BIRD COMMUNITIES AND FOREST STRUCTURE IN THE SIERRA NEVADA OF CALIFORNIA

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ABSTRACT.—I examined the relationship of forest structure and vegetation diversity to bird communities in the mixed conifer and red fir zones of the central Sierra Nevada. Bird populations were censused in open- and closed-canopy forests in both vegetation zones from June through September 1974 to test the prediction that structurally similar forests support similar avifaunas.

Comparisons of bird and vegetation data revealed that forest canopy cover was a primary factor influencing the size and composition of avian communities in the nesting and post-nesting seasons. Closed-canopy forests had lower bird densities, diversities, species richness and consuming biomasses than open-canopy forests in both vegetation zones. The composition of feeding guilds was similar in the two canopy types, but ground-understory foragers, hummingbirds and flycatchers were less abundant in the closed forests. When analyzed by dominance-diversity curves, bird communities in these conifer habitats generated geometric curves in the closed forests and lognormal curves in the open areas. Lognormal curves indicate more bird species of intermediate abundance. The open forests had well-developed understories and higher foliage-height diversities offering a greater array of foraging substrates for birds.

Previous studies have indicated that avian community organization is closely associated with habitat structure (MacArthur and MacArthur 1961, MacArthur 1964, Karr 1968, Karr and Roth 1971, Røv 1975, Holmes et al. 1979). The results of these studies have led to the prediction that structurally similar habitats should support avifaunas with similar species richness, density, diversity and guild structure. However, other workers (Tomoff 1974, Willson 1974, Roth 1976) have not found strong correlations between vegetational configurations and patterns of avian diversity. They recommended a deeper analysis into factors that may modify the composition of avian communities.

In coniferous forests of the Sierra Nevada, forest type and degree of canopy closure have been used as indicators of avian community size and composition (Verner et al. 1980). In the present study, I examined the relationship of forest type and canopy closure to bird communities with respect to species richness, densities, diversities and foraging guilds. In the mixed conifer and red fir zones (Rundel et al. 1977) of the central Sierra Nevada, I selected open- and closed-canopy forests in order to examine these relationships. I tested the prediction that bird populations in open-canopy forests differ in a significant and predictable manner from those in closed-canopy forests.

Bird populations of the western slope of the Sierra Nevada have received relatively little quantitative study. Only a few estimates of population densities have been published (Kingery and Cogswell 1951, Salt 1953, Robert 1966, Kilgore 1971). Thus, a second purpose of my study was to provide density estimates and indications of habitat preferences for birds occurring in the central Sierra Nevada.

STUDY AREAS

The general study area was a valley at the headwaters of the North Fork of the American River in Placer Co., California (39°15′N, 120°20′W). It was heavily glaciated during the Pleistocene, creating a steep and diverse topography. Mixed conifer forest occurs at lower elevations, but extensive stands of red fir (*Abies magni-*

fica) dominate above 2,000 m. Broadleaved forests of oak (*Quercus* sp.), aspen (*Populus tremuloides*), and cottonwood (*P. trichocarpa*) are present at lower elevations and along streams. Mountain meadows, montane chaparral, granite cliffs, lakes and creeks also are present.

The west slope of the Sierra Nevada has an extreme climate with cold, snowy winters and hot, dry summers. Climatological data used in this study were taken at the Soda Springs Snow Laboratory, U.S. Forest Service, Nevada Co., California, located about 15 km from the study site at an elevation of 2,057 m. A ten-year summary (1965–1975) of temperatures from there showed maximum summer readings in excess of 30°C, and minimum readings of −19°C. Temperatures were relatively constant during this ten-year period. In contrast, average annual precipitation in this period ranged from 119 to 201 cm, with an average of 157 cm. In 1974, the year of the study, precipitation was 142 cm. Despite this relatively low precipitation, the snow pack remained in large patches in the red fir forests until the first week of July.

I selected four types of forest in the North Fork of the American River drainage to use as study sites. I measured and marked areas 30 m wide in each forest, avoiding discontinuities such as creeks, meadows and extensive rock outcrops. Transects varied in length depending upon the size of suitable conifer stands.

MIXED CONIFER—OPEN CANOPY

This level census area (1.6 ha) lay between 1,825 and 1,835 m. Conifers on the site were Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*P. contorta*), white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*). Firs and cedars were evenly distributed throughout the transect, whereas lodgepole pines grew in dense stands where the soil was coarse or gravelly. Most Jeffrey pines were large, reaching maximum heights of 60 m. The dense understory of shrub species included huckleberry oak (*Quercus vaccinifolia*), mountain whitethorn (*Ceanothus cordulatus*), and gooseberries (*Ribes roezlii*) along with conifer seedlings. Numerous granite outcrops were present, and the soil appeared to be rather shallow.

MIXED CONIFER—CLOSED CANOPY

This site (2.4 ha) had a southwest exposure (elevation 1,890–1,900 m). The dominant conifers were incense cedar and white fir, most of which were rather small and grew in dense stands. Large Jeffrey pines, white firs and a few cedars rose above the dense lower canopy. Black oaks (*Quercus kelloggii*) also occurred in small patches throughout the transect. The soil was deep, but shade limited understory plants to open areas of dead trees or rock outcrops.

RED FIR—OPEN CANOPY

This site (2.3 ha) lay between 2,145 and 2,225 m in a glacial valley with a southwest exposure. Red fir (*Abies magnifica*) was the dominant conifer, but small numbers of white fir, Jeffrey and lodgepole pine also occurred in the area. The soil was coarse and rocky, causing trees to be widely spaced. Shrubs, including huckleberry oak, mountain whitethorn, gooseberries and willow (*Salix* sp.) provided a luxuriant understory. Forbs, a variety of grasses, as well as bracken fern (*Pteridium aquilinum*) formed a ground cover over much of the forest.

RED FIR—CLOSED CANOPY

This steep site (2.8 ha) had a southern exposure, at elevations ranging from 2,225 to 2,310 m. Red fir was the dominant conifer, but white fir, Jeffrey pine and western white pine (*P. monticola*) also were present. Most red firs were mature and formed a nearly continuous canopy. The forest floor was well shaded, but in places where the canopy was discontinuous, manzanita (*Arctostaphylos patula*) grew sparsely with mountain whitethorn, huckleberry oak and a few grass and forb species. The soil was deep, and covered by a thick layer of forest litter and logs in various stages of decomposition.

METHODS

VEGETATION

At each transect a 30-m-diameter circle was randomly selected and within the circle eight radii were marked at 45° angles from the center point. The vegetation was sampled at 15 points 1 m apart along each radius (n = 120 points per plot).

As an indirect measure of vegetation cover, I determined the amount of light reaching the ground using ozalid paper indicators (Friend 1961), which measure the total light intercepted by all layers of vegetation. I placed 120 of these devices on the forest floor at each transect for a 24-h period during four consecutive, cloudless days in August. On each date, 10, to serve as controls, were placed on an open, rocky ridge near the transect being measured. I later calibrated and compared these control indicators to assess the effects of daily and elevational differences upon the rates of bleaching of the ozalid paper booklets. Percent shade values were calculated from the formula: $100(U - S)/U$, where U represented the average number of pages bleached per booklet in the unshaded areas, and S the shaded areas beneath the canopy.

MacArthur and Horn (1969) described a method for calculating foliage profiles and percent cover values by a combination of sightings through a camera and a plumb-line suspended below a tripod. They suggested using a grid on the viewfinder of the camera in order to make a series of measurements from each tripod position. I modified this method by making a single estimate of canopy height from each of 120 camera positions. A 35 mm camera was equipped with a 200 mm lens, and was mounted vertically on the tripod at a height of 1.5 m. I focused upon the lowest piece of living vegetation directly above the focusing screen, and read the height from the distance scale of the lens. For understory cover, a plumb-line was dropped from the camera. Vegetation strikes were measured with a meter stick and identified as seedlings, shrubs, grasses or forbs. Infinity was recorded if no foliage was sighted above the camera, and zero was noted if the plumb-line hit the ground without touching vegetation. Foliage profiles for each transect were produced by categorizing each measurement according to the following height intervals: ground-understory (0–1.5 m), low canopy (1.6–5.0 m), mid-canopy (5.1–15 m) and high canopy (15.1–>50m). The numbers of leaves per height interval were calculated by the formulae given in MacArthur and Horn (1969). Percent canopy coverages were calculated as fractions of the total sampling points (120) with living foliage directly above the camera. Understory coverages were calculated as percent strikes of vegetation by the plumb-line of the total (120) measurements.

In each transect I counted and identified all trees having at least half their foliage extending within the 30-m circle. I measured the diameter breast height (dbh) of each of these trees and categorized them into the following size classes: 10–15 cm, 15.1–30 cm, 30.1–45 cm, 45.1–60 cm, 60.1–75 cm, 75.1–90 cm, >90 cm. The methods of James and Shugart (1970) were used

to convert these data into estimates of tree densities (numbers/ha) and basal areas (m²/ha).

I applied three measures of diversity to the vegetation and bird data (Simpson 1949, Shannon and Weaver 1949, Hill 1973). Although each of these indices generated the same relative values for foliage height diversity (FHD), tree species diversity (TSD) and bird species diversity (BSD), I selected the Shannon-Weaver index because it varied least with sample size. These diversity values were calculated from the equation: $H' = -\sum_{i=1}^{s} p_i \ln p_i$, where s was the number of categories, and p_i the proportion of individuals in the "i^{th}" category.

BIRD POPULATIONS

Bird populations were censused from 17 June to 11 September 1974. In each of the four transects, 12 censuses were conducted, six each in the nesting (17 June–31 July) and post-nesting seasons (1 August–11 September). Although montane avifaunas have asynchronous breeding cycles (Winternitz 1976), in this study I determined that most species had completed nesting by the end of July. Data for the nesting and post-nesting seasons were analyzed separately because censuses taken in August and September had many immatures and migrants from other localities.

I conducted censuses using the strip-transect method (Kendeigh 1944, Salt 1957). Fixed-width transects were used in preference to the variable-strip method (Emlen 1971) because it was extremely difficult to estimate accurately the lateral distances to vocalizing birds in these coniferous forests. Many birds could not be seen, owing to the density of foliage in forest canopies. More than 85% of the bird detections were based on vocalizations alone. On any census, it was unlikely that all birds actually present on the transects were noted. Thus, there was no way to determine absolute densities, and the values reported here should be regarded as minimum relative densities. Transect counts were taken between 07:00 and 10:00. I recorded all birds noted within a 15-m band on either side of a measured trail marked with surveyor's flagging. At first sighting, I recorded the approximate foraging substrate, location and behavior for each bird. Individuals seen flying overhead, such as raptors, were not counted. Birds in the genera *Empidonax* and *Carpodacus* were not identified to species. On the basis of geographic distribution, habitat, appearance, behavior and call notes, I believe the flycatchers were *E. hammondi* and *oberholseri*. The finches certainly were either *C. purpureus*, *cassinii* or both. In order to determine if density estimates or species richness values differed significantly between the transects, I used a paired *t*-test. Significance was defined as having $P < 0.05$.

Willson (1974) characterized foraging guilds according to primary food items, foraging stratum and behavior. I used a similar system of classification, and divided species into feeding guilds using the following criteria: 1) location of foraging: (U) ground-understory, (B) bark, (F) foliage, (V) various; 2) foraging method: (H) hover feeding, (S) sallying, (D) drilling, (G) gleaning surfaces; 3) major foods: (N) nectar, (I) insects, (P) plant material (usually seeds), (O) omnivore. Each species was assigned to a foraging guild based upon a three-letter code; thus, the Yellow-rumped Warbler was in guild FGI (foliage-gleaning insectivore), and the White-headed Woodpecker was in guild BDI (bark-drilling insectivore). Feeding habits were based upon individual food preferences given in Martin et al. (1961). Insect-feeding was defined here as 75% or more insect material (adults or larvae), plant feeding as 75%

or more seeds or other vegetable material, and omnivores exhibited no specific feeding preferences.

Since the transects differed somewhat in size, I multiplied the density estimates for each bird species by conversion factors to determine relative numbers of individuals per hectare. These values are expressed as numbers per 40 ha for comparative purposes. Biomass figures were derived by multiplying these average values by the species' weight in grams. The biomass data for each species were taken from specimens in the Museum of Vertebrate Zoology, University of California, Berkeley. The values used were average breeding season weights of individuals taken from populations nearest the study site. Salt (1957), Karr (1968) and Bock and Lynch (1970) argued for the use of consuming biomass, instead of biomass, in the analysis of food consumption or energy intake by an avifauna. Consuming biomass provides a means of equilibrating the energy demands of large and small birds with differing metabolic rates. These values were calculated in the present study by taking the body weight of each species to the 0.62 exponent, according to the equations of Kendeigh (1970). These figures were then multiplied by the average number of individuals per 40 ha for each species and summed for all foraging guilds. Differences in consuming biomass values were compared using a paired *t*-test. Dominance-diversity curves (Whittaker 1975) based upon consuming biomasses were used to examine the relative importance of all species in these communities.

RESULTS

VEGETATION

In both the mixed conifer and red fir zones, total tree densities and basal areas were greater in the closed-canopy sites (Table 1). Tree species diversity (TSD) values were highest in the mixed conifer forests, although tree species richness was similar for all transects.

As measured by the techniques of MacArthur and Horn (1969), the foliage profiles (Fig. 1) for the two open-canopy forests were similar for all layers except the lowest. The open red fir transect had 0.8 leaves in the lowest interval as compared with 0.4 in the open mixed conifer area. The closed-canopy areas had most of their foliage concentrated in the highest layer (>15 m). Because it had more small trees, and fewer mature ones, the closed mixed conifer site had more foliage in the low canopy (5–15 m) than the closed red fir area.

Percent shading, the summation of foliage from all vegetation layers, was high for all transects (Table 2). Canopy cover varied inversely with understory development (Table 2). The open-canopy forests, with relatively lower coverage of conifer foliage, had higher percent coverage values in the seedling-shrub, and grass-forb layers.

BIRD POPULATIONS

Bird densities were significantly higher ($P < 0.05$) in open-canopy forests, and dur-

TABLE 1.   Tree species composition of mixed-conifer and red fir forests, Placer Co., California.

| | Mixed conifer | | | | Red fir | | | |
| | Open canopy | | Closed canopy | | Open canopy | | Closed canopy | |
Species	D[a]	BA[b]	D	BA	D	BA	D	BA
Western white pine	—	—	—	—	—	—	28	21
Jeffrey pine	84	34	70	29	14	9	—	—
Lodgepole pine	70	16	—	—	14	2	28	3
White fir	364	22	224	36	14	4	14	5
Red fir	—	—	—	—	364	97	546	113
Incense cedar	84	13	630	42	—	—	—	—
Black oak	—	—	56	6	—	—	—	—
Snag	—	—	14	8	14	5	42	—
Total	602	85	994	121	420	117	658	23
TSD[c]	1.10		1.03		0.58		0.68	165

[a] Tree densities, numbers (>10 cm dbh) per hectare.

[b] Total basal areas of trees (m²/ha).

[c] Tree species diversity. $H' = -\sum_{i=1}^{s} p_i \ln p_i$.

ing the post-nesting season (Table 3). I found no significant differences in densities between the mixed conifer and red fir forests. Species richness was significantly higher in open forests, during the post-nesting season and in the mixed conifer zone. Bird species diversity values were highest in open forests, but were quite similar between seasons (Table 3).
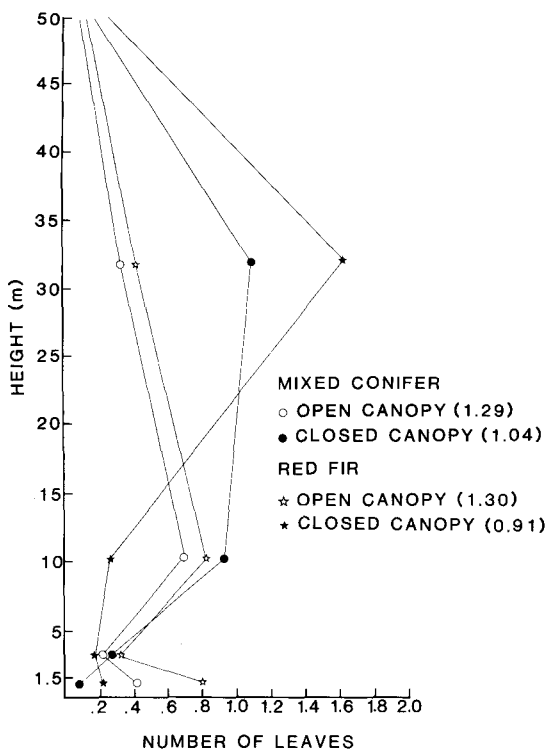
The open-canopy transects, in both the

FIGURE 1. Average foliage profiles for each of the transects. Height intervals were: ground–1.5 m, 1.6–5.0 m, 5.1–15 m, 15.1–>50 m. The numbers in parentheses indicate foliage height diversity values, calculated from the Shannon-Weaver index H'.

mixed conifer and red fir zones, supported a greater consuming biomass of birds than did either of the closed-canopy sites (Table 4). This community pattern was shown primarily by species in three understory guilds (UGI, UGH, UGO), and the air-sallying insectivores (ASI). In the nesting and post-nesting seasons, Hermit Thrushes, *Carpodacus* finches, Dark-eyed Juncos, Chipping Sparrows and Fox Sparrows were relatively common (>5 individuals/40 ha) in the understory of the open mixed conifer transect. The open red fir area also supported large numbers of understory foragers, but *Carpodacus* finches and Chipping Sparrows were not as common. The closed mixed conifer area was almost totally lacking in shrubs, herbs, forbs, or grasses (Table 2), and it supported very few understory species. In this transect, only Dark-eyed Juncos were common, and they frequently were seen foraging in conifers. In the closed red fir site, Hermit Thrushes were observed in occasional patches of shrubs and herbs, but Dark-eyed Juncos were the only ubiquitous understory foragers.

The White-headed Woodpecker was consistently the most common bark-drilling species. Its presence was dependent upon suitable large trees, especially snags, for foraging. Canopy structure and forest type appeared to have little effect upon woodpecker abundances. Birds of the bark-gleaning guild, particularly Red-breasted Nuthatches and Brown Creepers, were abundant in all types of forest.

Numbers of individuals and consuming biomasses of foliage-gleaning insectivores were similar in the four transects. Seven species in this guild were found to be relatively common (>5 individuals/40 ha) in open-canopy forests including Mountain

TABLE 2. Vegetation cover listed as percentages of the total sampling points (120) in each transect.

	Mixed conifer		Red fir	
	Open canopy	Closed canopy	Open canopy	Closed canopy
Percent shading[a]	88.7	97.2	90.1	95.6
Percent cover[b]				
Conifer foliage	67.2	89.1	69.3	86.0
Seedlings and shrubs	17.2	0.1	30.3	14.5
Grass and forbs	28.3	3.0	43.4	7.2

[a] Includes all vegetation layers, data derived from methods of Friend (1961).
[b] Data were derived from methods of MacArthur and Horn (1969).

Chickadees, Golden-crowned Kinglets, Warbling Vireos, Yellow-rumped, Hermit, and Wilson's warblers and Western Tanagers. The closed-canopy areas supported a similar array of foliage gleaners, except that Warbling Vireos and Wilson's Warblers were not as common. Foliage-gleaning insectivores were dependent upon conifer foliage as a foraging substrate, but changes in foliage density appeared to have little influence on abundance patterns for most species.

Air-sallying insectivores including *Empidonax* flycatchers, Western Wood Pewees and Olive-sided Flycatchers were considerably more common in the open forests, as their foraging behavior required exposed perches and unobstructed air space to scan for flying insects. Dense, closed-canopy forests provided relatively few suitable perching sites for these species.

Nectar-feeding species, including Anna's and Rufous hummingbirds, occurred exclusively where the canopy was sufficiently open to support patches of gooseberries or other nectar sources.

Species importance curves (Whittaker 1975) for the nesting bird populations (Fig. 2) were constructed by plotting the abundances of all species in a sample on a logarithmic scale in descending order of rank. Consuming biomass was used because it re-

Table 3. Relative densities (no./40 ha) of bird species in four forest sites in the North Fork of the American River Drainage, Placer Co., California.

			Mixed conifer				Red fir			
			Open canopy		Closed canopy		Open canopy		Closed canopy	
Species	Foraging guild[a]	Body weight (g)	N[b]	PN	N	PN	N	PN	N	PN
Anna's Hummingbird (*Calypte anna*)	VHN	4.2	2	1	—	—	5	3	—	—
Rufous Hummingbird (*Selasphorus rufus*)	VHN	3.9	1	5	—	—	27	41	—	—
Common Flicker†[c] (*Colaptes auratus*)	VGO	159.9	2	3	3	4	2	2	2	4
Pileated Woodpecker (*Dryocopus pileatus*)	BDI	291.6	—	—	2	—	—	—	—	—
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	BDI	50.7	8	13	—	—	1	3	—	—
Hairy Woodpecker† (*Picoides villosus*)	BDI	70.0	4	4	7	5	3	5	1	2
White-headed Woodpecker† (*Picoides albolarvatus*)	BDI	62.2	16.	13	11	14	10	13	11	18
Empidonax flycatchers† (*Empidonax* sp.)	ASI	11.5	11	17	1	1	5	6	3	4
Western Wood Pewee† (*Contopus sordidulus*)	ASI	13.9	9	14	1	—	11	4	3	3
Olive-sided Flycatcher† (*Nuttallornis borealis*)	ASI	33.3	5	5	1	—	7	1	—	—
Steller's Jay† (*Cyanocitta stelleri*)	VGO	107.3	46	38	41	63	37	55	12	22
Mountain Chickadee† (*Parus gambeli*)	FGI	12.3	83	103	75	114	67	109	83	101
White-breasted Nuthatch (*Sitta carolinensis*)	BGI	17.2	10	9	—	9	—	—	1	2

Table 3.   Continued.

Species	Foraging guild[a]	Body weight (g)	Mixed conifer				Red fir			
			Open canopy		Closed canopy		Open canopy		Closed canopy	
			N[b]	PN	N	PN	N	PN	N	PN
Red-breasted Nuthatch† (*Sitta canadensis*)	BGI	10.2	77	116	54	66	21	40	77	94
Brown Creeper† (*Certhia familiaris*)	BGI	7.9	41	45	50	63	17	26	44	66
American Robin† (*Turdus migratorius*)	VGO	80.6	30	21	62	41	59	32	39	35
Hermit Thrush† (*Catharus guttatus*)	UGI	26.3	16	10	—	5	39	26	13	12
Townsend's Solitaire† (*Myadestes townsendi*)	UGI	31.9	5	5	—	2	—	4	—	—
Golden-crowned Kinglet† (*Regulus satrapa*)	FGI	6.0	14	27	47	71	20	33	66	81
Ruby-crowned Kinglet (*Regulus calendula*)	FGI	6.8	2	13	—	7	3	4	—	—
Solitary Vireo (*Vireo solitarius*)	FGI	13.9	—	—	2	8	—	—	—	—
Warbling Vireo† (*Vireo gilvus*)	FGI	12.6	18	10	—	2	11	6	—	—
Orange-crowned Warbler (*Vermivora celata*)	FGI	8.5	1	2	—	3	—	6	—	5
Nashville Warbler† (*Vermivora ruficapilla*)	FGI	8.1	2	3	—	—	2	5	—	—
Yellow Warbler (*Dendroica petechia*)	FGI	9.2	—	1	—	—	1	3	—	2
Yellow-rumped Warbler† (*Dendroica coronata*)	FGI	11.9	32	29	18	32	44	28	27	22
Black-throated Gray Warbler (*Dendroica nigrescens*)	FGI	8.5	—	—	—	2	—	—	—	—
Hermit Warbler† (*Dendroica occidentalis*)	FGI	9.3	20	13	10	4	28	15	13	9
Wilson's Warbler (*Wilsonia pusilla*)	FGI	7.7	5	11	—	2	21	32	—	3
Brown-headed Cowbird (*Molothrus ater*)	VGO	41.0	3	3	—	—	—	—	—	—
Western Tanager† (*Piranga ludoviciana*)	FGI	27.3	13	6	7	9	22	14	10	6
Black-headed Grosbeak (*Pheucticus melanocephalus*)	FGO	43.3	—	—	—	2	—	—	—	—
Evening Grosbeak (*Hesperiphona vespertina*)	FGO	48.7	21	11	—	—	10	5	5	11
Carpodacus finches† (*Carpodacus* spp.)	UGH	28.0	12	6	1	3	4	7	4	2
Pine Grosbeak (*Pinicola enucleator*)	FGO	49.6	—	—	—	—	2	6	—	—
Dark-eyed Junco† (*Junco hyemalis*)	UGH	17.7	123	140	30	44	120	146	70	115
Chipping Sparrow† (*Spizella passerina*)	UGO	12.2	28	19	4	6	4	4	—	—
White-crowned Sparrow (*Zonotrichia leucophrys*)	UGO	29.1	—	8	—	—	—	—	—	—
Fox Sparrow† (*Passerella iliaca*)	UGO	30.1	10	6	5	7	16	11	5	9
Total			670	730	432	588	619	695	489	628***[d]
Species richness			32	34	21	27	30	32	20	23***
Bird species diversity (BSD)			2.87	2.81	2.42	2.57	2.84	2.79	2.41	2.43

[a] Foraging guilds: UGS = understory-gleaning insectivores; UGH = understory-gleaning herbivores; UGO = understory-gleaning omnivores; BDI = bark-drilling insectivores; BGI = bark-gleaning insectivores; FGI = foliage-gleaning insectivores; FGO = foliage-gleaning omnivores; ASI = air-sallying insectivores; VHN = various hovering nectarivores; VGO = various gleaning omnivores.
[b] N = nesting season (17 June–31 July); PN = post-nesting season (1 August–14 September).
[c] † = definite evidence of nesting on at least one of the transects.
[d] Significant ($P < .05$) difference between: *nesting and post-nesting; **mixed conifer and red fir; ***open and closed canopies.

TABLE 4. Consuming biomass totals (grams/40 ha) summed for each foraging guild.

	Mixed conifer				Red fir				
	Open canopy		Closed canopy		Open canopy		Closed canopy		
Guild	N[a]	PN	N	PN	N	PN	N	PN	
Understory-Gleaning Insectivores (UGI)	163	123	—	55	292	228	99	90	**b ***
Understory-Gleaning Herbivores (UGH)	824	884	186	288	744	920	445	686	* ***
Understory-Gleaning Omnivores (UGO)	216	197	60	40	151	105	44	7	** ** ***
Bark-Drilling Insectivores (BDI)	352	364	321	244	190	161	156	269	N.S.
Bark-Gleaning Insectivores (BGI)	528	701	406	559	152	259	485	645	*
Foliage-Gleaning Insectivores (FGI)	883	951	687	1,090	1,016	1,116	850	949	N.S.
Foliage-Gleaning Omnivores (FGO)	238	119	—	25	132	123	52	121	N.S.
Air-Sallying Insectivores (ASI)	146	196	14	6	139	65	27	33	***
Various-Hovering Nectarivores (VHN)	7	12	—	—	75	103	—	—	—c
Various-Gleaning Omnivores (VGO)	1,370	1,102	1,762	1,842	1,605	1,542	860	1,034	N.S.
Total	4,727	4,649	3,436	4,149	4,496	4,622	3,018	3,834	***

[a] N = nesting season, PN = post-nesting season.
[b] Significant ($P < .05$) differences between: *nesting and post-nesting; **mixed conifer and red fir; ***open and closed canopies.
[c] Insufficient data to test the hypothesis.

flects a species' use of food resources more clearly than individual abundance alone (Salt 1957). The relative species consuming biomass values ($-\ln p_i$ consuming biomass) were divided into the following categories: 1–3 common, >3–5 intermediate, >5–8 rare. The closed-canopy forests (2–4) approached a straight line with six or seven common, nine intermediate and four or six rare species. The post-nesting curves (Fig. 3) were similar to the nesting curves, except that more rare species were observed. The dominant species in these closed transects included two generalists, Steller's Jay and American Robin, and a variety of bark- and foliage-gleaners. Only a single understory forager, the Dark-eyed Junco, was common on either of these transects. Generally,

understory- and air-foraging species tended to be uncommon. Transects 1 and 3 were similar in shape during both seasons (Figs. 2 and 3), having fewer common, but more intermediate (>17) species than the closed transects. Almost 60% of the species in the open forests fell into this intermediate category, accounting for higher diversity values for these areas (Table 3). The common species in the open forests tended to be the same as those observed in closed forests, but the intermediate species included many more air, foliage and understory foragers.

DISCUSSION

Willson (1974) found that different sorts of forests with similar foliage profiles did not support similar avian communities. Furthermore, she found that increases in the vertical layering or total volume of foliage did not alter species presence or the total avian biomass of guilds in any predictable
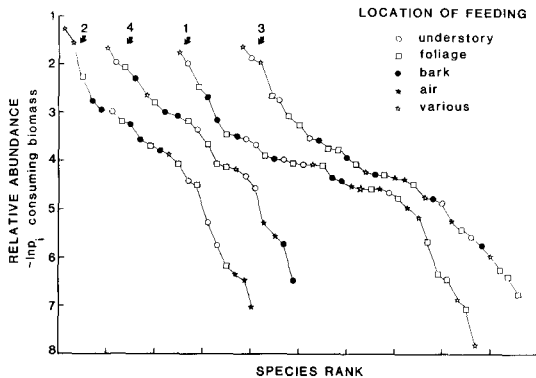

FIGURE 2. Dominance-diversity curves for nesting bird species on the four transects. The points represent the relative abundances of species on a logarithmic scale (ordinate) plotted in sequence from most to least abundant (abscissa). Numbers indicate transect sites: 1) open canopy—mixed conifer, 2) closed canopy—mixed conifer, 3) open canopy—red fir, 4) closed canopy—red fir.
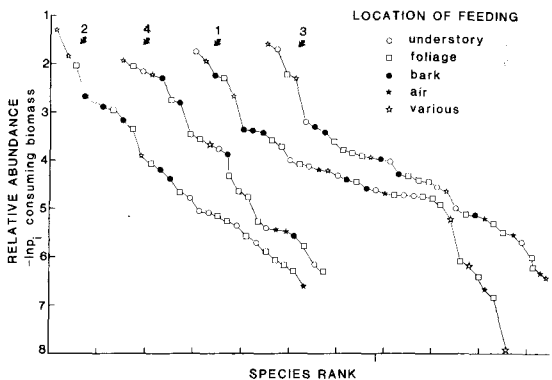

FIGURE 3. Dominance-diversity curves for post-nesting bird species on the four transects. The transect numbers are the same as in Figure 2.

manner. In my study, avian populations in closed-canopy forests differed significantly and predictably from those in the open-canopy areas (Tables 3 and 4). With the exception of the hummingbirds, all guilds were present in each transect. However, in closed-canopy forests, reductions in understory vegetation and forest clearings caused pronounced decreases in three understory guilds as well as in the flycatchers.

My results agree with those of Holmes et al. (1979), that the understory provided a distinct foraging environment, and that certain bird species were highly dependent on it. In closed-canopy forests, guilds contracted but were not eliminated when understory vegetation was lacking. The foliage profiles were nearly identical in the two open-canopy forests, suggesting that these areas offered a similar vertical array of foraging substrates for birds. Foraging guilds reflected this similarity, as the species lists for these two transects were identical with only four exceptions (White-breasted Nuthatches, Brown-headed Cowbirds, Pine Grosbeaks, and White-crowned Sparrows).

MacArthur and MacArthur (1961), MacArthur et al. (1966), Karr (1968) and others have found strong correlations between BSD and FHD, and have suggested that FHD is a good predictor of BSD. Other workers have cast doubt upon the validity of this general relationship (Tomoff 1974, Willson 1974, Roth 1977, Franzreb and Ohmart 1978). In my study, FHD and BSD followed similar trends (Fig. 1 and Table 3), as both were higher in open- than in closed-canopy forests. Generally, my findings were in agreement with Karr and Roth (1971) who predicted low avian diversities in dense, uniform stands of conifers.

Holmes et al. (1979) suggested that FHD is an index to the presence and development of foraging areas from the ground to the top of the canopy. An area with a high FHD value, indicating the presence of foliage in a variety of vertical zones, would have a high BSD because it provides increased foraging opportunities for birds. TSD was not related to BSD in any obvious manner (Tables 1 and 3). It is clear that FHD is only one of many factors (such as food, patch size, climate and elevation) that modify avian diversities in conifer forests of the Sierra Nevada.

The presence of black oaks in the closed mixed-conifer transect (Table 1) was one factor which significantly affected BSD. Solitary Vireos, Yellow, Black-throated Gray, and Wilson's warblers were seen only in

these deciduous trees in this transect. Von Haartman (1971) found that deciduous forests supported more insects than conifer forests, and many workers have observed that deciduous or deciduous-conifer forests have greater bird species richness than do conifer forests alone (Salt 1957, Winternitz 1976, Winkler and Dana 1977). Patches or islands of black oak within the mixed conifer forests added significantly to the vegetational variability on a horizontal plane, creating an edge effect, increasing foraging opportunities for birds. Despite the presence of black oaks in the closed-canopy mixed conifer forest, avian densities, species richness and BSD were lower than for either of the open-canopy transects.

Whittaker (1975) reviewed the uses and interpretations of species importance curves in the analysis of dominance and diversity in communities. In structurally simple habitats, or communities with low species richness, these curves approach a straight line or geometric form. Such communities are dominated by a few abundant species, followed by a continuum of rare ones. Species-rich communities, or non-homogeneous samples from a range of habitats, tend to have similar numbers of common and rare species, and more of intermediate importance. In such communities where diversity is higher, species importance curves approach the lognormal form of Preston (1948). Species importance curves have been used to infer competitive interactions and patterns of niche partitioning in avifaunas (Røv 1975). The shapes of these curves are probably affected by competition for food, but no general agreement exists regarding their theoretical implications or the conclusions that can be drawn from them (Whittaker 1975).

Able and Noon (1976), and Sabo (1980) found that species importance curves for bird populations became increasingly steep along elevational gradients from hardwood to subalpine forests. They indicated that severe environmental conditions may have promoted dominance by a few well-adapted species. All the transects I censused were exposed to similar environmental conditions, but the closed-canopy forests were relatively simple habitats with conifer bark and foliage as primary foraging substrates. Dominance by a few common species, as expressed by the geometric progression, suggested that these areas provided a limited food supply that only a few bird species could use effectively. The open-canopy forests, with greater structural complexity, of-

fered a greater variety of foraging opportunities for birds. These forests were a combination of foliage and bark, as well as understory vegetation and open air space. The greater availability of food permitted greater avian diversity, (with more species of intermediate importance) because there were simply more ways to subdivide the environment.

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