cover of each plant species on each subplot (Mueller-Dombois and Ellenberg 1974:63). Because the birds we studied foraged almost exclusively in trees, we excluded other plant species from preference analyses (see below). Vertical vegetation structure was determined by estimating on each subplot the total cover (all species combined) in each of eight height classes: 0–0.5 m, 0.5–2 m, 2–5 m, 5–10 m, 10–15 m, 15–20 m, 20–30 m, and >30 m. To represent the Forest as a whole, tree species and height class cover values for all 820 subplots were averaged to obtain a mean cover for each species and height class. Using weighted averages, the values for the eight height strata were assigned to the five strata used to record bird foraging heights (see below). The means for each tree species and height class were then converted to proportions of total cover in all classes of each variable for comparison with relative use of each class by bird species.

Bird relative abundance. On each plot used to characterize habitat, we recorded the numbers of individuals of each bird species seen or heard during each of 20 consecutive 10-min periods, beginning 0.5 h after sunrise on one morning between late April and early July (Dedon and Barrett 1982). Boundaries of plots were checked with a range finder and either marked with surveyor's flagging or recognized from natural landmarks. The observer remained at the center of the plot during surveys, except for brief forays to check bird distances. We calculated relative frequency of each species by summing the number of individuals recorded per period. Relative abundance of each species was estimated by dividing the species' relative frequency by the sum of all species frequencies. In this study, we use only bird abundance data from 1977, since the method of plot selection was randomized for the whole Forest only in this year.

One source of bias may have affected our relative abundance values. We counted birds over a 2.5-month period and sampled each plot on only one day. Detectability possibly differed owing to behavioral changes through the breeding season. Since plots were selected randomly and only relative abundances are considered, however, we believe bias is relatively slight.

Foraging data. Foraging behaviors and substrates used by birds were recorded on sample plots during 1977 and 1978, and in "opportunistic" observations made in transit to and from plots and in transects walked in various parts of the Forest. Although starting points

and directions of transects were not selected at random, we attempted to sample a variety of geographic areas, irrespective of vegetation composition. Most observations were made from sunrise to 10:30 and from 16:00 to 19:00, from mid-April to early August. When we saw a bird attempting to take food, the following data were recorded: bird species, foraging height, tree species or other substrate used, foraging site, and foraging technique. Foraging heights were assigned to one of five height classes: 0–1 m, 1–3 m, 3–7 m, 7–20 m, >20 m. Substrates recorded other than tree species were shrub species, snags, and ground. "Foraging site" indicates the tree part or other location from which the bird attempted to take food: trunk, branch (>1 cm diameter), twig (<1 cm), foliage, and air. Foraging techniques were recorded as: *hawking* (flying from a perch to take aerial insects), *hovering* (taking insects from foliage while in flight), *lunging* (leaping from a stationary position to take insects moving inside the tree crown), and *gleaning* (taking stationary insects from a substrate while perched). Foraging sites and techniques were recorded only during 1978. Because birds were often difficult to see owing to foliage height and density, we recorded consecutive foraging observations for some individuals to increase the amount of information collected. To reduce the bias that multiple records may create (Wagner 1981, Morrison 1984), we treated each individual bird as an observation when determining frequencies and sample sizes for statistical tests. Thus, when *n* consecutive observations of an individual were recorded, each observation contributed to the species' total frequency by a value of $1/n$, and all observations of the individual in the period contributed $\sum_{i-1}^{n} 1/n = 1$ to the species' frequencies. By this method, we incorporated all data taken, without biasing species frequencies toward individuals which contributed multiple observations. We report sample sizes for both the number of individuals observed and the total number of observations obtained.

ANALYSIS

Preference. "Preference" refers to the difference between the proportional use of a substrate class (tree species or foliage height class) and the proportion available in the environment. Preference is described by Strauss' (1979) index:

$$L = p_i - q_i$$

where: L is the preference value, p_i is the proportion of all uses of substrates, that is of class *i*, and q_i is the proportion of the same class that is available in the environment. The index ranges from +1 to −1, with positive values indicating selection for a substrate class by the bird, 0 indicating non-selective use, and negative values indicating avoidance.

To test for significance of L, 95% confidence intervals (C.I.s), based on the estimated sampling variance of L (Strauss 1979), were constructed by Dunn's (1961) method. This method sets a procedure-wise error rate for a series of comparisons (e.g., a bird species' preferences for six different tree species) so that the chance that a single type 1 error occurs within the series of comparisons is equal to α. A preference value was considered to be significantly different from non-selective use if the 95% C.I. of L did not overlap the L value of 0 (where use equals availability).

Niche breadth. Patterns of use within and between niche axes were compared using single-axis niche breadths. Niche breadths of birds on individual axes were calculated by the percent similarity (*PS*) method (Feinsinger et al. 1981).

$$PS = \sum_{i=1}^{R} min(p_i, q_i)$$
$$= 1 - 0.5 \sum_{i=1}^{R} |p_i - q_i|,$$

where R is the number of defined niche axis states. The *PS* value sums the absolute values of L, and indexes the sum to between 0 (total dissimilarity) and 1 (use equals availability).

No availabilities were defined for the foraging site and technique axes. Percent similarity was used to evaluate niche breadth on these two axes, however, by setting availabilities as equal for all variable states on each axis. Thus, *PS* measured deviation in use from a uniform distribution for these axes. Calculation of all niche breadths with the same measure permitted comparison of breadths between axes. Niche breadths on the tree species axis were based only on the birds' use of the dominant tree species, which included 94% of foraging observations.

We could not calculate complete multi-dimensional niche breadths, as recommended by May (1975) and Inger and Colwell (1977), because foraging sites and techniques were recorded in only one year. We calculated partial composite measures for two components of the multi-dimensional niche, one based on use of height class and tree species (two years of data), and the other on foraging site and technique. The use frequencies for each combination of the niche states in the two combined axes (height/tree and site/technique) were used to calculate two-dimensional niche breadths.
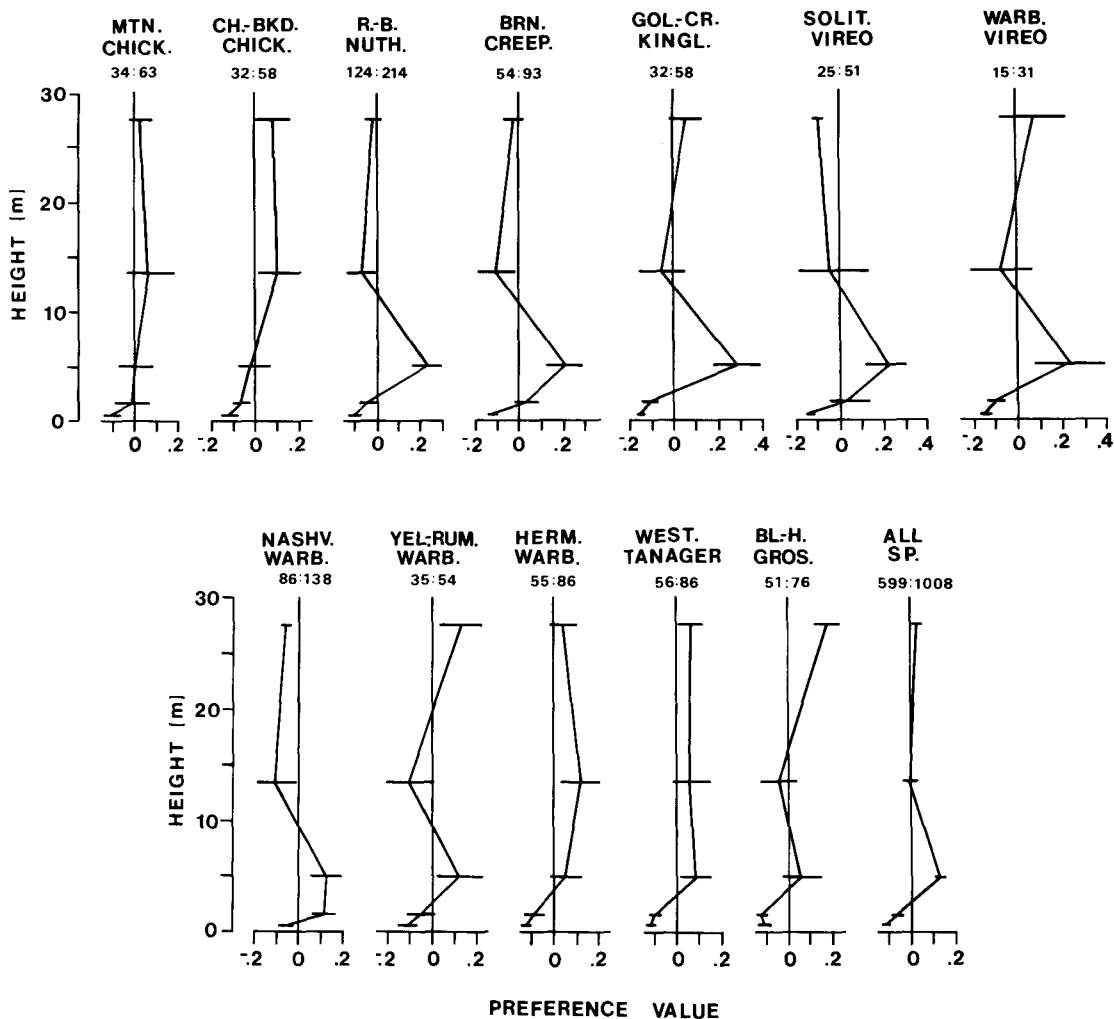
FIGURE 2. Foraging height preferences of insect-gleaning birds at Blodgett Forest. Each preference value equals the proportion of foraging observations in a height class minus the proportion of total foliage available in the same height class. Horizontal lines indicate 95% confidence intervals (see text). Sample sizes are reported under species names, indicating (before colon) the number of individuals observed which was used in statistical analyses, and (after colon) the total number of observations made. The latter value includes multiple observations of single individuals, incorporated into species totals as described in Methods.

These niche breadths were calculated by the equation $H = \Sigma \ [P_i \ln(P_i)]$ (Shannon and Weaver 1949, Levins 1968) scaled from 0 to 1 by dividing by the maximum H value achieved when all categories are equally used. H was used because it does not require resource availability, and thus permits all used substrates to be included. We approximated the composite foraging niche breadth (all axes) by averaging breadths on the two-dimensional axes. We considered this method preferable to either calculating multi-dimensional breadths using only one year's data, or averaging breadths calculated independently for each of the four axes. Correlations of relative abundances of birds and niche breadth values were calculated to test hypotheses concerning abundance in relation to specialist vs. generalist foraging habits.

Niche overlap. We calculated niche overlap for each pair of species using Horn's (1966) information theory index,

$$O_{ij} = [(p_{ik} + p_{jk})\log(p_{ik} + p_{jk}) - p_{ik}\log p_{ik} - p_{jk}\log p_{jk}]/2 \log 2$$

where O_{ij} equals the overlap of species i and j, p_{ik} equals the proportion of niche category k used by species i, and p_{jk} equals the proportion of k used by species j. Overlaps were calculated for each pair of species on individual foraging niche axes, and on the two-dimensional axes (as described for niche breadths). We approximated total overlap among species pairs on all foraging axes by multiplying the two-dimensional axes. This procedure is appropriate when the axes are independent (May 1975); in fact, they showed a

TABLE 1. Common and scientific names, seasonal residency, relative abundances, and niche breadth values for members of the insect-gleaning guild at Blodgett Forest.

| | Resi-dency[b] | Relative abundance | Niche breadths[a] | | | | | |
| | | | Single axes | | | | Combined axes | |
			HT	TR	SI	TE	HT:TR	SI:TE
Mountain Chickadee (*Parus gambeli*)	P	0.072	0.88	0.59	0.50	0.25	0.68	0.46
Chestnut-backed Chickadee (*Parus rufescens*)	P	0.068	0.80	0.71	0.43	0.35	0.66	0.51
Red-breasted Nuthatch (*Sitta canadensis*)	P	0.162	0.78	0.72	0.73	0.34	0.80	0.75
Brown Creeper (*Certhia americana*)	P	0.018	0.76	0.84	0.20	0.25	0.83	0.00
Golden-crowned Kinglet (*Regulus satrapa*)	P	0.159	0.70	0.76	0.41	0.38	0.64	0.51
Solitary Vireo (*Vireo solitarius*)	M	0.059	0.74	0.78	0.64	0.45	0.72	0.75
Warbling Vireo (*Vireo gilvus*)	M	0.028	0.70	0.51	0.48	0.33	0.58	0.46
Nashville Warbler (*Vermivora ruficapilla*)	M	0.107	0.76	0.73	0.52	0.29	0.72	0.53
Yellow-rumped Warbler (*Dendroica coronata*)	M	0.035	0.74	0.63	0.64	0.50	0.66	0.82
Hermit Warbler (*Dendroica occidentalis*)	M	0.180	0.78	0.51	0.56	0.27	0.63	0.52
Western Tanager (*Piranga ludoviciana*)	M	0.060	0.78	0.85	0.55	0.62	0.71	0.74
Black-headed Grosbeak (*Pheucticus melanocephalus*)	M	0.053	0.76	0.68	0.45	0.53	0.68	0.65
Mean			0.76	0.69	0.51	0.38	0.69	0.56

[a] HT = foraging height, TR = tree species, SI = site, TE = technique.
[b] P = permanent resident, M = migrant.

weak, but significant, negative association ($r = -0.27$, $P = 0.01$).

Similarity patterns within the guild were shown by cluster analysis (Dixon 1981:448, Program 1M), using the product of foraging overlap values of species pairs as similarity measures. Groups were combined based on average similarity (Dixon 1981).

The magnitude of overlaps between each species and the rest of the guild on each axis was approximated by averaging the pairwise overlaps of each species with all other guild members. This index is designated "guild overlap." Using the Mann-Whitney test (Sokal and Rohlf 1969), we compared the magnitudes of guild overlap values of all species on each pair of niche axes to assess the degree to which each axis distinguished guild members in foraging.

RESULTS

FORAGING HEIGHT

As a group, the guild foraged selectively by height (Fig. 2). The two lowest canopy classes were avoided ($L = -0.11$ and -0.05 for 0–1 m and 1–3 m heights, respectively), the middle and highest layers were preferred ($L = 0.14$ and 0.04, respectively), and the upper middle layer was used in proportion to its availability ($L =$

0.00). A summary of the individual species' height use patterns (Fig. 2) shows that of 60 possible comparisons, 26 (43%) were significant and positive, 15 (25%) were significant and negative, and 19 (32%) did not differ significantly. This degree of selectivity indicates nonrandom use of foliage layers.

Individual species showed a variety of foliage height use patterns. The birds can be classified into five categories of height preference: (1) high—Chestnut-backed Chickadee (see Table 1 for scientific names), Black-headed Grosbeak; (2) medium and high—Yellow-rumped Warbler, Hermit Warbler, Western Tanager; (3) medium—Red-breasted Nuthatch, Brown Creeper, Golden-crowned Kinglet, Solitary Vireo, Warbling Vireo; (4) low and medium—Nashville Warbler; and (5) no preference—Mountain Chickadee. Foraging heights did not differ between resident and migrant groups (Table 1; Wilcoxon rank sum tests, comparisons at 0–1 m [$P = 0.50$], 1–3 m [$P = 0.38$], 3–7 m [$P = 0.44$], 7–20 m [$P = 0.44$], 20+ m [$P = 0.32$]).

TREE SPECIES

The guild used the six dominant tree species in 94% of our observations. Other substrates used were snags (3%), and tanoak (*Lithocarpus densiflora*), deerbrush (*Ceanothus integerri-*
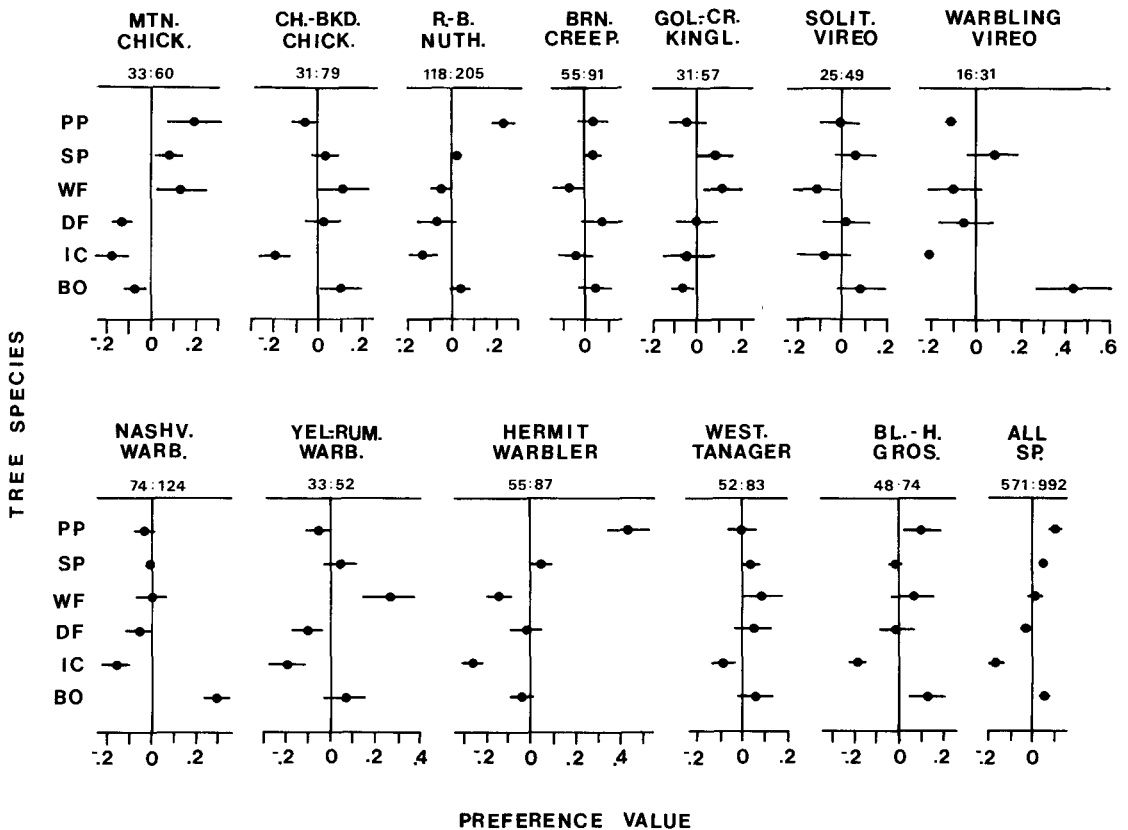
FIGURE 3. Tree species preferences of insect-gleaning birds at Blodgett Forest. Preference values and confidence intervals are calculated as described in Figure 2. Sample sizes are shown as described in Figure 2.

mus), and ground (1% each). Certain birds made substantial use of these minor foraging substrates. Snags were used by the Red-breasted Nuthatch and the Brown Creeper in 9% and 7% of observations, respectively. The Nashville Warbler used deerbrush 10% of the time, and the Solitary Vireo used tanoak in 9% of observations.

The guild as a whole showed marked differences in preferences for the six major tree species (Fig. 3). Ponderosa and sugar pine, and black oak were preferred (Ls = 0.11, 0.05, and 0.05, respectively). White fir was used in proportion to its availability, whereas Douglas-fir was weakly but significantly avoided (L = −0.03). Incense-cedar was strongly avoided (L = −0.17).

Individual bird species differed considerably in their preferences for tree species. Overall, their preferences were somewhat complementary, except that all birds avoided incense-cedar (significantly so for nine species). Ponderosa pine, white fir, and black oak each were preferred significantly by four species, and sugar pine was preferred by three. Douglas-fir was not preferred by any bird. Of 72 possible bird/tree comparisons, 15 (21%) were significant and positive, 18 (25%) were significant and

negative, and 39 (54%) were not significantly different. These results indicate non-random use of trees by foraging birds.

We assigned the birds to seven categories of tree species preference, based on their selection of certain combinations of the three most important tree types, pine (ponderosa and sugar), white fir, and oak: (1) pine—Hermit Warbler, Red-breasted Nuthatch; (2) white fir—Golden-crowned Kinglet, Yellow-rumped Warbler, Western Tanager; (3) oak—Warbling Vireo, Nashville Warbler; (4) pine-fir—Mountain Chickadee; (5) oak-pine—Black-headed Grosbeak; (6) oak-fir—Chestnut-backed Chickadee; and (7) no preference—Brown Creeper, Solitary Vireo.

Analysis of tree species preferences based on residency indicated that, as a group, migrant species (seven species, Table 1) used greater amounts of hardwood foliage (28%), and less conifer foliage (72%), than did resident species (12% hardwood, 88% conifers; Wilcoxon rank-sum test, P = 0.02). This pattern, however, was not uniform within groups: the Chestnut-backed Chickadee, a resident, used a high amount of hardwood foliage (23%), whereas the Hermit Warbler, a migrant, seldom used hardwoods (8%).
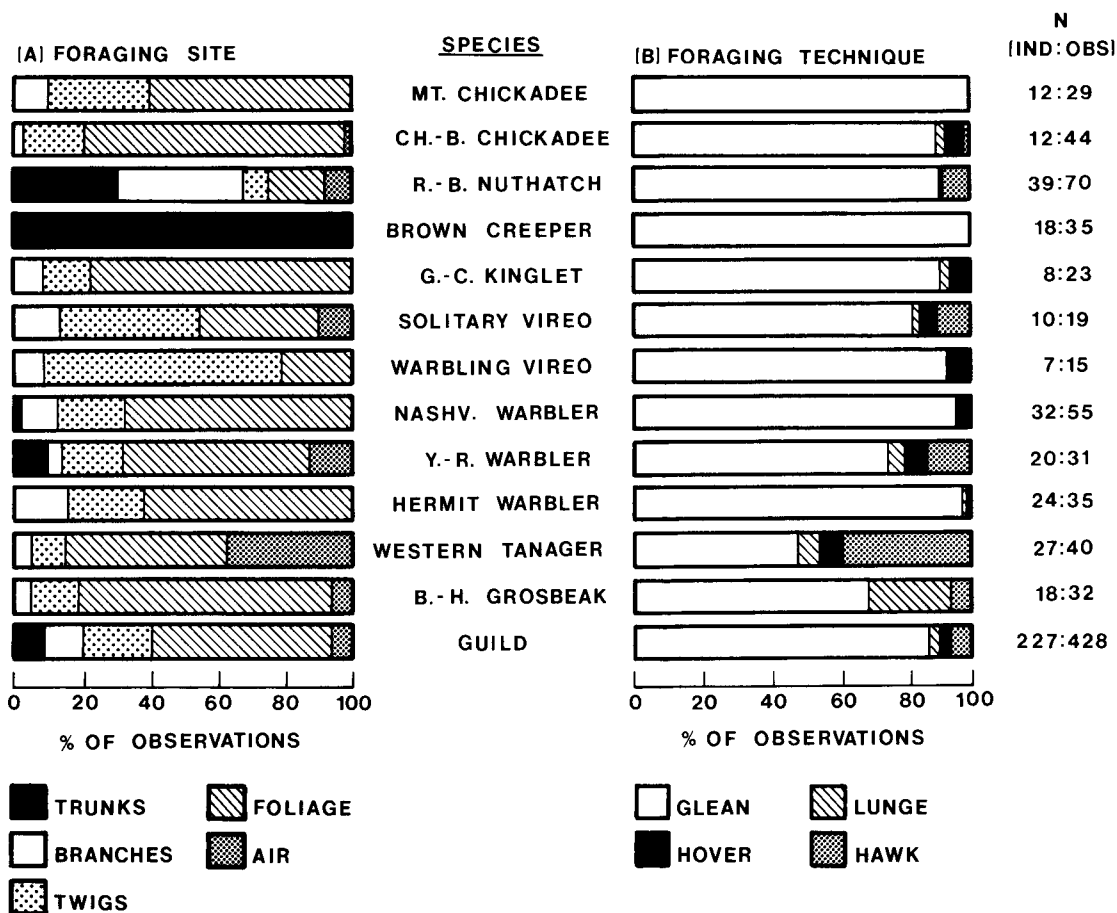
[A] FORAGING SITE	SPECIES	[B] FORAGING TECHNIQUE	N (IND:OBS)
	MT. CHICKADEE		12:29
	CH.-B. CHICKADEE		12:44
	R.-B. NUTHATCH		39:70
	BROWN CREEPER		18:35
	G.-C. KINGLET		8:23
	SOLITARY VIREO		10:19
	WARBLING VIREO		7:15
	NASHV. WARBLER		32:55
	Y.-R. WARBLER		20:31
	HERMIT WARBLER		24:35
	WESTERN TANAGER		27:40
	B.-H. GROSBEAK		18:32
	GUILD		227:428

% OF OBSERVATIONS   % OF OBSERVATIONS

TRUNKS FOLIAGE BRANCHES AIR TWIGS

GLEAN LUNGE HOVER HAWK

FIGURE 4. Foraging sites and techniques used by insect-gleaning birds at Blodgett Forest. Sample sizes are as described in Figure 2.

FORAGING SITES

The guild members used a variety of foraging sites (Fig. 4). Eight birds used tree foliage most often. The two vireos foraged most frequently on twigs. The Brown Creeper searched only on tree trunks, whereas the Red-breasted Nuthatch fed mainly on trunks and large branches. The Western Tanager hawked insects from the air to the greatest extent. The resident and migrant species groups did not differ in their uses of substrates (Wilcoxon rank-sum tests for air [$P = 0.13$], foliage [$P = 0.50$], twigs [$P = 0.10$], branches [$P = 0.44$], and trunks [$P = 0.27$]).

FORAGING TECHNIQUES

The guild showed little variation in foraging techniques (Fig. 4). Gleaning greatly exceeded hawking, hovering, and lunging; eight species gleaned in 90% or more of our observations. The Solitary Vireo and Yellow-rumped Warbler used a higher proportion of other techniques. The two largest species, Western Tanager and Black-headed Grosbeak, differed considerably from other species. The tanager hawked nearly three times more often than any other guild member, while the grosbeak lunged

nearly four times more often than any other species. Although certain migratory species used nongleaning techniques most often, we found no consistent differences in techniques used between the migrant and resident groups (Wilcoxon rank-sum tests for glean [$P = 0.10$], hover [$P = 0.15$], lunge [$P = 0.17$], and hawk [$P = 0.19$]).

NICHE BREADTH

Species' scaled values for niche breadth differed significantly between all four foraging niche axes (Table 1; Mann-Whitney test, $P < 0.05$), except between foraging height and tree species, which approached significance ($P = 0.08$). The guild was least specialized in its selection of foraging heights ($\bar{x}$ niche breadth = 0.76) and tree species ($\bar{x} = 0.69$), intermediate in its selection of foraging positions ($\bar{x} = 0.51$), and most specialized in its use of foraging techniques ($\bar{x} = 0.38$). Niche breadths did not differ between the resident and migrant groups on any of the niche axes (Mann-Whitney test, $P > 0.10$ for all comparisons).

Correlations of species abundance with niche breadths on single, two-dimensional, and four-

TABLE 2. Correlations between relative abundance of bird species and niche breadths on four single niche axes, two two-dimensional axes, and the mean of the two-dimensional axes.

Niche axis	All species ($n = 12$)		Residents ($n = 5$)		Migrants ($n = 7$)	
	r	P	r	P	r	P
One-dimensional						
Height	0.04	0.44	−0.39	0.26	0.64	0.06
Tree	−0.15	0.31	−0.15	0.40	−0.25	0.29
Site	0.35	0.12	0.72	0.08	0.02	0.48
Technique	−0.27	0.19	0.75	0.07	−0.58	0.08
Two-dimensional						
Ht:Tr	−0.05	0.43	−0.26	0.33	0.02	0.48
Si:Te	0.19	0.26	0.82	0.04	−0.42	0.17
Four dimensional						
$\bar{x}$ 2-d axes	0.20	0.26	0.81	0.05	−0.31	0.25

dimensional axes indicated no significant relationships, using either all guild members or only migrants (Table 2). Correlations approached significance, however, between migrant abundance and both height ($P = 0.06$) and technique ($P = 0.08$) breadths. We consider the marginal relationship between migrant abundance and height breadth to be spurious, given the similarity of breadth values for this group (Table 1). Residents showed positive relationships between abundance and niche breadths that were: (1) nearly significant for individual foraging site ($P = 0.08$) and techniques ($P = 0.07$) axes; (2) significant for the multi-dimensional site-techniques axis ($P = 0.04$); and (3) significant for the four-dimensional niche breadth ($P = 0.05$, Table 2).

NICHE OVERLAP

Insect-gleaning birds overlapped to different extents on various components of the foraging niche (Table 3). Based on comparisons of guild overlaps on pairs of single-dimension axes, species' overlapped least in their use of foraging sites (Mann-Whitney tests, $P < 0.05$ for comparisons of site and each other axis). Tree species use showed the next-to-lowest guild overlap ($P < 0.05$), and overlaps on the heights and techniques axes were higher and of similar magnitude ($P > 0.05$).

The pattern of overlap between species on the two-dimensional axes differed slightly from that on individual axes. The height-tree overlaps were lower than those on the site-techniques axis (Mann-Whitney test, $P = 0.05$; Table 3). The relative magnitudes of overlap on the two-dimensional axes (calculated from multi-dimensional niche states) were opposite from what would have resulted simply from multiplying single-axes overlaps.

Similarities in species' foraging niches are summarized in a cluster diagram based on four-dimensional overlaps (Fig. 5). At the 50% sim-

ilarity level, four groups are evident: (1) a trunk-gleaner (Brown Creeper); (2) a branch and trunk-gleaner (Red-breasted Nuthatch); (3) three species that preferred oaks and either foraged low or used twigs (vireos and Nashville Warbler); and (4) seven upper canopy foliage-feeders. Within group 3, the Warbling Vireo was distinguished by its greater use of twigs and higher foraging. Within group 4, the Mountain Chickadee and Hermit Warbler sub-group was distinguished by preference for pine and avoidance of fir, greater use of branches and twigs, and dependence on gleaning. The Chestnut-backed Chickadee and the Golden-crowned Kinglet were segregated by their greater use of foliage as a foraging site and consistently high similarity on other axes. The Yellow-rumped Warbler, Western Tanager, and Black-headed Grosbeak sub-group was distinguished by use of high foliage and use of a greater variety of foraging sites and techniques. Migrant and resident species were not separated distinctly.

DISCUSSION

The strong selectivity shown by the insect-gleaning birds, both as a guild and as separate species, indicates that vegetation structure and tree species composition are important habitat attributes to them. Our preference measures incorporate habitat selection by birds at two levels: the selection of breeding habitat, and the use of occupied habitat. We suggest that foraging preferences offer reasonable explanations as to which vegetation conformations may be occupied by the various guild members, provided that other needs (e.g., nest sites and song perches) are met.

One interpretational problem with preferences is that values may underestimate the importance of abundant food resources. For example, the 7–20-m foliage layer contained 45% of available foliage, and was used by the guild

TABLE 3. Mean niche overlaps among each species and other guild members. Two-dimensional overlaps are cal-culated from multi-dimensional niche categories. Four-dimensional overlaps are means of the products of the overlaps on the two-dimensional axes (see text).

Species	One-dimensional overlaps				Two-dimensional		Four-dimensional
	Height	Tree species	Site	Technique	Height: tree sp.	Site: tech.	Ht:Tr × Si:Te
Mountain Chickadee	0.95	0.83	0.89	0.92	0.65	0.76	0.49
Chestnut-backed Chickadee	0.94	0.90	0.88	0.95	0.67	0.77	0.52
Red-breasted Nuthatch	0.96	0.88	0.69	0.94	0.71	0.60	0.43
Brown Creeper	0.94	0.89	0.08	0.92	0.73	0.08	0.06
Golden-crowned Kinglet	0.93	0.85	0.79	0.94	0.70	0.77	0.53
Solitary Vireo	0.89	0.86	0.78	0.94	0.64	0.76	0.48
Warbling Vireo	0.95	0.78	0.66	0.92	0.58	0.62	0.36
Nashville Warbler	0.90	0.83	0.81	0.95	0.63	0.78	0.49
Yellow-rumped Warbler	0.95	0.88	0.80	0.92	0.66	0.78	0.52
Hermit Warbler	0.97	0.75	0.80	0.94	0.62	0.78	0.48
Western Tanager	0.96	0.84	0.71	0.80	0.73	0.68	0.49
Black-headed Grosbeak	0.93	0.87	0.80	0.87	0.68	0.72	0.49
Mean	0.95	0.85	0.72	0.92	0.67	0.68	0.45

in 45% of our observations. Despite the lack of a positive preference value, we cannot conclude that the layer was not important to the guild. Similarly, white fir foliage was abundant and was used in proportion to its availability.

Birds may selectively use foliage at different heights for several reasons. Avoidance of the two lower foliage layers was expected, as foliage here consists primarily of shrubs, herbs, forbs, and grasses, whereas the guild was defined as those insect-gleaners that predominantly use forest trees. The lower layers are used mainly by ground-feeding granivores and insectivores, and by other foliage-gleaning birds characteristic of shrubs. The Nashville Warbler, although primarily a gleaner of forest trees, used low shrub foliage more than the other guild members.

Several factors may explain why the middle foliage layer was strongly preferred. This layer incorporates the understory of stands with a sparse overstory favored by the Nashville Warbler and Solitary Vireo, and the overstory of younger stands favored by many other species. The preference by the Brown Creeper and the Red-breasted Nuthatch for this layer reflects their use of furrowed bark, which is more abundant on the older, lower portions of trees (Travis 1977, Jackson 1979); moreover, because we defined the middle height class as including a greater vertical extent, it contained more trunk surface area than the two lowest layers.

The highest layer was preferred to a moderate extent by the guild as a whole, and strongly by certain species. The Yellow-rumped Warbler and Western Tanager both hawk insects frequently and may have been attracted to the upper layer because its small amount of foliage aided their aerial maneuverability. Gleaners frequently used high foliage soon after it was exposed to sunlight. Balda (1969) also reported early use of high foliage, which he attributed to increased insect activity in the newly-warmed foliage.

Preferences of birds for various tree species reflect the abundance, type, and accessibility of prey items on trees, plus the morphological and behavioral characteristics of the birds (Franzreb 1978, Holmes and Robinson 1981, Sabo and Holmes 1983). The guild's consistent avoidance of incense-cedar foliage may have been because: (1) the small scale-like needles may mature quickly, reducing the period of susceptibility to phytophagous insects, and,
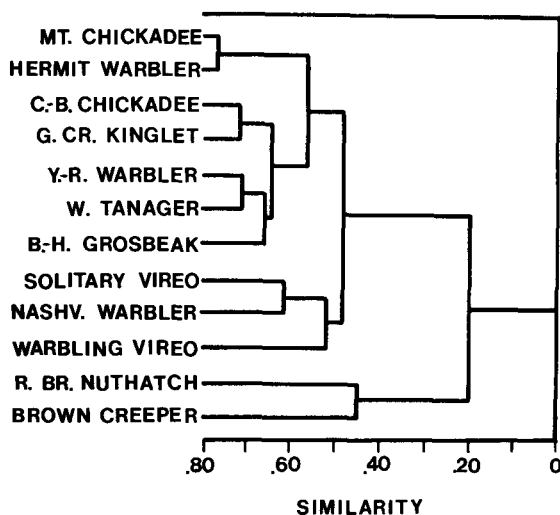

FIGURE 5. Dendrogram of foraging similarities of insect-gleaning birds at Blodgett Forest. Similarities are based on 4-dimensional niche overlaps (see text).

thus, lowering insect densities; (2) essential oils, which make incense-cedar wood resistant to decay (Anderson 1963) and are present in foliage (Zarvarin 1958), may also reduce foliage digestability and, hence, insect abundance; (3) cedar's dense growth form and hanging foliage may make it difficult for birds to search for insects; and (4) much of the cedar in the study area grew in dense understory thickets, which may have hindered the birds' foraging maneuverability. The relatively low use of Douglas-fir may be a result of its physiognomy: much of the foliage grows on small hanging branches that provide poor support for the less maneuverable guild members. Preference for the deciduous black oak is probably due to the abundance of insects available on emergent spring foliage. Further study of insect productivity and bird foraging efficiency in white fir and pines will be needed before one can explain these preferences.

The pattern of tree species preferences shown by the insect-gleaners indicates the importance of tree species in determining habitat suitability. Except for the consistent avoidance of incense-cedar, the birds generally used different tree species in a complementary way. We suggest that the greater diversity of tree species in the mixed-conifer forest, in comparison with other habitats in the Sierra Nevada (Rundel et al. 1977, Verner and Boss 1980:4), promotes a higher diversity of insect-gleaning birds. More species of forest insect-gleaners breed in this type of forest than in any other forested habitat in the Sierra (summarized from Verner and Boss 1980:86–90).

Preferences by insect-gleaning birds for certain tree species have been reported for other geographic areas (Hartley 1953, Balda 1969, Holmes and Robinson 1981). Studies of breeding birds in Arizona, which included some of the bird and tree species that we studied, have reported different patterns. Franzreb (1978) found that the three most common foliage-gleaning species in a mixed-conifer forest preferred Douglas-fir and white fir, and avoided ponderosa pine. Balda (1969) found that pines (*Pinus leiophylla*) and oaks were preferred by foliage feeders in an oak-juniper woodland. In a forest dominated by ponderosa pine, he found pine and Douglas-fir used according to their availabilities. In a pine-juniper ecotone, ponderosa pine was under-used by insect-gleaners (Laudenslayer and Balda 1976). More work is needed to describe fully the regional and seasonal patterns of tree species preferences and to describe the effect of tree species availability on preference within regions.

The predominant use of stationary gleaning, rather than hovering, by all guild members is striking. Alatalo (1982) found similar results in a Finnish conifer forest, whereas Robinson and Holmes (1982) found that hovering was used much more frequently by foliage insect-feeders in a northeastern United States hardwoods forest. These differences may reflect bird responses to fundamental differences in the structure of trees in the two forest types (cf. Sabo and Holmes 1983). Many conifers have foliage arrayed along rigid horizontal branches. In our study area, this configuration is characteristic of white fir, sugar pine, and, to a lesser extent, ponderosa pine. This structure allows birds to hop along branches and twigs, and glean insects from a relatively large amount of foliage. In contrast, hardwood foliage in the eastern U.S. generally occurs at the ends of branches, where birds must expend more energy hovering to take insects (Robinson and Holmes 1982). The only deciduous hardwood in our area, black oak, bears leaves on sturdy, upright twigs. Hence, birds have little difficulty gleaning from its foliage.

The foraging techniques of the tanager and grosbeak differed from those of the other guild members, owing to attempts by these large birds to capture large prey. Both are "variable-distance searchers" (*sensu* Robinson and Holmes 1982) that not only take insects of all sizes by gleaning, but also search for larger insects at greater distances. The tanager hawks large, slow insects from exposed perches, often between bouts of gleaning. Although it usually gleans, the grosbeak also appears to search for larger insects at greater distances within the tree crown below it. Upon finding larger flying or stationary prey up to 3 m away, the grosbeak lunges down upon it. No other species at Blodgett Forest used this technique regularly.

The relative rankings of overlap values on various foraging axes among insect-gleaning species at the Forest are similar to results of other recent studies. At Blodgett, species differed from one another most often in their use of foraging sites, then followed by tree species, and least (and nearly equally) by height and technique. That foraging technique differentiated these species minimally is in part a trivial result of our use of gleaning as a criterion to define the guild. Alatalo's (1982) study of this guild in a Finnish conifer forest ranked foraging site most important, followed in decreasing order by tree species, technique, and height. In oak woodlands in Mexico and California, Landres and MacMahon (1983) found technique and food site to be most important, and height least important, in differentiating between members of the foliage- and bark-gleaning guilds. (They did not quantify plant species use.)

Other studies have shown different rankings of niche overlaps within similar guilds. Root (1967) found foraging technique, plant species, and foraging site to be decreasingly important in distinguishing foliage-gleaners in mixed oak-chaparral in California. Tits (*Parus* spp.) in an English woodland differed decreasingly by plant species use, height, and foraging site (Hartley 1953). Hutto (1981) found that four riparian western wood warblers differed most in foraging heights and least in technique and site during both summer and winter.

The above-mentioned differences in patterns of niche segregation probably reflect real differences among habitats and geographic areas. This conclusion remains somewhat uncertain, however, owing to differences in the way various workers have defined guilds and niche components. More comparative studies using standardized methodologies are clearly needed.

Our analysis revealed few fundamental differences in the foraging niches of resident and migratory species during the breeding season. Most striking was the greater use of conifers by residents and the greater use of oak by migrants. Most residents avoided deciduous foliage, and used substrates that were available year-round (conifer foliage, branches, and tree trunks). Presumably, this reflects ancestral adaptations of the palearctic-derived residents (Mayr 1976), and these species' need to retain abilities to forage efficiently on substrates available during the winter when prey are scarce (Sabo and Holmes 1983). In contrast, most migrants preferred the productive, seasonal, hardwood foliage more characteristic of neotropical areas from where these species are derived (Mayr 1976). We emphasize, however, that differences in foliage-type preferences were only relative. Migrant species have adapted to make substantial use of conifer foliage. Among his foliage-gleaning birds, Alatalo (1982) also found that migrants used greater amounts of deciduous foliage than did residents.

Residents and migrants also differed in the relationship of species foraging-diversity and abundance. The positive correlation between resident species' abundances and niche breadths is consistent with the idea that birds with greater behavioral flexibility may achieve higher populations. We do not suggest that such population regulation is likely to occur during the breeding season; rather, if it occurs at all, it is more likely to do so in winter. The lack of a relationship between abundance and niche breadth in migrants supports the widely held view that a more complex set of factors regulates the abundance of migrant species on the breeding grounds (Keast and Morton 1980).

Species abundance has been positively correlated with niche breadth in a number of other bird communities (e.g., Balda 1969, Szaro and Balda 1979). Among foliage-gleaning birds, Alatalo (1982) found, as we did, a stronger positive relationship between niche breadth and abundance of residents than that of migrants. Also, the relationship was stronger for residents in winter than in summer, suggesting that population regulation may occur at that time.

Our results have implications for management of the Sierra Nevada type of mixed-conifer forest. Insect-gleaning birds appear especially likely to be affected by forest management practices that alter tree species diversity. Fire suppression and early logging have altered tree species composition in much of the mixed-conifer type forests, increasing incense-cedar and white fir, and reducing the extent of pines (Kilgore 1971, Rundel et al. 1977). Use of prescribed fire and other techniques to re-establish natural species composition may be beneficial to this guild. Current timber management and fuelwood cutting practices have also substantially affected tree species diversity and other habitat conditions in this forest type (Verner 1980). Based on our results, we believe that efforts should be increased to maintain a high diversity of tree species in stands managed for timber, by using both even- and uneven-aged forest management techniques to encourage a variety of tree species, by planting a mixture of trees in clearcuts, and by retaining oaks and managing for their replacement over time.

ACKNOWLEDGMENTS

LITERATURE CITED

AIROLA, D. A., AND R. H. BARRETT. 1981. Vertebrates of Blodgett Forest Research Station, El Dorado County, California—an annotated species list. Univ. Calif. Div. Agric. Sci., Special Publ. 3267, Berkeley.

ALATALO, R. V. 1982. Multidimensional foraging niche organization of foliage-gleaning birds in northern Finland. Ornis Scand. 13:56–71.

ANDERSON, A. B. 1963. The chemistry of decay resistance and its decrease with heartwood aging in incense-cedar (Libocedrus decurrens Torrey). Holzforschung 17:1–5.

BALDA, R. P. 1969. Foliage use by birds of the oak-juniper woodland and ponderosa pine forest in southeastern Arizona. Condor 71:399–412.

DEDON, M., AND R. H. BARRETT. 1982. An inventory system for assessing wildlife habitat relationships in forests. Calif.-Neva. Wildl. Trans. 55–60.

DIXON, W. J. [ED.]. 1981. BMDP Statistical Software. Univ. of California Press, Berkeley.

DUNN, O. J. 1961. Multiple comprisons among means. J. Am. Stat. Assoc. 56:52–64.

FEINSINGER, P., E. E. SPEARS, AND R. W. POOLE. 1981. A simple measure of niche breadth. Ecology 62:27–32.

FRANZREB, K. E. 1978. Tree species used by birds in logged and unlogged mixed coniferous forests. Wilson Bull. 90:221–238.

FRANZREB, K. E., AND R. D. OHMART. 1978. The effects of timber harvesting on breeding birds in a mixed-conifer forest. Condor 80:431–441.

HARTLEY, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. J. Anim. Ecol. 22:261–288.

HOLMES, R. T., AND S. K. ROBINSON. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia (Berl.) 48:31–35.

HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419–424.

HUTTO, R. L. 1981. Seasonal variation in the foraging behavior of some migratory western wood warblers. Auk 98:765–777.

INGER, R. F., AND R. K. COLWELL. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. Ecol. Monogr. 47:229–253.

JACKSON, J. A. 1979. Tree surfaces as foraging substrates for insectivorous birds, p. 69–94. In J. G. Dickson, R. N. Conner, R. F. Fleet, J. C. Knoll, and J. A. Jackson [eds.], The role of insectivorous birds in forest ecosystems. Academic Press, New York.

KEAST, A., AND E. S. MORTON [EDS.]. 1980. Migrant birds in the Neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, DC.

KILGORE, B. M. 1971. Responses of breeding birds to habitat changes in a giant sequoia forest. Am. Midl. Nat. 85:135–152.

LANDRES, P. B., AND J. A. MACMAHON. 1983. Community organization of arboreal birds in some oak woodlands of western North America. Ecol. Monogr. 53:183–208.

LAUDENSLAYER, W. F., JR., AND R. P. BALDA. 1976. Breeding bird use of a pinyon-juniper-ponderosa pine ecotone. Auk 93:571–586.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ.

MAY, R. M. 1975. Some notes on estimating the competition matrix, α. Ecology 56:737–741.

MAYR, E. 1976. History of the North American bird fauna, p. 565–588. In E. Mayr [ed.], Evolution and the diversity of life: selected essays. Belknap Press, Cambridge, MA.

MORRISON, M. L. 1984. Influence of sample size and sampling design on analysis of avian foraging behavior. Condor 86:146–150.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

ROBINSON, S. K., AND R. T. HOLMES. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet and habitat structure. Ecology 63:1918–1931.

ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37:317–349.

RUNDEL, P. W., D. J. PARSON, AND D. T. GORDON. 1977. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges, p. 559–599. In M. G. Barbour and J. Major [eds.], Terrestrial vegetation of California. John Wiley and Sons, New York.

SABO, S. R., AND R. T. HOLMES. 1983. Foraging niches and the structure of forest bird communities in contrasting montane habitats. Condor 85:121–138.

SHANNON, C. E., AND W. WEAVER. 1949. The mathematical theory of communication. Univ. of Illinois Press, Urbana.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

STRAUSS, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio and a proposed linear index of food selection. Trans. Am. Fish. Soc. 108:344–352.

SZARO, R. C., AND R. P. BALDA. 1979. Bird community dynamics in a ponderosa pine forest. Stud. Avian Biol. 3.

TRAVIS, J. 1977. Seasonal foraging in a Downy Woodpecker population. Condor 79:371–375.

VERNER, J. 1980. Bird communities of mixed-conifer forests of the Sierra Nevada, p. 198–224. In R. M. DeGraff [tech. coor.], Management of western forests and grasslands for nongame birds. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-86.

VERNER, J., AND A. S. BOSS [tech coor.]. 1980. California wildlife and their habitats: western Sierra Nevada. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PSW-37.

WAGNER, J. L. 1981. Visibility and bias in avian foraging data. Condor 83:263–264.

ZAVARIN, E. 1958. The extraneous substances of incense-cedar (Heyderia decurrens Torrey). California Forestry and Forest Products, No. 5. Univ. California Agricultural Experiment Station, Berkeley.

Department of Forestry and Resource Management, University of California, Berkeley, California 94720, and USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Arcata, California 95521. Address of second author: Department of Forestry and Resource Mangement, University of California, Berkeley, California 94720. Present address of first author: USDA Forest Service, Lassen National Forest, Chester, California 96020.