THE STRUCTURE OF A FOREST BIRD COMMUNITY DURING WINTER AND SUMMER

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ABSTRACT.—We examined the abundance and use of habitat by birds during winter and summer in a mixed-conifer forest of the western Sierra Nevada. Of the species present during both seasons, four had significantly higher indices of abundance in winter, whereas none had higher summer indices. Bird species differed significantly in habitat use during summer as identified by discriminant function analysis (DFA). The spacing of large trees separated birds along the first DFA axis; the second axis was defined by the size of foraging trees. There was also a significant difference in habitat use among species during winter. The size of foraging trees and the diameter of small (11–30 cm dbh) trees defined the first function; the second function was defined by high canopy cover. In both seasons, however, an unbiased classification procedure separated all species poorly. There was a significant difference in the overall pattern of habitat use by permanent resident birds between winter and summer as identified by DFA. All species showed significant differences in habitat use vs habitat availability during both winter and summer. Overwintering birds used areas characterized by high, heavy canopy cover and heavy subcanopy cover relative to summer use. Our results suggest that forest managers should give increased attention to the structure and species composition of managed forests. *Received 16 Sept. 1985, accepted 22 Nov. 1985.*

Species composition, abundance, and behavior of birds are known to vary seasonally (Willson 1970, 1971; Travis 1977; Conner 1980, 1981; Rice et al. 1980; Hutto 1981; Lewke 1982; Morrison et al. 1985). Some species are permanent residents in an area; others occupy an area only during winter or summer. In addition, the quantity and quality of the habitat, both in terms of plant condition (e.g., leaf abscission) and food resources (e.g., abundance), vary seasonally. The description of the structure of bird communities is thus complicated by many factors.

Our objective was to describe habitat use by birds during winter and summer in the western Sierra Nevada, California; we examined both community and species-specific habitat use. Possible changes in habitat use may indicate a response to environmental differences between seasons, and they are important to recognize if the habitat requirements of birds are to be met by forest managers.

STUDY AREA

The study was conducted at the Blodgett Forest Research Station (University of California–Berkeley), El Dorado County, California. This 1200-ha forest is in the mixed-conifer zone

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at 1200–1450 m elevation in the western Sierra Nevada. Predominant tree species, in decreasing order of canopy coverage, included incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), California black oak (*Quercus kelloggii*), and sugar pine (*P. lambertiana*) (Morrison et al., unpubl. data). During the spring and summer (May through August, hereafter referred to as the summer season) of 1983 and 1984, and during winter (November through March) of 1982–83 and 1983–84, four areas totaling about 100 ha (range = 16–35 ha) were used as the study site. Because of limited access to much of Blodgett Forest during winter, we selected areas within the forest that allowed both summer and winter access.

METHODS

Bird abundance. — Sampling points were placed along a preexisting grid used for surveying the forest vegetation for silvicultural purposes. Points ("growth-stocking points") were located about every 120 m along the grid; we randomly selected 40 of these points for counting birds in both winter and summer. All birds seen or heard in a 30-m-radius plot around each point were recorded for 5 min during the first 3 h after sunrise on four occasions each during the summer and winter. Bird abundance was calculated as the mean number of birds recorded per count (=index of abundance). Because many species were sexually monomorphic, data for males and females were combined to determine abundance. Spearman's rank correlation indicated that the relative order of species by abundance was similar ($P < 0.05$) between years within a season, and we combined count data for both years of study in the analysis presented here.

Habitat use. — The habitat use by winter, summer, and permanent-resident bird species was recorded. During summer, each area was visited for 2–4 h on 4–5 occasions (at 7–10 day intervals between visits). During winter, each area was visited for about 7 h (total) during a 2–3 day period on 4–6 occasions (at 2–3 week intervals).

Analysis of habitat use was based on the activities of foraging individuals. An observer would walk systematically through an area; when an actively foraging bird was encountered, the substrate (i.e., tree, shrub, ground) the bird was using served as the center of a 10-m-radius plot. Within each plot, a visual estimate of shrub and seedling cover by species and cover of dead and down material by size class (≤ 10, 11–30, 31–90, and >90 cm diameter) was made. The point-centered quarter method (Mueller-Dombois and Ellenberg 1974:110–115) was used to determine species composition and dbh of trees in 11–30 cm dbh and >30-cm dbh size classes surrounding the foraging substrate. The species and dbh of the foraging tree were also recorded. A randomly oriented 20-m line transect bisecting the center point was used to measure cover by height layers. Presence or absence of live vegetation was noted at each of six heights (1, 4, 10, 20, 30, and 40 m) at 2-m intervals along the transect. Foliage height diversity (FHD; Shannon and Weaver 1949) was calculated. Habitat available to the birds was determined by collecting the same data used to describe bird habitat use at the 40 plots at which birds were counted.

Previous work (Morrison 1984) indicated that a sample of >35 individuals adequately described habitat use. Because we could not obtain this size sample for each species each season, data were combined for the two winters and two summers of our study. Data for males and females were combined for this analysis. Whereas rare species of birds may be important in influencing interspecific relationships in a bird community, they are difficult to analyze because of inadequate sample sizes. Therefore, we examined overall community structure (all species present regardless of sample size) separately for winter and summer, but restricted more detailed statistical treatments to species with adequate samples. Given the problems associated with violations of assumptions and related sample size problems

TABLE 1
ABSOLUTE TREE DENSITY ON STUDY PLOTS AT BLODGETT FOREST RESEARCH STATION, CALIFORNIA

Species	No. trees per 100 m²		Total
	11–30 cm dbh	>30 cm dbh	
Incense cedar	0.72	0.44	1.16
White fir	0.37	0.39	0.76
Douglas-fir	0.25	0.23	0.48
Ponderosa pine	0.06	0.20	0.26
Sugar pine	0.02	0.13	0.15
Black oak	0.00	0.07	0.07
Other	0.06	0.03	0.09
Total	1.48	1.49	2.97

in the use and interpretation of multivariate analysis (Johnson 1981, Noon 1981, Morrison 1984), such a procedure is preferable to one ignoring such concerns and reporting questionable results. All analyses were run using the SPSSX computer package (SPSS 1983).

Data were analyzed using discriminant function analysis (DFA) with stepwise inclusion of variables. Standardized discriminant function coefficients were used to interpret the functions (ecologically); correlations of the discriminant scores with the original variables yielded the same conclusions. Our data seldom met the assumption of equality of variance-covariance matrices. Transformation (e.g., log, arcsine; see Sokal and Rohlf 1969:380–387) of original data did not substantially enhance normality. Most classification procedures conducted using DFA were run after first dividing the data set randomly into two parts: one containing about 70% of the original observations with which the DFA was performed, and the second containing the remaining observations for determination of the ability of the first data set to classify the second (an "unbiased" classification procedure; Norusis 1985: 87–88). Such a procedure was especially important given the nonnormality of many of our data sets. For comparisons with large differences in sample sizes, the DFA was run using a random subset of the group with the large *n*. Mahalanobis' distances were calculated to examine all pairwise comparisons between species in habitat use.

Correlation coefficients were calculated for all combinations of original variables. When correlations exceeded 0.5, the variable with the least discriminating power (based on analysis of variance) among species was removed from subsequent analysis. Variables created from combinations of other variables (e.g., total vegetation cover) were not used in any multivariate analysis; FHD was not included in these analyses because of high intercorrelations and low discriminating power relative to other (cover) variables.

RESULTS

Vegetation Availability

About one-half of the trees in the 11–30-cm dbh size category (SMDBH) were incense cedar (Table 1). White fir and Douglas-fir, with one-half to one-third the density of cedar, were the only other tree species with densities over 0.1 trees/100 m² in this size range (Table 1). Cedar and white

TABLE 2

AVAILABILITY OF HABITAT MEASURED IN 40 PLOTS AT THE BLODGETT FOREST RESEARCH STATION, CALIFORNIA

Variable	Mnemonic	$\bar{x}$	SD
Percent cover of down material (cm diameter)			
≤10	DWN1	16.3	13.7
11–30	DWN2	4.0	5.4
31–90	DWN3	1.7	2.4
>90	DWN4	0.1	0.5
Total		22.1	17.2
Percent cover by height (m)			
1.0	CVR1	17.3	23.7
4.0	CVR2	15.0	17.0
10.0	CVR3	29.8	22.7
20.0	CVR4	36.8	23.3
30.0	CVR5	23.6	28.4
40.0	CVR6	3.4	8.3
Total		125.9	54.5
Tree distribution (m)			
11–30 cm dbh	SMDIST	5.4	1.7
>30 cm dbh	LGDIST	6.3	2.3
Tree dbh (m)			
11–30 cm dbh	SMDBH	19.3	3.7
>30 cm dbh	LGDBH	55.0	11.3

fir were roughly codominant in the larger (>30 cm dbh; LGDBH) size class. Ponderosa pine and Douglas-fir were about one-half as abundant as cedar and fir; sugar pine and black oak were present but in low density.

Total cover of down material was only about 22%; most of this was branches and twigs (<10 cm diameter; DWN1) (Table 2). The forest canopy extended to between 30–40 m in height. The densest cover was at 10 m and 20 m, although cover at all heights under 40 m exceeded 15%. The distribution of small (11–30 cm dbh) and large (>30 cm dbh) trees was about equal. The mean dbh of the smaller size category of trees approached 20 cm, whereas trees in the larger category averaged 55 cm dbh.

Bird Abundance

Thirty-five species were considered resident in the study area during summer. Only eight of these had indices of abundance over 0.4; the

majority (24 or 69%) had indices less than 0.4 (Table 3). The Dark-eyed Junco (scientific names of birds are in Table 3) and Hermit Warbler were the only species with indices over 1.0.

Twenty-one species were resident during winter. Seven had indices of abundance greater than or equal to 0.4, and 10 had indices greater than or equal to 0.2 (Table 3). The remaining 11 species had indices under 0.2. The American Robin and Golden-crowned Kinglet were the only species with indices over 1.0, although the Red-breasted Nuthatch had an index of 0.99.

Of the species present in both winter and summer, four had significantly higher indices of abundance in winter than in summer; none had significantly higher summer indices (Table 3). The American Robin had a winter abundance about four times greater than its summer abundance; the Chestnut-backed Chickadee, Golden-crowned Kinglet, and Red-breasted Nuthatch had winter abundances about twice that of their summer abundances.

Bird Habitat Use

Summer residents. — There was an overall significant difference in habitat use among bird species during summer as identified by discriminant function analysis (Table 4). Three functions accounted for 100% of the explainable variation in our data set. The spacing of large trees (LGDIST) separated species along the first DFA axis (Fig. 1). The Pileated Woodpecker was associated with areas with relatively closely spaced large trees; the Dusky Flycatcher was found in areas with relatively widely spaced large trees. The remaining species were located between these two extremes.

The second axis was defined by size of foraging trees (FGDBH) used. This axis was influenced most drastically by the Pileated Woodpecker and the Golden-crowned Kinglet, which used the largest and smallest trees for foraging, respectively. The kinglet was, however, barely separated from the remaining species. The two-dimensional graph (Fig. 1) showed that most species were located near the center of the plot. Only 67 of the 190 (35%) pairwise comparisons (Mahalanobis' distances) between species were significant (Table 5). The Pileated Woodpecker and Dusky Flycatcher were significantly separated from all other species (and accounted for over one-half of the significant comparisons). The Mountain Chickadee, Purple Finch, and Black-headed Grosbeak were also significantly different from most of the other species (Table 5).

The unbiased classification analyses separated all species poorly, showing only 10% correct classification. For species on extremes of the axes,

TABLE 3
INDICES OF ABUNDANCE OF BIRDS RECORDED DURING WINTER AND SUMMER AT THE
BLODGETT FOREST RESEARCH STATION, CALIFORNIA

Species	Summer $\bar{x} \pm SD$	Winter $\bar{x} \pm SD$
Red-breasted Sapsucker (*Sphyrapicus ruber*)	0.34 ± 0.36	0
Downy Woodpecker (*Picoides pubescens*)	0.17 ± 0.53	0.09 ± 0.37
Hairy Woodpecker (*P. villosus*)	0.13 ± 0.29	0.19 ± 0.22
White-headed Woodpecker (*P. albolarvatus*)	0.08 ± 0.26	0.17 ± 0.29
Northern Flicker (*Colaptes auratus*)	0.09 ± 0.24	0.11 ± 0.26
Pileated Woodpecker (*Dryocopus pileatus*)	0.17 ± 0.38	0.08 ± 0.23
Olive-sided Flycatcher (*Contopus borealis*)	0.11 ± 0.32	0
Western Wood-Pewee (*C. sordidulus*)	0.11 ± 0.27	0
Hammond's Flycatcher (*Empidonax hammondii*)	0.44 ± 0.30	0
Dusky Flycatcher (*E. oberholseri*)	0.27 ± 0.34	0
Steller's Jay (*Cyanocitta stelleri*)	0.33 ± 0.56	0.21 ± 0.39
Mountain Chickadee (*Parus gambeli*)	0.34 ± 0.38	0.46 ± 0.69
Chestnut-backed Chickadee (*P. rufescens*)	0.35 ± 0.56	0.74 ± 0.51[a]
Red-breasted Nuthatch (*Sitta canadensis*)	0.38 ± 0.36	0.99 ± 0.42[b]
Brown Creeper (*Certhia americana*)	0.30 ± 0.46	0.34 ± 0.65
Winter Wren (*Troglodytes troglodytes*)	0.30 ± 0.49	0.38 ± 0.26
Golden-crowned Kinglet (*Regulus satrapa*)	0.86 ± 0.36	1.60 ± 0.99[b]
Ruby-crowned Kinglet (*R. calendula*)	0	0.19 ± 0.32
Western Bluebird (*Sialia mexicana*)	0	0.10 ± 0.40
Townsend's Solitaire (*Myadestes townsendi*)	0.08 ± 0.27	0.14 ± 0.47
Hermit Thrush (*Catharus guttatus*)	0.14 ± 0.29	0
American Robin (*Turdus migratorius*)	0.35 ± 0.20	1.68 ± 0.56[c]
Varied Thrush (*Ixoreus naevius*)	0	0.17 ± 0.45
Solitary Vireo (*Vireo solitarius*)	0.61 ± 0.20	0
Warbling Vireo (*V. gilvus*)	0.80 ± 0.21	0
Nashville Warbler (*Vermivora ruficapilla*)	0.30 ± 0.32	0
Yellow-rumped Warbler (*Dendroica coronata*)	0.35 ± 0.40	0.18 ± 0.43
Hermit Warbler (*D. occidentalis*)	1.01 ± 0.13	0
MacGillivray's Warbler (*Oporornis tolmiei*)	0.24 ± 0.22	0
Western Tanager (*Piranga ludoviciana*)	0.62 ± 0.22	0
Black-headed Grosbeak (*Pheucticus melanocephalus*)	0.40 ± 0.29	0
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	0.14 ± 0.26	0.86 ± 2.58
Fox Sparrow (*Passerella iliaca*)	0.15 ± 0.25	0
Dark-eyed Junco (*Junco hyemalis*)	1.05 ± 0.18	0.89 ± 1.10
Brown-headed Cowbird (*Molothrus ater*)	0.17 ± 0.36	0
Purple Finch (*Carpodacus purpureus*)	0.21 ± 0.27	0.10 ± 0.32
Pine Siskin (*Carduelis pinus*)	0.19 ± 0.52	0
Evening Grosbeak (*Coccothraustes vespertinus*)	0.22 ± 0.45	0

[a] $P < 0.05$ of a seasonal difference using a *t*-test.
[b] $P < 0.01$ of a seasonal difference using a *t*-test.
[c] $P < 0.001$ of a seasonal difference using a *t*-test.

TABLE 4

HABITAT USED BY BIRDS DURING WINTER AND SUMMER, AND A COMPARISON OF WINTER
VS SUMMER (ALL BIRD SPECIES COMBINED PER SEASON) AT THE BLODGETT FOREST
RESEARCH STATION, CALIFORNIA, AS ANALYZED BY DISCRIMINANT FUNCTION ANALYSIS

	Winter[a]		Summer[b]			Winter vs summer[c]
	I	II	I	II	III	I
Eigenvalue	0.126	0.051	0.324	0.275	0.153	0.474
Relative % variation	61.5	25.1	43.1	36.7	20.3	100.0
Cumulative % variation	61.5	86.6[d]	43.1	79.7	100.0	100.0
Canonical correlation	0.335	0.221	0.494	0.465	0.364	0.567
Wilks' lambda	0.822	0.926	0.514	0.680	0.868	0.678
χ^2	72.535	28.566	156.76	90.74	33.44	112.76
df	27	16	57	36	17	5
P	<0.001	<0.05	<0.001	<0.001	<0.01	<0.001

[a] Box's M: $F = 1.47$; df = 54, 17,833.6; $P < 0.05$.
[b] Box's M: $F = 1.93$; df = 114, 10,057.2; $P < 0.001$.
[c] Box's M: $F = 3.43$; df = 15, 256,880.8; $P < 0.001$. Winter N = 266, which represents a random subsample of 511 plots. This subsample was taken to approximate more closely the summer sample of 181.
[d] The third function accounted for the remaining 13.4% of the variation but was nonsignificant ($P < 0.2$).

the percent classification was above average: 100% for the Pileated Wood-pecker, 40% for the Dusky Flycatcher, and 25% for the grosbeak; no kinglets were correctly classified, however.

Winter residents.—There was a significant difference in habitat use among species during winter as identified by DFA (Table 4). Two func-tions were significant and accounted for most of the explainable variation in the data set. The diameter of foraging trees and the diameter of the small size class of trees defined the first function. Except for the Pileated Woodpecker, which used areas typified by large foraging trees and the largest of the smaller size class of trees, little obvious separation was noted along the first axis (Fig. 2).

The second function was defined by high canopy cover (CVR5). Here again, little separation was noted among species except for the Pileated and Hairy woodpeckers. The Hairy Woodpecker tended to use areas with heavy canopy cover, and the Pileated Woodpecker used areas with low canopy cover.

About one-half (25 or 56%) of the 45 pairwise comparisons between species were significant (Table 5). The Pileated Woodpecker, Ruby-crowned Kinglet, and Dark-eyed Junco were significantly separated from all or nearly all of the other species. The generally poor separation among species

•PIWO

FGDBH

DUFL•

•PUFI

•MOCH

•WAVI •BHGR

−1 •RBSA ▪RBNU 1 2
WHWO• HAWO• •NAWA
BRCR •YRWA LGDIST→
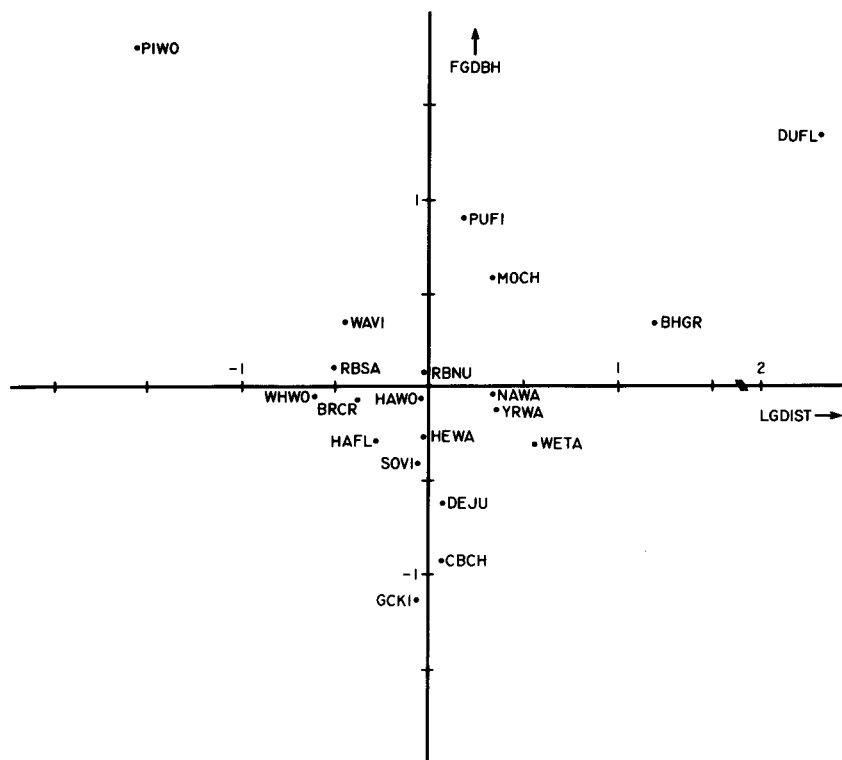HAFL• ▪HEWA •WETA
SOVI•

•DEJU

•CBCH
−1
GCKI•

Fig. 1. Two-dimensional ordination of bird habitat use during summer at Blodgett Forest, California, as determined by discriminant function analysis. The species and their associated mnemonics and sample sizes are given in Appendix 1. See Table 4 for statistics associated with this analysis. Variables defining the axes are FGDBH (dbh of the foraging tree) and LGDIST (distribution of large trees).

was reflected in the unbiased classification; only 14% were correctly classified. The two species on the extremes of the axes did show correct classification rates higher than average (100% for the pileated and 22% for the hairy).

Permanent residents, winter vs summer. — There was a significant difference in the overall pattern of habitat use by permanent resident birds between winter (all species combined) and summer (all species combined) as identified by DFA (Table 4). There was a greater use of high cover and more widely scattered large trees during winter. Use of cover in the second (CVR2) layer was also greater during winter. The overall use of larger diameter trees was greater during summer. The discriminant analysis was fairly strong, showing an unbiased classification of 69%.

TABLE 5

SIGNIFICANCE[a] BETWEEN PAIRS OF SPECIES AS DETERMINED BY MAHALANOBIS' DISTANCE (ASSOCIATED WITH DISCRIMINANT FUNCTION ANALYSIS) (TABLE 4) FOR BIRD HABITAT USE AT BLODGETT FOREST, CALIFORNIA, DURING SUMMER (LOWER-LEFT TRIANGLE) AND WINTER (UPPER-RIGHT TRIANGLE)

	RBSA[b]	HAWO[c]	WHWO[c]	PIWO[c]	HAFL	DUFL	MOCH[c]	CBCH[c]	RBNU[c]	BRCR[c]	GCKI[c]	RCKI[c]	SOVI	WAVI	NAWA	YRWA	HEWA	WETA	BHGR	DEJU[c]
HAWO[c]	—			*			*		*	*	*								*	*
WHWO[c]	*	—		*					*	*	*								*	*
PIWO[c]	*	*	—	*		*			*	*	*									—
HAFL	*	*	*	—	*		—	*	—											
DUFL	*	*	*	*	—	—	*	*	*	*							*	*	
MOCH[c]	*	*	*	*	*	—	*	*	*	*	*									
CBCH[c]	*	*	*	*	*	*	—	—	*	*										
RBNU[c]	*	*	*	*	*	*	—	—	—											
BRCR[c]	*	*	*	*	*	*	—	*	*	—										
GCKI[c]	*	*	*	*	*	*	—	*	—	*	—									
RCKI[c]	*	*	*	*	*	*	*	—		—										
SOVI	*	*	*	*	*	*						—								
WAVI	*	*	*	*	*	*					—									
NAWA			*	*	*	*	*		*			—								
YRWA					*	*					*		—							
HEWA					*	*			*		*			—						
WETA					*	*			*		*	*			—						
BHGR	*		*		*	*	*	*	*		*	*	*	*	*	—	—			
DEJU[c]	*	*	*	*	*	*	*	*	*	*	*	*	—		—			—	*	—
PUFI	*	*	*	*	*	*	*	*	*	*	*				*	*	*	*	*	—

[a] $P < 0.05$.
[b] See Appendix 1 for species abbreviations.
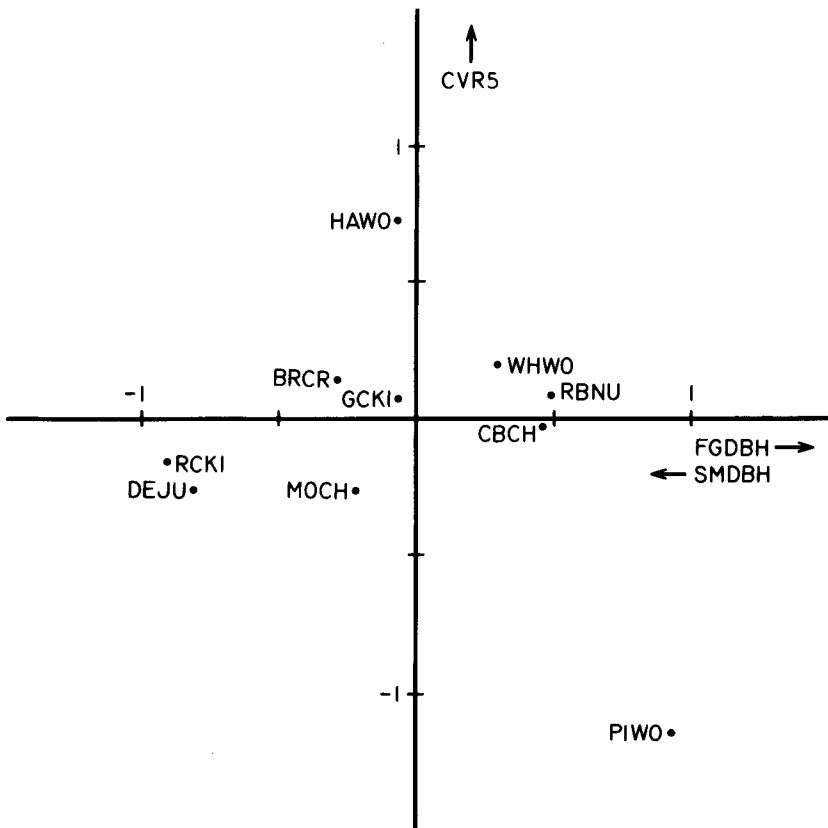[c] Species present during winter.

FIG. 2.   Two-dimensional ordination of bird habitat use during winter at Blodgett Forest, California, as determined by discriminant function analysis. The species and their associated mnemonics (except for the Ruby-crowned Kinglet, RCKI) and sample sizes are given in Appendix 1. See Table 4 for statistics associated with this analysis. Variables defining the axes are CVR5 (canopy cover), FGDBH (dbh of the foraging tree), and SMDBH (dbh of the small size class of trees).

All permanent resident species analyzed used areas typified by greater use of high (canopy) cover or widely scattered large trees in winter versus summer, except for the Golden-crowned Kinglet, which showed no significant differences between seasons (Appendix 1). The White-headed Woodpecker and Mountain Chickadee also used smaller foraging trees during winter; low (subcanopy) cover was also of higher use in winter by the nuthatch.

Species-specific habitat use vs availability: summer. — All 20 species analyzed showed significant differences between habitat use and habitat avail-

ability during summer (Appendix 1). Only 11, however, showed greater than 70% correct unbiased classification; an additional four species showed over 60% unbiased classification. The diameter of the foraging tree was the primary variable separating summer habitat use from availability for 15 species, with these species using larger trees for foraging in proportion to those available randomly (Appendix 1). The distribution of large diameter or small diameter trees separated the remaining species, except for the Dark-eyed Junco and Black-headed Grosbeak.

Species-specific habitat use vs availability: winter. —All nine species analyzed during winter showed significant differences between habitat use and availability (Appendix 1). Four showed over 70% correct unbiased classification; the remaining five species had classification rates from 55% to 69%. All species except the Pileated Woodpecker used greater cover in the second, third, or fifth height layer relative to that available randomly as either the primary, secondary, or tertiary variable separating use from availability of habitat. The Chestnut-backed Chickadee and Pileated Woodpecker used significantly larger trees for foraging than those available randomly, and the Hairy Woodpecker used areas with smaller diameter trees relative to those available randomly.

<div align="center">DISCUSSION</div>

Blodgett Forest is a true mixed-coniferous forest; all predominant tree species can usually be seen at any point in the forest. The subcanopy and canopy layers were similar in foliage cover up to 30–40 m in height, and the distribution of trees in both size classes was similar. This structure of the forest vegetation may account for our finding that most species had similar abundance—low to moderate—relative to the two or three species with the highest abundances (during either season). It thus appeared that the forest vegetation offered adequate habitat for many species, but few species were able to attain relatively high abundance. This supposition is supported by results of analysis of habitat use. Except for the Pileated Woodpecker, little obvious separation was seen among species on the discriminant plots during either season, using the variables we measured.

More species were considered resident during summer than winter (35 vs 21). Of the year-round residents, four species had higher abundances in winter than summer, whereas none had higher abundances in summer than winter. This could result from a change in the detectability of a species between seasons; interpretation of the indices is hampered because many species formed interspecific foraging flocks during winter. If our results reflect actual shifts in abundance, it appears that while relatively few species overwinter in our study area, those that do, do so at higher numbers than in the summer.

The bird community overwintering at Blodgett used areas characterized by high, heavy canopy cover provided by large, widely spaced trees; heavier cover in the subcanopy was also used during winter compared to summer. We attributed this difference in habitat use to the protection from wind and precipitation supplied by relatively large trees with dense canopies that formed an "umbrella" over the forest floor and the denser subcanopy that further protected the birds from adverse weather (i.e., thermal cover; see Thomas et al. 1979; also Kittredge 1953, Gary and Troendle 1982). Although we do not have adequate data to present an energetics model, others have shown that such habitat is preferred by numerous species of animals in an attempt to escape inclement weather (see reviews by Moen 1973:286–292, Thomas et al. 1979).

Morrison et al. (1985) showed that the use of trees with smaller diameters for foraging during winter at Blodgett Forest was primarily a reflection of the use of small incense cedar. Birds increased use of cedar because of the presence of a readily accessible insect (incense cedar scale, *Xylococculus macrocarpae*) overwintering just under the loose bark of small trees. The presence of this food source may explain the higher winter abundance of certain species shown in this paper.

Species-specific analysis of habitat use (vs availability) generally paralleled results for our community-level analyses—larger diameter trees were used for foraging in summer and areas with high canopy cover at one or more heights were used in winter. During summer, birds apparently were using relatively large trees as singing and foraging sites—our data were often collected on individuals alternately singing and foraging in large trees. During winter, when song perches were not usually used, thermal protection became important and small cedars apparently were preferred.

Our results suggest a word of caution to forest managers. In the western Sierra Nevada (and elsewhere), forests are being managed for preferred commercial species (e.g., Douglas-fir, ponderosa pine, fir) and short (e.g., 70 years) rotation. Therefore, the habitat conditions used by birds during winter in our study—dense canopy with an understory of young incense cedar—are being replaced by relatively monotypic stands of younger trees. Although our results are descriptive and not predictive, it is apparent that more attention needs to be given to the structure and species composition of managed forests.

APPENDIX 1

SUMMARY OF DISCRIMINANT FUNCTION ANALYSIS (DFA) OF HABITAT USE VS HABITAT AVAILABILITY (N = 40 PLOTS), AND WINTER VS SUMMER HABITAT USE, FOR BIRDS AT BLODGETT FOREST RESEARCH STATION, CALIFORNIA, DURING SUMMER AND WINTER[a]

	Summer use vs availability					Winter use vs availability	
	DFA (P) (N)	Standardized discriminant function coefficients			% Classification	DFA (P) (N)	Standardized discriminant function coefficients
Red-breasted Sapsucker (RBSA)	<0.001 (20)	FGDBH (0.741)	CVR2 (0.656)	LGDIST (-0.511)	77.8		
Hairy Woodpecker (HAWO)	<0.001 (18)	FGDBH (1.000)			72.2	<0.001 (28)	LGDBH (-0.945)
White-headed Woodpecker (WHWO)	<0.001 (20)	FGDBH (0.916)	CVR3 (0.622)	SMDBH (-0.530)	76.5	<0.05 (35)	CVR2 (1.000)
Pileated Woodpecker (PIWO)	<0.001 (15)	FGDBH (1.000)			95.0	<0.001 (12)	FGDBH (0.900)
Hammond's Flycatcher (HAFL)	<0.001 (29)	FGDBH (0.560)	CVR3 (0.476)	LGDIST (-0.716)	63.6		
Dusky Flycatcher (DUFL)	<0.01 (10)	SMDIST (0.754)	LGDIST (0.767)		75.0		
Mountain Chickadee (MOCH)	<0.001 (21)	FGDBH (0.925)	CVR2 (0.758)	LGDBH (-0.670)	68.4	<0.001 (58)	CVR2 (0.661)
Chestnut-backed Chickadee (CBCH)	<0.001 (19)	SMDIST (0.644)	LGDIST (0.754)		80.0	<0.001 (38)	FGDBH (0.824)
Red-breasted Nuthatch (RBNU)	<0.01 (27)	FGDBH (0.712)	LGDIST (-0.620)		50.0	<0.001 (79)[b]	SMDBH (-0.574)
Brown Creeper (BRCR)	<0.001 (23)	FGDBH (0.755)	LGDIST (-0.672)		72.2	<0.001 (69)	CVR2 (0.761)

APPENDIX 1
CONTINUED

	Summer use vs availability					Winter use vs availability	
	DFA (P) (N)	Standardized discriminant function coefficients			% Classification	DFA (P) (N)	Standardized discriminant function coefficients
Golden-crowned Kinglet (GCKI)	<0.001 (12)	FGDBH (0.878)	CVR2 (−0.592)	LGDIST (0.565)	73.7	<0.001 (55)c	CVR3 (0.579)
Solitary Vireo (SOVI)	<0.05 (21)	FGDBH (0.585)	SMDIST (−0.565)	LGDIST (−0.704)	50.0		
Warbling Vireo (WAVI)	<0.05 (14)	LGDIST (1.000)			36.8		
Nashville Warbler (NAWA)	<0.001 (13)	FGDBH (1.236)	DWN3 (0.797)	LGDBH (−0.671)	68.8		
Yellow-rumped Warbler (YRWA)	<0.01 (25)	FGDBH (1.066)	DWN3 (0.785)	LGDBH (−0.760)	75.0		
Hermit Warbler (HEWA)	<0.001 (21)	FGDBH (0.637)	CVR3 (0.646)	LGDIST (−0.588)	70.0		
Western Tanager (WETA)	<0.05 (12)	FGDBH (1.000)			68.8		
Black-headed Grosbeak (BHGR)	<0.01 (13)	DWN3 (1.000)			52.6		
Dark-eyed Junco (DEJU)	<0.01 (13)	CVR2 (−0.687)	LGDIST (0.807)		52.2	<0.001 (19)	CVR2 (0.881)
Purple Finch (PUFI)	<0.05 (13)	FGDBH (1.000)			75.0		

[a] Mnemonics given in Table 2 (FGDBH = dbh of foraging tree).
[b] Represents a subsample of 125 plots.
[c] Represents a subsample of 127 plots.

APPENDIX 1
CONTINUED

	Winter use vs availability				Winter vs summer use			
	Standardized discriminant function coefficients		% Classification	DFA (P)	Standardized discriminant function coefficient			% Classification
Red-breasted Sapsucker (RBSA)								
Hairy Woodpecker (HAWO)	CVR5 (0.836)	CVR2 (0.626)	55.2	<0.05	CVR5 (1.000)			80.0
White-headed Woodpecker (WHWO)			56.0	<0.01	CVR5 (0.805)	FGDBH (−0.718)		41.7
Pileated Woodpecker (PIWO)	LGDBH (−0.568)		85.0	<0.05	LGDIST (1.000)			100.0
Hammond's Flycatcher (HAFL)								
Dusky Flycatcher (DUFL)								
Mountain Chickadee (MOCH)	CVR3 (0.542)	FGDBH (0.528)	75.9	<0.001	CVR5 (0.918)	FGDBH (−0.797)		55.6
Chestnut-backed Chickadee (CBCH)	CVR2 (0.849)		83.9	<0.001	LGDIST (0.853)	CVR5 (0.797)		58.3
Red-breasted Nuthatch (RBNU)	CVR5 (0.488)	CVR2 (0.462)	87.8	<0.001	SMDBH (−0.679)	CVR5 (0.500)	CVR2 (0.463)	80.5
Brown Creeper (BRCR)	CVR3 (0.516)	LGDIST (−0.566)	67.6	<0.001	LGDBH (−0.862)	LGDIST (0.842)	CVR5 (0.608)	54.6
Golden-crowned Kinglet (GCKI)	SMDBH (−0.504)	SMDIST (−0.481)	64.0	>0.05				

APPENDIX 1
CONTINUED

	Winter use vs availability			Winter vs summer use	
	Standardized discriminant function coefficients	% Classification	DFA (P)	Standardized discriminant function coefficient	% Classification
Solitary Vireo (SOVI)					
Warbling Vireo (WAVI)					
Nashville Warbler (NAWA)					
Yellow-rumped Warbler (YRWA)					
Hermit Warbler (HEWA)					
Western Tanager (WETA)					
Black-headed Grosbeak (BHGR)					
Dark-eyed Junco (DEJU)	LGDBH (−0.497)	69.6	<0.01	LGDIST (0.750) CVR5 (0.841)	75.0
Purple Finch (PFUI)					

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