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FORAGING NICHES AND THE STRUCTURE OF FOREST BIRD COMMUNITIES IN CONTRASTING MONTANE HABITATS

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ABSTRACT.—The foraging niche patterns of woodpeckers and insectivorous passerines in two montane forests in New Hampshire were characterized and compared in separate and joint multivariate analyses. Comparisons of these two communities occurring in contrasting environments help to identify and assess the relative importance of the factors determining their species compositions and niche structures. The most important of these are shown to be the interrelated effects of climate, habitat physiognomy, competitive interactions, food resource base, wintering habits, and biogeographic origin of the avifaunas. Subalpine birds had lower and more variable population densities, plus lower niche diversity but greater niche overlap than birds of northern hardwoods. Niche ordinations showed that canopy height and foraging substrate were important gradients in the organization of both communities. We conclude that the patterns of bird community structure in these particular habitats are responses to diverse evolutionary and ecological events that determine individual species' patterns of habitat selection and resource exploitation.

Current understanding of niche partitioning and guild organization in bird communities has been largely derived either from studies of one group of bird species occupying one habitat (e.g., Hartley 1953, MacArthur 1958, Root 1967, Morse 1968, Wiens 1969, Feinsinger 1976, Wolf et al. 1976, Eckhardt 1979) or from comparisons of bird community patterns in similar habitat types (e.g., Cody 1968, Morse 1971, 1976b, Diamond 1975, Pearson 1975, 1977, Karr 1976b, Rabenold 1978, Noon and Able 1978). The few studies that have compared communities in contrasting habitats have generally focused on bird distributions along environmental gradients (e.g., Johnston and Odum 1956, Bond 1957, Terborgh 1971, 1977, Able and Noon 1976, but cf. Karr 1971, 1976a). Furthermore, most studies have neither considered quantitative differences in avian niche responses to the resource structure of different habitats, nor used the contrasting environments to evaluate the relative importance of the factors influencing those communities.

In this paper we analyze the niche structure, food resource relationships, and phylogenetic affinities of the woodpeckers and insectivorous passerines in two distinct but nearby forest habitats and use this comparative approach to identify and assess the factors that determine the observed bird community patterns. To do this we quantified the foraging behavior and habitat use of syntopic breeding birds in two forest systems along an elevational gradient in the White Mountains of New Hampshire. One bird community occurs in the relatively tall, broad-leaved northern hardwoods forests at 600 m elevation and is composed of bird species most similar to those found in more southerly deciduous forests (Holmes and Sturges 1975, Holmes et al. 1979). The other occurs in largely coniferous subalpine forests at 850 to 1,400 m elevation and is comprised primarily of boreal species (Sabo 1980). Moreover, since environmental adversity increases with elevation in these mountains, the subalpine community is subject to greater climatic instability and seasonality. Here we consider how these differences in habitat structure, environmental factors, and species origins affect the species compositions, guild configurations, and species niche relationships of these two bird communities. In addition, the occurrence of several species in both communities offers an opportunity for a "natural experiment" to

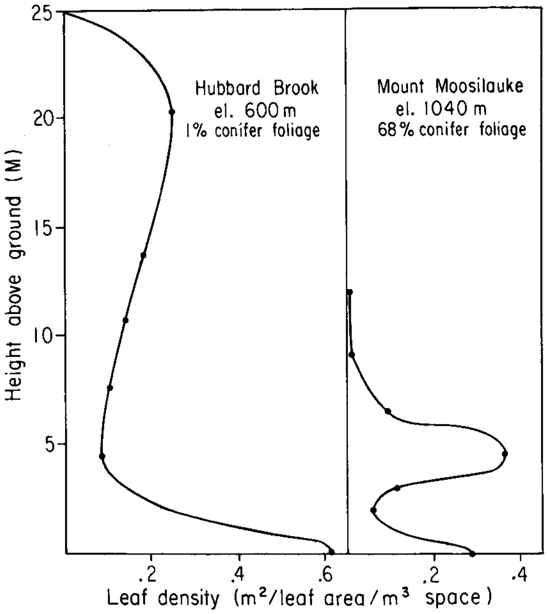

FIGURE 1. Foliage height profiles of northern hardwoods and subalpine sites.

examine the effects of habitat and community interactions on their niches.

STUDY SITES

The northern hardwood community was studied on a 10-ha plot at elevation 600 m, adjacent to watershed 6 of the Hubbard Brook Experimental Forest, White Mountains National Forest. Sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), and yellow birch (*Betula lutea*) are the dominant trees, with some red spruce (*Picea rubens*) sparsely interspersed (see Holmes and Sturges 1975 for details). The subalpine community was studied on Mount Moosilauke, 8 km northwest of the Hubbard Brook site; most observations were made on a 50-ha tract of relatively homogeneous forest in a broad valley of the upper reaches of the Baker River watershed at 950–1,150 m elevation. Subalpine dominant trees are balsam fir (*Abies balsamea*) and red spruce, with substantial numbers of paper birch (*Betula papyrifera*) and some mountain ash (*Sorbus americana*) (see Sabo 1980 for details). Comparing the climate at 1,000 m and 600 m elevation, the subalpine is colder (12°C vs. 16°C mean June temperature), wetter (150 vs. 120 cm annual precipitation), and windier (30 vs. 12 km/h mean above-canopy wind speed). The northern hardwoods canopy averages 22 m in height, 90% coverage, whereas the subalpine canopy averages 7 m height, 60% coverage. The average diameter (DBH) of the live trees greater than 2.5 cm DBH is 16 cm in the northern hardwoods, 10 cm in the subalpine zone; the lower community also has fewer dead trees (5% vs. 14% basal area percentage). Foliage volume is about 1% coniferous at the northern hardwood site, 68% at the subalpine site. Foliage height profiles for the two areas are shown in Figure 1. Both sites have been logged in this century (ca. 1909–1939), but subalpine regeneration appears slower, and more dead woody brush has accumulated on the subalpine forest floor than in the northern hardwoods.

METHODS

BIRD DENSITIES

Both studies relied on fixed study plots and modifications of Kendeigh's (1944) spot-map method to determine bird densities. All censuses were conducted during the main breeding season, late May to mid-July, in the years 1976 to 1978. The northern hardwood populations were monitored on the 10-ha plot using (1) standardized timed censuses, twice weekly between 06:00 and 08:00 with two observers each time, (2) mist-netting and color-banding, once or twice weekly using 40 mist-nets, and (3) systematic observations and territory mapping (see Holmes and Sturges 1975 for further details). Subalpine populations were censused on a 5-ha plot centered in the 50-ha tract using (1) standardized time censuses, once to twice weekly between 05:00 and 09:00 with a single observer each time, (2) mist-netting and color-banding once weekly during 1977 using five mist-nets, in order to evaluate census accuracy, and (3) systematic observations and territory mapping. Subalpine populations were also censused (but not mist-netted) each year on a supplemental 5-ha plot located on the exposed forested ridge above the 50-ha tract at 1,250 m elevation. Over 20 h of observation time were accumulated each season for each plot, with boundaries and adjacent areas closely inspected for bird territories lying partially in the plot. Four additional 5-ha plots were also censused (but not mist-netted) in 1977 in other sections of the Baker River watershed to characterize variation in bird densities across the subalpine landscape.

Bird densities were averaged over the 1976–1978 seasons. To evaluate the relative stability of populations, the coefficient of variation ($CV = SD/\bar{x}$) was computed for the 1976–1978 seasons. The coefficient of variation is equivalent to the standard deviation of a population with a mean density of unity. When comparing three years, it reaches an upper limit of $\sqrt{3}$ for species present in only a single year.

FORAGING BEHAVIOR

Both studies sought foraging birds and recorded data on a given bird for as long as it was in sight. Data for the northern hardwoods community were taken exclusively on the 10-ha study site. About 70% of the subalpine foraging data were taken on the 50-ha tract, with the remainder from adjacent areas on Mt. Moosilauke of similar habitat between 850 and 1,200 m elevation. Data on foraging maneuvers were recorded by bird species, time of day, type of maneuver, substrate to which the maneuver was directed, height above ground, plant species, and, when in a tree, whether it was along the inner (proximal) or outer (distal) half of the crown. Although techniques used in the studies were standardized in most respects, minor differences in foraging maneuvers required some adjustments in the subalpine data set (Sabo 1980): (1) "hawk" and "hover" were combined to equal the "hover" of Holmes et al. (1979), (2) for branch and trunk substrate classes, "hawk" and "hover" were included in "glean" and (3) "twig-peck" was merged with "twig-glean."

For this comparative analysis, foraging behavior was quantified by 22 variables that fell into four groups (see Table 3): (1) 12 maneuver-substrate combinations, with frequencies adding to unity; (2) two positions for tree crown maneuvers; (3) three foliage variables; and (4) five height strata, with frequencies adding to unity. To compare the two communities in a joint ordination (see below), we had to make two adjustments to compensate for differences in physiognomy and vegetative composition. First, canopy trees in the northern hardwoods average three times taller than those in the subalpine zone. As noted in other studies (Cody 1974, Hutto 1981), some bird species appear to scale the vertical foraging component to relative foliage strata. Therefore, we categorized the foraging heights into five strata for each community: (1) forest floor; (2) shrub layer, from just above the ground level to 1.5 m in both forests; (3) sapling layer, 1.5–7.5 m in the northern hardwoods and 1.5–4.5 m in the subalpine forest; (4) the mid-canopy, 7.5–15 m in the northern hardwoods and 4.5–7.5 in the subalpine forest; and (5) upper canopy, the foliage above 15 m in the northern hardwoods, and above 7.5 m in the subalpine forest. Second, the relative use of coniferous vs. deciduous foliage seems primarily a response to the relative amounts of these two foliage types (compare Table 3 with Fig. 1). These two variables dominated the preliminary joint ordinations (see below), producing separate clusters for the two communities and were subsequently excluded from the data set in order to compare foraging techniques in the two communities.

Multivariate analyses were used to reduce this complex, redundant, data structure to axes expressing the major underlying relationships. Each community was ordinated separately, and the axes of these ordinations compared to examine whether foraging was patterned similarly in the two communities. Then, the data matrices for the two communities were combined and ordinated together (=joint ordination) so that the ecological relations between species in different communities could be examined. The technique used, detrended correspondence analyses (DCA), is a form of principal components analysis (PCA) modified to handle moderate outliers and distortion on higher axes. Mathematical derivation is given in Hill and Gauch (1980), and a computer implementation in FORTRAN has been written by Hill (1979). DCA has given better recovery of synthetic data matrices than PCA, reciprocal averaging, or nonmetric multidimensional scaling (Hill and Gauch, unpubl. data). It yields axes that are homologous to PCA components that are defined by eigenvectors of birds and foraging variables; these represent the major trends of variation in foraging behavior. Unlike other eigenanalyses, DCA axes are scaled in SD units (mean species standard deviations along axes) as well as eigenvalues. Correlations of foraging variables to the axes are used to give biological interpretations to the axes.

NICHE MEASUREMENTS

Niche overlap and niche breadth were measured on the foraging data set in order to compare the two communities. To simplify the problem of redundancy among the variables, two subsets were considered: foraging manner as characterized by the 12 substrate-maneuver combinations, and foraging heights as characterized by the five scaled height intervals. Variables of both crown position and foliage type were not considered because (1) tree crown position was often correlated with certain foraging styles (e.g., woodpecking with proximal positions, and sallying with distal ones), (2) the foliage-type categories cover several tree species exclusive to a particular community, and (3) both groups of variables apply only to tree-directed maneuvers. On the other hand, since foraging height and foraging maneuver are mostly independent (the exception being terrestrial maneuvers), composite measures giving overall breadth or overlap can be estimated as the product of the height and maneuver measurements. For niche overlap between a species pair we chose the Proportional Similarity (PS),

$$\mathrm{PS} = \sum_i \min(p_i, q_i),$$

i.e., the actual area of intersection between two frequency distributions p and q. For niche breadth we took the Shannon-Weiner diversity index,

$$H' = -\sum_i p_i \ln p_i,$$

as a measure of dispersion within the 12 maneuver and five height categories. Although measurements that are calculated from the community-wide resource distribution have many advantages (cf. Colwell and Futuyma 1971, Feinsinger et al. 1981), they may not be appropriate when comparing two contrasting communities whose food resource distributions are not known independently of the foraging data.

RESULTS AND DISCUSSION

BIRD SPECIES COMPOSITION AND ABUNDANCE

We found 22 principal species of insectivorous birds in the northern hardwoods site and 20 in the subalpine site (Table 1). The percent similarities between the communities calculated from densities were 19.9% at the species level and 38.6% at the genus level. Six species occurred in both communities: Winter Wren, Swainson's Thrush, Solitary Vireo, Black-throated Green Warbler, American Redstart, and Dark-eyed Junco. Several other species occurred sporadically in both communities or at densities too low for us to measure. These will be discussed in a later section.

Woodpeckers were notably rare in the subalpine zone (Table 1). None of the woodpeckers characteristic of the northern hardwoods was found breeding in the subalpine sites on Moosilauke, but Black-backed [Three-toed] Woodpeckers (*Picoides arcticus*) bred in some well-timbered subalpine areas with numerous snags. The species composition also reflects the foliage of the two communities: kinglets, highly dependent on conifers, were absent from the northern hardwoods, and the *Dendroica* warblers, many specializing on conifers, had fewer species and lower densities in the northern hardwoods. Also, groups with more tropical and warm-temperate distributions ("centers of radiation"), such as thrushes, vireos, and tanagers, were commoner and had more species in the northern hardwoods (see below).

The northern hardwoods supported greater bird populations than the subalpine zone (178 birds/10-ha as compared to 110 birds/10-ha in the subalpine valley and 62 birds/10-ha on the subalpine ridge). The four additional subalpine plots also had low bird densities ($\bar{x}$ = 114 ± 41 SD birds/10-ha). Although this difference might have arisen partly from the more intense censusing effort in the northern hardwoods, it is consistent with other studies comparing bird densities in temperate deciduous and coniferous forest (Udvardy 1957). The community in the subalpine zone was dominated by fewer species than that in the northern hardwoods, as indicated by Simpson index ($C = \Sigma P_i^2$) values of 0.180–0.183 for the subalpine plots versus 0.113 for the northern hardwoods.

Bird populations appeared to fluctuate annually more in the subalpine forest than in the northern hardwoods (Table 2). The mean coefficient of variation (CV) for the 22 northern hardwood species was 0.45 ± 0.42 SD, for the 20 subalpine valley species 0.82 ± 0.56 SD, and for the 13 subalpine ridge species 0.19 ± 0.54 SD. The northern hardwoods CV was significantly less than either subalpine CV (Mann-Whitney U-test, $t_U = 2.45$ and 2.31, $P < .05$). The greater yearly fluctuation in the subalpine populations was also indicated by the number of species absent from the plots for one or two of the three seasons. Of the 22 northern hardwood species, two were absent one year, and only one was absent in two years (Black-capped Chickadee). Of the 20 subalpine valley species, five were absent one year, and four were absent two years (Red-breasted Nuthatch, Ruby-crowned Kinglet, Solitary Vireo, and Bay-breasted Warbler). Of the 13 subalpine ridge species, three were absent one year, and three were absent two years (Ruby-crowned Kinglet, Magnolia Warbler, and Purple Finch). The northern hardwoods thus had a greater proportion of "full-time" species than both subalpine areas ($\chi^2 = 5.05$ and 4.52, $P < .05$). While the differences in CVs between the northern hardwood and subalpine sites could conceivably be attributed to different plot sizes and census procedures, given the intensity of our study, it is unlikely that a species breeding on or adjacent to any plot was completely overlooked.

The mean CV did not differ between the subalpine valley and subalpine ridge sites, primarily because a number of "part-time" species at the valley site contributed high CV values. However, when only the 13 species occurring at both sites were analyzed, we found that populations in the subalpine valley fluctuated less. The greater exposure of the ridge may make it a poorer quality habitat for breeding than the subalpine valley. Since these birds are mostly migratory and redistribute themselves across the landscape each breeding season, they may prefer sites like the valley, leaving the ridge for population overflow. Variation in population density between the sites (e.g., the White-throated Sparrow was common on the ridge

TABLE 1. Principal insectivorous birds breeding in the northern hardwoods at Hubbard Brook and in the subalpine sites on Mt. Moosilauke, N.H.

Code	Species	Live weight (g)	Foraging height (m) ($\bar{x}$ ± SD)	Conifer use (%)	General foraging pattern*	Sample size** (*n*)
		Northern Hardwoods Community				
YBS	Yellow-bellied Sapsucker (*Sphyrapicus varius*)	48.3	10.3 ± 4.2	0	B-P	169
HWP	Hairy Woodpecker (*Picoides villosus*)	66.9	9.8 ± 3.4	0	B-P	121
DWP	Downy Woodpecker (*P. pubescens*)	26.7	10.8 ± 4.8	0	B-P	189
LF	Least Flycatcher (*Empidonax minimus*)	10.5	11.1 ± 5.2	0	C-H/F	609
BLC	Black-capped Chickadee (*Parus atricapillus*)	11.5	12.7 ± 5.3	1	C-Gl	451
WBN	White-breasted Nuthatch (*Sitta carolinensis*)	21.0	12.0 ± 4.8	2	B-Gl	285
WW	Winter Wren (*Troglodytes troglodytes*)	9.2	1.7 ± 1.1	3	S-Gl, G-Gl	243
WT	Wood Thrush (*Hylocichla mustelina*)	49.0	0.2 ± 1.0	0	G-P	193
HT	Hermit Thrush (*Catharus guttatus*)	30.0	2.5 ± 3.9	0	G-Gl, S-H/Gl	177
ST	Swainson's Thrush (*C. ustulatus*)	30.8	2.7 ± 5.2	1	G-Gl, S-H/Gl	344
VT	Veery (*C. fuscescens*)	31.9	0.6 ± 1.4	0	G-Gl	106
SV	Solitary Vireo (*Vireo solitarius*)	16.4	10.5 ± 4.5	14	B-Gl/H, C-Gl	114
REV	Red-eyed Vireo (*V. olivaceus*)	17.6	11.5 ± 4.8	1	C-H/Gl	1,719
PV	Philadelphia Vireo (*V. philadelphicus*)	12.1	14.4 ± 6.5	1	C-H/Gl	628
BLW	Black-throated Blue Warbler (*Dendroica caerulescens*)	9.9	5.8 ± 4.1	2	S-H/Gl	193
GW	Black-throated Green Warbler (*D. virens*)	9.1	13.9 ± 4.8	7	C-Gl/H	587
BNW	Blackburnian Warbler (*D. fusca*)	10.4	15.0 ± 4.2	18	C-Gl/H	570
OB	Ovenbird (*Seiurus aurocapillus*)	19.5	0.2 ± 0.9	2	G-Gl	404
ARS	American Redstart (*Setophaga ruticilla*)	8.2	11.0 ± 4.8	1	C-H	1,233
TAN	Scarlet Tanager (*Piranga olivacea*)	28.1	12.8 ± 4.9	3	C-H/F	207
RBG	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	43.9	11.4 ± 5.4	1	C-Gl/H	378
J	Dark-eyed Junco (*Junco hyemalis*)	19.8	1.9 ± 3.2	3	S-Gl, G-Gl	375
		Subalpine Community				
YBF	Yellow-bellied Flycatcher (*Empidonax flaviventris*)	11.8	4.6 ± 1.8	42	C-H	361
BRC	Boreal Chickadee (*Parus hudsonicus*)	10.2	5.0 ± 2.8	82	C-Gl, S-Gl	272
RBN	Red-breasted Nuthatch (*Sitta canadensis*)	11.0	7.0 ± 3.3	49	B-P, C-Gl	640
WW	Winter Wren	9.2	0.2 ± 0.5	6	G-Gl/P	286
ST	Swainson's Thrush	30.8	1.4 ± 1.9	12	G-Gl, S-Gl/H	282
GCT	Gray-cheeked Thrush (*Catharus minimus*)	27.5	0.4 ± 0.7	26	G-P/Gl	140
GK	Golden-crowned Kinglet (*Regulus satrapa*)	6.8	6.0 ± 3.0	94	C-Gl/H	1,217
RK	Ruby-crowned Kinglet (*R. calendula*)	7.0	7.8 ± 2.3	99	C-Gl/H	272
SV	Solitary Vireo	16.4	6.6 ± 2.0	58	C-Gl, B-Gl	179
NVW	Nashville Warbler (*Vermivora ruficapilla*)	9.0	4.8 ± 2.4	45	C-Gl/H	211
MGW	Magnolia Warbler (*Dendroica magnolia*)	9.2	4.6 ± 2.9	72	C-Gl, S-Gl	682
MRW	Yellow-rumped Warbler (*D. coronata*)	12.1	5.5 ± 2.7	60	C-Gl/H, S-Gl	1,043
GW	Black-throated Green Warbler	9.1	6.2 ± 2.0	43	C-Gl/H	1,242
BYW	Bay-breasted Warbler (*D. castanea*)	13.0	6.7 ± 1.7	40	C-Gl	753
BPW	Blackpoll Warbler (*D. striata*)	12.8	5.1 ± 2.3	54	C-Gl	2,160
CNW	Canada Warbler (*Wilsonia canadensis*)	10.5	3.8 ± 1.4	36	S, C-Gl/H	884
ARS	American Redstart	8.2	4.2 ± 1.7	9	C-H, S-H/Gl	1,024
PFN	Purple Finch (*Carpodacus purpureus*)	26.8	6.0 ± 2.1	22	C-Gl	228
J	Dark-eyed Junco	19.8	3.2 ± 3.0	58	S-Gl, G-P	684
WTSP	White-throated Sparrow (*Zonotrichia albicollis*)	26.8	2.0 ± 2.2	37	G-P, S-Gl	1,058

* Major foraging patterns: strata (C = canopy, S = shrub, G = ground, B = bark); foraging method (Gl = gleaning, P = probing or pecking, H = hovering, F = flycatching associated with foliage).

** Sample size for numbers of foraging maneuvers observed and for foraging heights.

TABLE 2. Mean population densities (birds/10 ha) and coefficients of variation for principal insectivorous species. Data for 1976–1978 breeding seasons. Main study site for the subalpine community was the valley site.

Species	Northern hardwoods		Subalpine valley		Subalpine ridge	
	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV
Yellow-bellied Sapsucker	4.3	0.27	—	—	—	—
Hairy Woodpecker	2.3	0.25	—	—	—	—
Downy Woodpecker	3.0	0.17	—	—	—	—
Yellow-bellied Flycatcher	—	—	6.7	0.35	5.3	0.43
Least Flycatcher	28.0	0.21	—	—	—	—
Black-capped Chickadee	0.7	1.73	—	—	—	—
Boreal Chickadee	—	—	0.9	0.93	0.5	1.08
White-breasted Nuthatch	2.3	0.33	—	—	—	—
Red-breasted Nuthatch	—	—	0.3	1.73	—	—
Winter Wren	2.0	1.32	5.7	0.37	—	—
Wood Thrush	7.0	0.29	—	—	—	—
Hermit Thrush	3.5	0.52	—	—	—	—
Swainson's Thrush	5.3	0.29	7.5	0.07	2.1	0.94
Gray-cheeked Thrush	—	—	3.2	0.33	2.0	0.50
Veery	3.2	0.24	—	—	—	—
Golden-crowned Kinglet	—	—	1.0	1.00	3.7	1.10
Ruby-crowned Kinglet	—	—	0.2	1.73	0.3	1.73
Solitary Vireo	2.5	0.72	0.3	1.73	—	—
Red-eyed Vireo	25.0	0.32	—	—	—	—
Philadelphia Vireo	3.0	0.33	—	—	—	—
Nashville Warbler	—	—	3.2	0.63	2.3	0.89
Magnolia Warbler	—	—	1.3	1.15	0.3	1.73
Black-throated Blue Warbler	11.2	0.07	—	—	—	—
Yellow-rumped Warbler	—	—	3.0	0.88	7.7	0.33
Black-throated Green Warbler	7.5	0.07	7.3	0.16	—	—
Blackburnian Warbler	2.0	0.50	—	—	—	—
Bay-breasted Warbler	—	—	0.3	1.73	—	—
Blackpoll Warbler	—	—	42.3	0.26	18.3	0.33
Ovenbird	13.5	0.35	—	—	—	—
Canada Warbler	—	—	6.0	1.00	—	—
American Redstart	39.5	0.16	10.7	0.69	—	—
Scarlet Tanager	3.0	0.44	—	—	—	—
Rose-breasted Grosbeak	5.3	0.29	—	—	—	—
Purple Finch	—	—	1.0	1.00	0.3	1.73
Dark-eyed Junco	2.7	1.15	4.3	0.33	4.2	0.46
White-throated Sparrow	—	—	4.3	0.35	15.0	0.58

but also fluctuated relatively more there) may also reflect the quantity of suitable habitat (open brush and edge is rarer on the valley site than on the ridge). The one species with the reverse pattern, the Yellow-rumped Warbler, not only had higher densities on the ridge site, but also was the most subordinate species in the subalpine warbler dominance hierarchy (see below). Possibly these warblers selected sites that were lower in densities of Black-throated Green and Magnolia warblers, thereby accounting for its distribution pattern.

We gained additional perspective on the nature of the population fluctuations by examining the patterns of the six species found in both the northern hardwoods and subalpine valley study plots. Here the CVs were not uniformly higher in the subalpine sites (Table 2); instead, the pattern appeared to reflect the habitat preferences of the species. We arranged the six species by their relative densities in the two communities, from those much commoner in the northern hardwoods (Solitary Vireo, American Redstart), through the Black-throated Green Warbler with approximately equal abundances in both communities, to those commoner in the subalpine forests (Swainson's Thrush, Winter Wren, and Dark-eyed Junco). These density trends correlated with the species' elevational distribution. The mean elevation of occurrence of a species, as determined in a survey of the White Mountains (for data, see Sabo 1980), may be used as a general index to the elevational preference of the species. In this case, the ratio of subalpine density to northern hardwood density, used as a relative index of subalpine preference, was correlated with the species' mean elevation (Spearman's $r = 0.83$, $P < .05$, $n = 6$). Moreover, all six species had higher CVs in the community where they had lower densities. These patterns agree with the general notion that populations fluctuate less in areas that are more "favorable." If the population response to a habitat gradient is pictured as a bell-shaped curve, then our results suggest that the demes

TABLE 3. Niche variables describing bird communities by foraging behavior: A. Community-wide unweighted averages with standard deviations of the frequencies of foraging maneuvers by species. B. Results of detrended correspondence analyses (DCA): eigenvectors (EV) and correlations with niche variables (r_n).

	A. Community averages				B. DCA ordination and correlations			
	Northern hardwoods		Subalpine		Axis I		Axis II	
Niche variable	Mean	SD	Mean	SD	EV	r_n	EV	r_n
Substrate-maneuver combinations (adding to unity for each species)								
Aerial sally	.080	.079	.013	.042	72	−.111	43	−.124
Leaf glean	.172	.159	.354	.172	47	−.492	15	−.649
Leaf hover	.264	.216	.181	.130	74	−.195	15	−.553
Twig glean	.017	.030	.203	.137	54	−.242	28	−.246
Twig hover	.003	.005	.043	.031	43	−.286	4	−.380
Branch peck	.034	.074	.012	.022	9	−.263	257	.797
Branch glean	.056	.066	.021	.022	29	−.347	121	.436
Trunk peck	.084	.194	.026	.079	0	−.259	280	.788
Trunk glean	.107	.129	.011	.025	66	−.128	181	.638
Litter peck	.071	.163	.064	.126	313	.750	94	−.049
Litter glean	.095	.157	.038	.082	304	.816	100	.001
Fallen log maneuvers	.015	.026	.035	.141	362	.492	123	.036
Crown position variables (adding to total fraction of maneuvers in trees)								
Proximal to trunk	.466	.342	.438	.160	43	−.652	99	.817
Distal to trunk	.281	.293	.412	.174	33	−.627	0	−.914
Foliage variables*								
Conifer foliage	.026	.047	.473	.260	*	−.353	*	−.343
Broadleaf foliage	.765	.302	.361	.265	*	−.513	*	.286
Herb foliage	.027	.048	.014	.038	262	.607	101	.042
Height strata (adding to unity for each species)								
Ground stratum	.222	.330	.132	.252	311	.969	105	.084
Shrub stratum	.131	.153	.065	.078	192	.565	105	.193
Sapling stratum**	.218	.154	.315	.190	50	−.496	76	.245
Mid-canopy stratum**	.331	.240	.343	.199	18	−.877	50	−.129
Upper canopy stratum**	.097	.125	.146	.128	7	−.616	6	−.502

* Conifer and broadleaf foliage variables not included in multivariate analyses.

** Actual height of strata varied between communities to account for vegetation configuration (see Methods, "Foraging Behavior" for descriptions).

lying towards the tails of the distribution will experience greater relative fluctuations.

FORAGING BEHAVIOR

Univariate comparisons between communities. The means and standard deviations for the foraging niche characters of birds in the northern hardwood and subalpine communities, unweighted by relative abundances of species, are given in Table 3. In both areas, birds chiefly obtained arthropods from leaves by gleaning and hovering, and made less use of branches, trunks, and the forest floor litter. Their use of the height strata was comparable for the two communities when these categories were scaled to forest stature.

Some differences between the community means may be attributed to habitat structure. Broadleaf or conifer foliage use would be strongly correlated with the habitat's plant species composition and structure. Some foraging maneuvers were more frequent in the northern hardwoods because of the more open and larger-leaved broadleaf canopy, where insects on leaf tips could not be reached by a stationary bird from the twig, where sufficient room existed for frequent sallies and hovers, and where trunks and branches were readily accessible. This may account for the more frequent use in the northern hardwoods of aerial sallying ($t = 3.47$, $P < .002$, $n = 42$ species unless otherwise indicated), leaf hovering ($t = 2.02$, $P = .05$, $n = 39$ passerine species), branch and trunk maneuvers ($t = 7.0$, $P \ll .001$), and broadleaf use ($t = 4.59$, $P < .001$). Similarly the more frequent occurrence of leaf gleaning ($t = 3.57$, $P < .001$), twig maneuvers ($t = 7.2$, $P \ll .001$) and conifer use ($t = 7.6$, $P \ll .001$) in the subalpine zone may have resulted from the dense conifer canopy, where birds could reach insect prey by gleaning, and where narrow twigs formed a large fraction of tree crown volume.

Comparison of separate community ordinations. Independent ordinations using detrended correspondence analysis (DCA) were performed on the northern hardwoods and subalpine data sets in order to compare patterns of foraging within each community (Fig. 2).

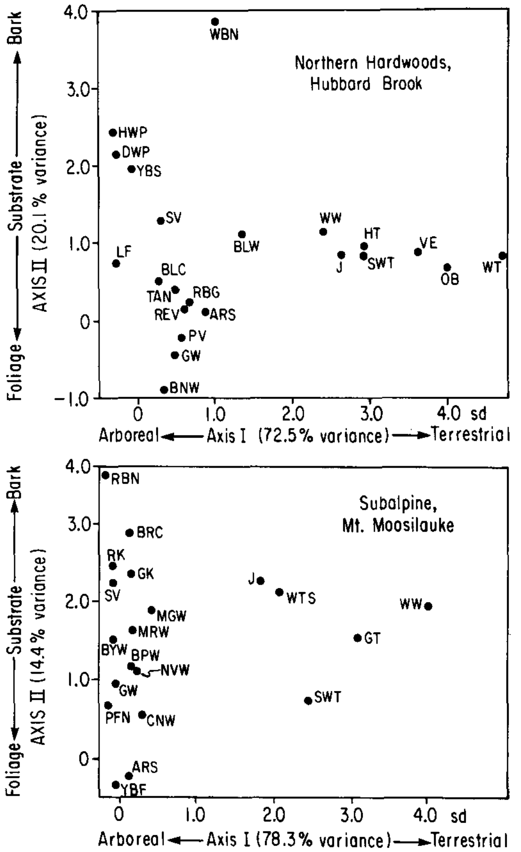

FIGURE 2. Species ordinations for northern hardwoods and subalpine communities using detrended correspondence analyses (DCA); both to same scale. In both graphs axis I corresponds to a terrestrial/arboreal foraging gradient, and axis II to a gradient from foliage to bark substrate use. Species acronyms listed in Table 1.

Axis I of the northern hardwoods community accounted for 72.5% of the variance and had a length equivalent to 3.85 standard deviations of species response. This axis described the terrestrial/arboreal niche division, left to right, suggesting the stem of a "T" ending in the ground-feeding Wood Thrush. Axis II (20.1% of the variance with a length of 2.38 standard deviations) arranged canopy species along the head of the "T" from proximal, bark-foraging niches above, to distal foliage-gleaning below. Axis III (4.9% of the variance and 1.62 standard deviations) portrayed an indistinct foraging method gradient from aerial flycatching and leaf-hovering by the Least Flycatcher and American Redstart to leaf- and twig-gleaning by the Solitary Vireo, Black-capped Chickadee, and Blackburnian Warbler. Although DCA is not designed to classify guild structure, it suggests the pattern of food exploitation (terrestrial foraging, bark-foraging, generalized canopy-feeding, canopy-gleaning) given by cluster analysis for the same community (Holmes et al. 1979). In this broadleaf community only two species could be considered relative specialists on conifer foliage, the Solitary Vireo and Blackburnian Warbler (Table 1; see also Holmes and Robinson 1981).

In the subalpine community, axis I accounted for 78.3% of the variance and represented 3.91 standard deviations of species response. It again described a terrestrial/arboreal niche division. Axis II (14.4% of the variance and 3.36 standard deviations) described a proximal-to-distal gradient from the Red-breasted Nuthatch's bark-pecking to aerial flycatching and leaf-hovering by the Yellow-bellied Flycatcher and American Redstart. While the proximal end of this gradient was shortened by the absence of woodpeckers, the distal end was extended by the use of open air between tree crowns for flycatching and hovering. Axis III of the subalpine (4.2% of the variance and 1.82 standard deviations) was complex and did not correspond to axis III in the hardwoods. It expressed the Solitary Vireo's branch-gleaning habit at one end, and gleaning and hovering on a variety of unrelated substrates by the thrushes and kinglets at the other.

The two ordinations show the same basic "T" structure, though with different lengths of the second axis and somewhat different representations of guilds. The food supply may be more finely subdivided in the subalpine canopy than in the northern hardwoods, as suggested by the closer and more even spacing of species on the second axis and the greater length of this axis in the subalpine. This is probably due to the larger number of species that feed in the foliage, using a greater range of foliage substrates (conifer to broadleaf) in the subalpine forest. Also, more congeneric species occur in the subalpine community, particularly the *Dendroica* warblers.

Joint ordination of both communities. The ordination of the combined northern hardwoods and subalpine communities using detrended correspondence analysis (DCA) shows the ecological position of the birds of one community in relation to those of the other (Fig. 3). The eigenvectors and their correlations with the niche variables for the DCA axes are the formal summary of the major relations within the data set (Table 3). The axes found in ordinating individual communities still dominate, with axis I arranging arboreal and terrestrial niches (and corresponding maneuvers) along a height gradient, and axis II structuring arboreal niches along a substrate gradient from fine distal leaves through heavy proximal trunks.

Axis I accounted for 62.7% of the variance, with a length of 3.62 standard deviations of

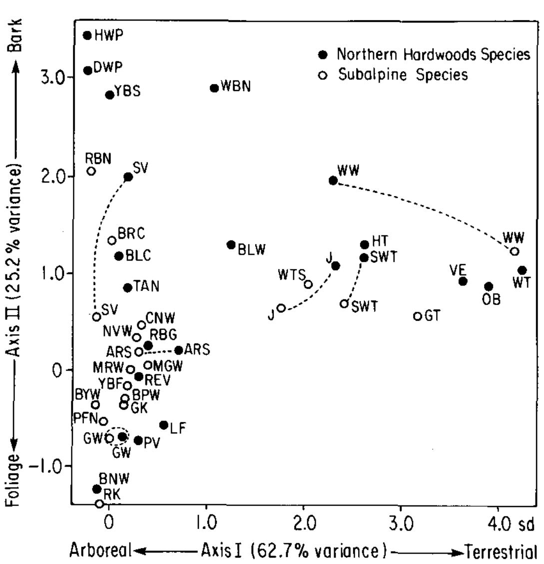

FIGURE 3. Position of 36 bird species along first two DCA niche axes in joint ordination. Axis I represents an arboreal to terrestrial gradient and accounts for 63% of the variance. Axis II represents a gradient from foliage to bark substrate use, accounting for 25% of the variance. Dotted lines connect the two positions for those species occurring in both communities. Species acronyms listed in Table 1.

species response. Seven northern hardwood and five subalpine species had terrestrial foraging patterns. Within each community the species graded from the arboreal niches to more terrestrial ones; the division between these groups seemed to lie at the shrub layer (ca. 1.5 m height), with terrestrial species using lower shrubs, herbs, litter, and fallen logs. In the northern hardwoods, the Black-throated Blue Warbler's use of the shrub layer placed it intermediate to terrestrial and arboreal foragers.

Axis II accounted for 25.2% of the variance, with a length of 2.80 standard deviations. It separated three woodpeckers and a nuthatch in the northern hardwoods that primarily forage on the proximal portions of tree trunks. From these, a species gradient started with the Red-breasted Nuthatch and the hardwoods' Solitary Vireo, which use both branch and some foliage resources, continued through species using progressively finer resources, and terminated with the Blackburnian Warbler and Ruby-crowned Kinglet, which hover extensively at leaves in the upper crown. Along this gradient from coarse to fine substrates, subalpine species were few at first, but came to outnumber northern hardwood ones (subalpine ordination scores were lower than northern hardwood ones on axis II, $t = 2.43$, $P < .05$). This reflects two phenomena: (1) woodpeckers were rare in the subalpine forest, probably because food was scarce, and (2) subalpine forests were smaller in stature, offering fewer large branches or tree boles to forage upon.

Axis III accounted for only 6.4% of the variance. It and higher axes were not readily interpretable, expressing minor components of unrelated species' niches (e.g., hovering by thrushes and kinglets). These higher axes probably obscure biologically meaningful data because the residual variance from axes I and II can swamp data that are important to only a few species pairs.

MEASUREMENTS OF FORAGING NICHE

Niche breadths were similar in both communities. Breadths of foraging maneuvers were nearly identical, while breadths of foraging height were only slightly greater in the northern hardwoods (Table 4). On the other hand, the niche overlaps computed from 231 northern hardwood and 190 subalpine species pairs averaged significantly higher in the subalpine community, particularly for foraging maneuver overlap. Even when the three woodpeckers were omitted from the calculations for foraging maneuver overlap in the northern hardwoods, this measurement (0.45) was still lower than that for the subalpine community ($t = 4.33$, $P < .01$). Thus species in both communities had about the same diversity of foraging activity, but those in the northern hardwoods were more broadly distributed across an abstract niche space (Fig. 3 where there are more northern hardwood species along the upper and right peripheries of the joint ordination). These findings agree with predictions from classical competition theory (MacArthur 1972) that niches should overlap more in communities with greater population fluctuations and more severe environmental conditions. A broader food supply in the northern hardwoods was evidenced by the presence of woodpeckers and by the lower niche overlaps. It would be misleading to draw conclusions on the intensity of competition from the niche measurements, however, because the differences between the resource bases of the two communities have not been quantified.

SPECIES FOUND IN BOTH COMMUNITIES

Six species regularly occurred in both northern hardwood and subalpine forests, and their relative foraging positions in both communities are shown in Figure 3. The ordination suggests that the Black-throated Green Warbler has almost identical niches in the two communities. Three species, Swainson's Thrush, American Redstart, and Dark-eyed Junco, have slightly different but overall similar niches, while the Winter Wren and the Solitary Vireo exhibit

TABLE 4. Summary of niche measurements in the northern hardwood and subalpine communities. Niche breadth is the Shannon-Weiner index computed for individual species. Niche overlap is the percent similarity for species pairs. There are 12 categories of foraging maneuver and 5 categories of foraging height.

	Northern hardwoods $\bar{x}$ ± SD	Subalpine $\bar{x}$ ± SD	t Statistic
Niche breadth	$n = 22$	$n = 20$	
Foraging maneuver	1.393 ± .348	1.393 ± .227	0.00
Foraging height	1.004 ± .257	1.036 ± .222	0.43
Niche overlap	$n = 231$	$n = 190$	
Foraging maneuver	.378 ± .239	.548 ± .218	7.55***
Foraging height	.479 ± .303	.552 ± .269	2.60**

** $P < .01$.
*** $P < .001$.

greater differences in their foraging patterns. We interpret these varying patterns as follows.

Since the Black-throated Green Warbler has been found to be socially dominant over several other parulid species (Morse 1971, 1976a, Sabo 1980), it may be less affected than subordinate species by the presence of potential competitors. It was about equally abundant in both communities; moreover, ecotonal forests are at the mode of its habitat selection pattern in the White Mountains (Sabo 1980). This warbler's foraging is relatively stereotyped (Morse 1971), and may require little modification to exploit the foliage configuration in either community.

The American Redstart is a behaviorally plastic species with a broad niche (Holmes et al. 1978, Sherry 1979) that may well modify its behavior in response to change in competitive context as well as to change in foliage structure. In the subalpine forest, redstarts have no major competitors, but in the northern hardwoods, Least Flycatchers are strong competitors and also social dominants that may affect how American Redstarts use their habitat (Sherry 1979). The Dark-eyed Junco may modify its foraging opportunistically in response to the lower understory and denser brush of the subalpine. Swainson's Thrush may also show this response, for its niche is similar to the junco's and shifts in the same direction. Winter Wrens, which specialize in foraging on fallen logs and branches in the subalpine forest, have a more general niche in the northern hardwoods. Fallen logs are noticeably fewer in the northern hardwood forests than in the subalpine, and the Winter Wren forages more commonly around the bases of living trunks in the northern hardwoods. Thus the niche shift of this species seems primarily a response to differences in the structure of the forest floor litter and perhaps in the relative abundance of foods found there.

The Solitary Vireo differs substantially on axis II, from foraging on distal twigs in the subalpine, to proximal branches and trunks in the northern hardwoods. Because its position in the northern hardwoods is shifted away from that of the northern hardwood Red-eyed and Philadelphia vireos, competition might be involved. Alternatively, the Solitary Vireo's shift from gleaning on branches in the northern hardwoods to gleaning on twigs in the subalpine zone could be due to the denser, more twiggy nature of the subalpine canopy and/or to different availability of insect prey on these substrates. Responses to both competition and resource levels have been suggested for this vireo in other subalpine communities (Rabenold 1978).

FOOD RESOURCE DIVISIONS WITHIN THE MAJOR GUILDS

Field observations and perspectives from ordinations permit some generalizations on the ways that ecologically and phylogenetically related avian species share their food resources.

Five related ground-feeding thrushes occur in the White Mountains. Each has its characteristic foraging style and modal habitat, and co-occurs with as many as three other thrushes. Their feeding niches range from pecking at ground litter to gleaning, hovering, and flycatching low in the trees, in the sequence: Wood Thrush, Hermit Thrush, Gray-cheeked Thrush, Veery, and Swainson's Thrush. This agrees with Dilger's (1956) field observations, except that the relative positions of the Hermit Thrush and Veery are reversed (see Fig. 3). These thrushes occupy habitats in an overlapping elevational series in the order: Wood Thrush, Veery, Hermit Thrush, Swainson's Thrush, and Gray-cheeked Thrush (Dilger 1956, Noon 1981). Noon (1981) found that interspecific competition strongly affected habitat selection in thrushes. Since more species and higher total densities of thrushes occur in the northern hardwoods than in the subalpine zone, competition may be more intense for thrushes on the northern hardwoods site. Moreover, the two subalpine thrushes differ in thermoregulatory adaptations to cold, while the four northern hardwoods ones do not (Holmes and Sawyer 1975).

Critical dimensions that separate woodpecker feeding niches include tree species, tree diameter, foraging style, and foraging height, agreeing with previous studies (Kilham 1964, 1965, 1970, Lawrence 1967, Jackson 1970, Conner 1979, Holmes et al. 1979). Food competition has been shown to be important among syntopic woodpeckers (Stallcup 1968, Williams and Batzli 1979), especially in winter. Thus niche differences among these species during the breeding season will reflect selection forces operating during winter.

Relations among the foliage insectivores are complex. Some of the montane congeneric pairs are elevational or foliage type replacements, such as Least/Yellow-bellied flycatchers and Black-capped/Boreal chickadees. For these pairs, habitat selection seems innate, possibly reinforced by bioenergetic requirements for thermoregulation and anatomical adaptations to different foliage structure. No evidence for direct on-going competition has been found (Rabenold 1978, Sabo 1980), but competition is implicated as having been important during the evolution of these congeneric pairs. However, complex behavioral interactions involving food competition and social dominance do affect the relations between other species (arranged as dominant/subordinate): Red-eyed/Philadelphia vireos (Rice 1978, Robinson 1981), Least Flycatcher/American Redstart (Sherry 1979), Black-throated Green/Magnolia, Yellow-rumped, and Blackburnian warblers (Morse 1971, 1976b). In these groups the dominant species has relatively rigid (stereotyped) foraging patterns while subordinates have more flexible styles. Some warblers further specialize by height strata (terrestrial: Ovenbird; shrub layer: Black-throated Blue and Canada warblers; upper canopy: Blackburnian Warbler), by foliage column density (brushy areas: Magnolia Warbler; more open areas: Yellow-rumped Warbler), by exploiting insect epidemics (Cape May and Bay-breasted warblers), and by foliage type (Blackburnian Warbler on coniferous in the northern hardwoods, American Redstart on deciduous in the subalpine). Specializations according to substrate and foraging maneuver are also frequent in the foliage insectivore guild in both communities (Holmes et al. 1979, Sabo 1980).

As with the thrushes, studies of individual sets of species indicate that interspecific competition appears to be more important in organizing relations among the foliage insectivores in the northern hardwoods than among the subalpine counterparts. In the northern hardwoods the three commonest species were involved in competition-dominance relations, while in the subalpine zone, only the warbler hierarchy occurred. The most common bird in the subalpine forest, the Blackpoll Warbler, appeared to entirely lack direct competitors excepting the rare Bay-breasted Warbler (Morse 1979, Sabo 1980). Furthermore, it may have thermoregulatory adaptations to the subalpine zone that are unique among warblers (cf. Sabo 1980). The apparent reduction of competition in the subalpine zone is probably related to its environmental severity. Not only are populations more variable here, thus blunting competition, but also the harsh climate has pressured some species to adapt to the conditions. These adaptations effectively expand the abstract niche space by serving as new axes for differentiation of species. Furthermore, insufficiently adapted species (e.g., Wood Thrush, Scarlet Tanager) cannot enter the subalpine habitat. A parallel trade-off between competition and environmental adversity exists in intertidal organisms, where physical factors chiefly determine community patterns in the higher, more exposed zone, while biological interactions including competition are more important in lower zones where conditions are less severe (Connell 1961).

Comparing niche ordinations and measures does not serve to demonstrate competition in the present study. We have inferred that competitive interactions organize species relations for numerous individual cases, based on intensive detailed studies of two to five species systems reported in the literature. In these studies, many of which were conducted on our study plots or in similar nearby forests, competition was reasonably conclusively shown to modify foraging behavior of the species involved. The emerging general picture is not that competition organizes the relations between every species in the community as some authors have maintained (e.g., Cody 1974). Rather, within certain groups of ecologically similar species, competitive interactions can be an important determinant of niche structure.

MINOR OR RARE SPECIES

In addition to the 20 to 22 principal bird species considered in the preceding sections, several other species occurred rarely or occasionally on or near the forest study sites (Table 5). These species were encountered too infrequently or were too widely dispersed for us to obtain accurate estimates of their densities or adequate samples of their foraging behavior. Despite this lack of data, however, a brief consideration of

TABLE 5. Rare or irregularly encountered species on the northern hardwoods and subalpine study sites, 1976–1978, grouped by general foraging patterns. Code names are used in Figure 4.

Bark probers	Pileated Woodpecker (PWP) (*Dryocopus pileatus*)	Black-backed [Three-toed] Woodpecker (B3W) (*Picoides arcticus*) [Northern] Three-toed Woodpecker (N3W) (*P. tridactylus*)
Bark gleaners	Brown Creeper (CRP) (*Certhia americana*) Black-and-white Warbler (B&W) (*Mniotilta varia*)	Brown Creeper (CRP)
Aerial salliers	Eastern Wood-Pewee (PEWEE) (*Contopus virens*)	Olive-sided Flycatcher (OSF) (*Contopus borealis*)
Foliage gleaners	Blue Jay (BJ) (*Cyanocitta cristata*)	Blue Jay (BJ) Gray Jay (GJ) (*Perisoreus canadensis*) Tennessee Warbler (TNW) (*Vermivora peregrina*) Cape May Warbler (CMW) (*Dendroica tigrina*)
Ground foragers	American Robin (ROB) (*Turdus migratorius*)	

these species provides insight into some of the factors affecting species distributions and into the structure of these montane bird communities.

Some species bred commonly in one community but were rare in the other. Such rarities represented the edges of populations distributed along an elevational gradient. Birds from the northern hardwoods that entered the subalpine zone were the Black-capped Chickadee, Hermit Thrush, Red-eyed and Philadelphia vireos, Black-throated Blue Warbler and Ovenbird. Only Purple Finches regularly reversed this pattern down into the northern hardwoods, although the Red-breasted Nuthatch and White-throated Sparrow appeared occasionally in the northern hardwood zone in appropriate habitat (conifer stands for the nuthatch or forest edge/fields for the sparrow). Why more northern hardwoods birds invaded the subalpine zone rather than the reverse may be due to (1) the greater geographic extent of northern hardwoods forests in the White Mountains, providing a larger number of potential colonizers, and (2) the scarcity of coniferous foliage in the northern hardwoods, making good breeding habitat and suitable foraging substrates/resources hard to find for conifer-dependent birds.

Other species (e.g., Pileated Woodpeckers in the northern hardwoods) were "rare" because they occupy large home ranges and could not be censused or observed adequately by our methods. Several species apparently found certain forest habitat to be marginal, as indicated by their irregular occurrences, low numbers in some years, and absence in others (e.g., Black-backed Woodpeckers, Three-toed Woodpeckers, Tennessee Warblers, and Cape May Warblers in the subalpine zone, Brown Creepers in both habitats and Black-and-white Warblers in the northern hardwoods). These irregular occurrences (apparently accompanied by breeding in most cases) may be related to specialized habitat or resource requirements that were not met regularly in the study areas. For example, two sallying flycatchers that require open perches, were rare in our study areas, the Eastern Wood-Pewee in the northern hardwoods and the Olive-sided Flycatcher in the subalpine forest, but both were commoner in more open areas within these habitats. Some species of irregular occurrence were at the southern limit of their geographical ranges (e.g., Gray Jay in the subalpine zone), and may have been limited by both climate and habitat. Blue Jays were infrequent at both study sites, which were located in large, relatively unbroken forest. This species appeared to be more common in lower elevation forests and in more disturbed and forest-edge habitats. Blue Jays seem to increase in the northern hardwoods at Hubbard Brook in years of high beech mast production (Holmes, unpubl. data). Likewise, the occurrence of American Robins in these forests may represent an overflow from massive populations in different but nearby habitats (forest edge and pasture lands); they increased at Hubbard Brook during an insect outbreak (Holmes and Sturges 1975) and thus may respond to the availability of certain kinds of food.

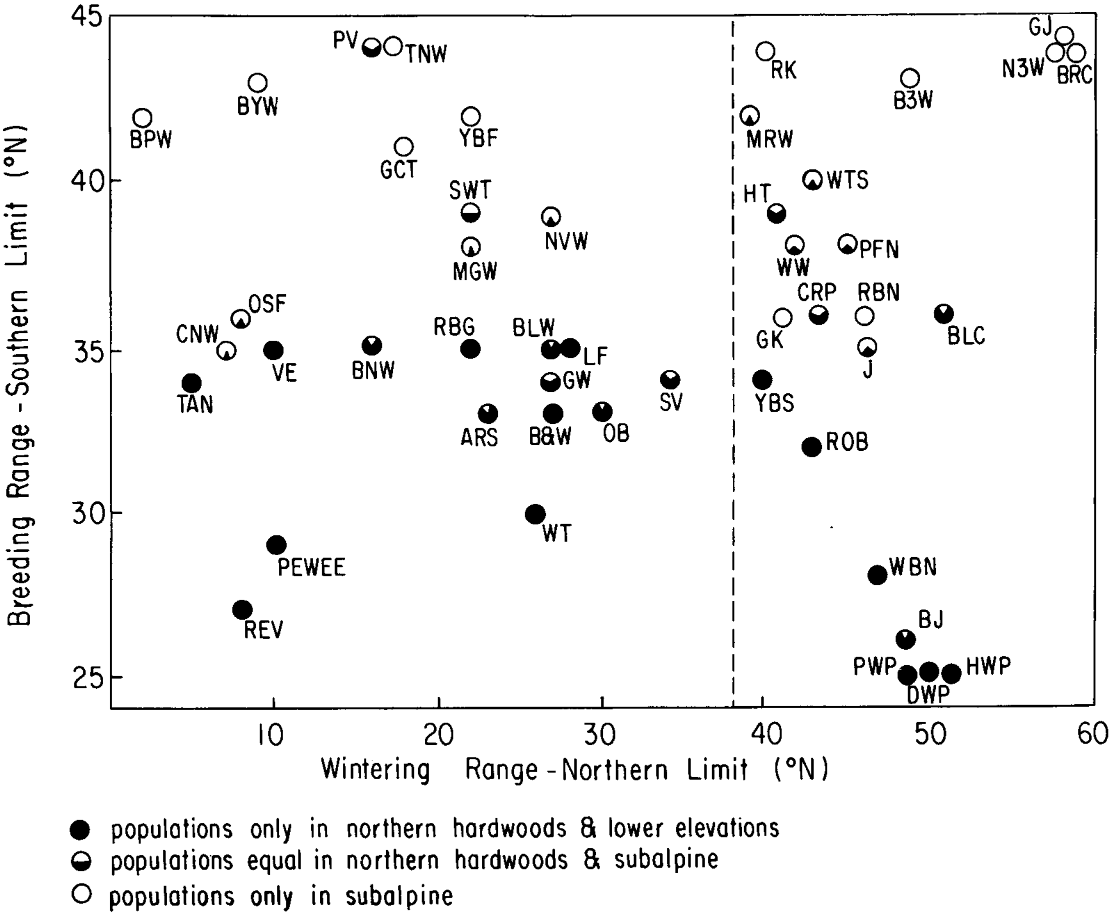

FIGURE 4. Biogeographic parameters of northern wintering and southern breeding limits for White Mountain bird species in eastern North America, graphed to show correspondence with elevational distribution in the White Mountains and geographic origin. All species of Old World origin winter north at least to 35°N latitude. Species acronyms listed in Tables 1 and 5.

The important point here is that each species appears to respond to the habitat in specific ways. This is most apparent among the incidental species that find these two communities marginal for a variety of reasons.

WINTERING PATTERNS, BIOGEOGRAPHY AND THE PLEISTOCENE: IMPLICATIONS FOR UNDERSTANDING TEMPERATE BREEDING BIRD COMMUNITIES

Cycles of Pleistocene glaciation, biogeographical origins of the North American avifauna, and wintering habits also probably affected the structure of the two communities. In Figure 4, we have plotted two parameters of the White Mountain bird species' annual cycles, the southern limit (in eastern North America) of breeding range and the northern limit of wintering range. The southern breeding limit roughly indicates tolerance to warm temperatures and fidelity to northerly biomes (although species breeding south on the Great Smoky Mountains tend to blur the pattern). The northern wintering limit indicates tolerance to cold temperatures and increasingly harsh seasonality. The graph shows the more southerly distribution of species occurring at lower elevations in the White Mountains, and a line of demarkation at about 37–38° N latitude, differentiating species that radiated in the New World from those primarily of palearctic origin. To what extent do these trends result from Pleistocene events and how might those events have affected the structure of these two bird communities?

Mayr (1976) discussed the probable geographic origins and secondary speciation centers for the North American avifauna. Of the species occurring in our forests, creepers, corvids, chickadees, nuthatches, kinglets, and the Purple Finch are from palearctic stock, and all have northern wintering grounds. Foods of these species on their breeding grounds reflect winter feeding centered on trunk, twig, and coniferous foliage, substrates that are available year round. Although the insect populations

TABLE 6. Biogeographic analyses of eastern North American species of woodpeckers and passerines by migration pattern, trophic level, and biogeographic derivation. Range data from the American Ornithologists' Union Check-list (1957), trophic data from Bent (1939–1968) and other sources.

General guild	Total species	Resident	Partly migratory	Fully migratory	Old World stock (%)*
Omnivore-scavengers	5	5			100
Tree-seed eaters	3		3		100
Carnivores	2		1	1	100
Bark insectivores	13	8	3	2	69
Foliage insectivores	65	7	8	50	19
Terrestrial and low understory herbivore/insectivores	53	5	12	36	6
Aerial insectivores	12			12	0
Totals*	153	25	27	101	
Old World stock	32	16	9	7	
New World stock	111	8	17	86	
Subspecies in eastern North America/Species					
Mean		2.37	2.00	1.17	
Standard Deviation		1.07	1.27	0.40	

* Species of unknown origin (three woodpeckers, six swallows, one waxwing) excluded from calculations but included in totals.

change seasonally, behavioral flexibility allows the birds to seek out these substrate types. In addition, many of these species are only seasonally insectivorous and feed on seeds and berries during winter. While Mayr considered the woodpeckers to be of unknown ancestral origin, *Picoides* (sensu lato) is thought to comprise a monophyletic group of species from palearctic stock (Short 1971); it also matches the pattern of the other species of palearctic derivation.

During the late Tertiary, evolution and radiation of the nine-primaried oscines took place in tropical North and South America (Mayr 1976). This process gave rise to about 200 genera encompassing 850 species (Morony et al. 1975), including vireos, warblers, tanagers, and sparrows, birds that now dominate seasonal passerine niches in the temperate zone. Ground-feeding birds are disabled by snow cover and they must retreat to southern wintering grounds. Foliage gleaners, particularly broadleaf users, encounter similar difficulties when leaves drop and insects undergo diapause. Figure 2 shows that the terrestrial guild in both communities is composed solely of species that have spread from the tropics (warblers, wrens, sparrows and catharine thrushes). The wood-pecking guild is dominated by palearctic species. Among foliage gleaners, palearctic derivatives are more restricted to conifers (e.g., kinglets), while New World derivatives mostly forage on broadleaf trees (Table 1). On our census plots, the CVs for passerine species of palearctic derivation ($\bar{x}$ = 1.28 ± 0.48 SD, $n = 11$) were much higher than those for species of tropical American derivation ($\bar{x}$ = 0.55 ± 0.45 SD, $n = 41$), probably reflecting harsher and more variable climate on their northern winter grounds. The three northern hardwoods woodpeckers had very low CVs ($\bar{x}$ = 0.23 ± 0.05 SD), differing from the other palearctic derivatives. The probable explanation is that one woodpecker is migratory while the other two resident species have access to a more dependable food source (bark-burrowing insects) and hence are less vulnerable to winter conditions.

In order to seek wider biogeographic trends in community assembly, we analyzed the woodpeckers and passerines that breed in eastern North America (east of the Great Plains and excluding the Florida peninsula and Greenland) (Table 6). Seasonal niches involving aerial, terrestrial, and foliage insectivory correlate with migratory New World species. Niches based on year-round resource bases correlate with residential birds of palearctic derivation. Subspeciation is more pronounced in resident species than in migrant ones ($t = 6.04$, $P < .001$, cf. Table 6 and Sabo 1980), perhaps indicating greater gene flow in populations of migratory species.

The contributions of neotropical and palearctic stocks to the foliage-using guilds in the two montane communities can be further related to the glacial history of the vegetation zones. On the one hand, 91% of the common foliage-using species in the northern hardwoods, but only 67% of those in the subalpine forest are derived from New World stock. On the other hand, only four warbler species feed in the northern hardwoods canopy, but eight use the subalpine canopy. This apparent contradiction may result from Pleistocene events. During climatic change vegetation zones shift extensively, fragmenting migrants' breeding ranges and facilitating speciation (cf. Mengel 1964). Temperate mixed forests, similar to the northern hardwoods, occurred at 30–34°N latitude in eastern North America during glacial epochs; isolated boreal and spruce forests similar to subalpine forests occurred at 26–40°N in several regions (Davis 1969, Flint 1971). Thus the pool of bird species for eastern deciduous forests and the northern hardwoods subset may include more New World foliage-users because of closer proximity and habitat similarity to centers of tropical speciation. The boreal communities that contribute to the subalpine forest are comprised of mostly palearctic elements with fewer neotropical derivatives. Furthermore, since the distance and ecological dissimilarity of boreal areas from tropical ones filter out most species, adaptive radiation might occur in those neotropical lines that did colonize boreal areas (e.g., wood warblers). The warblers in particular seem able to rapidly evolve isolating mechanisms, with the result that closely related species may have quite disparate appearances (e.g., Golden-winged *Vermivora chrysoptera* and Blue-winged *V. pinus,* Bay-breasted and Blackpoll warblers; cf. Mayr and Short 1970).

Migration allows birds to exploit seasonal productivity but requires a wintering ground with ample food supply to sustain the population (see Keast and Morton 1980). Competition and niche displacement patterns may influence evolution in these wintering-ground communities, which often exist amidst a residential low-latitude bird community—with consequently different niches and habitats for breeding and for wintering. Although a palearctic species entering the New World may have a breeding-ground niche that fits into a nearctic temperate or subalpine community, we speculate that a suitable wintering niche at low latitudes could be difficult for a newcomer to find. As this newcomer species migrated southward in the New World searching for viable wintering grounds, it would encounter progressively richer, more tightly co-evolved communities that might thwart the invasion (some temperate species are in fact territorial on the wintering ground, e.g., Rappole and Warner 1980). Moreover, palearctic stock could have been disadvantaged by being geared for competition with the palearctic low latitude fauna. Pleistocene diffusion of warm-temperate forms from the palearctic was doubtless further impaired by boreal habitats along the transoceanic connections, although milder conditions occurred during the Pliocene. For palearctic derivatives that did penetrate temperate North America, selection may have favored a residential habit or a northern wintering ground, as found in the New Hampshire communities. Thus wintering ground competition may allot broadleaf canopy and terrestrial niches to tropical-origin New World elements, while leaving pecking and conifer foliage niches largely to palearctic derivatives in these two communities.

Two important points emerge from these considerations. First, present-day species composition and patterns of resource partitioning in communities must be partly attributed to Pleistocene, and perhaps earlier, events occurring on a large geographical scale. Second, events and processes on the north temperate summering grounds, as well as those on the wintering grounds and even during migration, can significantly affect bird community patterns. This is counter to the general views developed by Fretwell (1972) and Wiens (1974, 1977) i.e., the winter season almost exclusively has the most influence on migratory species. Thus, in identifying the determinants of avian community structure at a site, one must consider many interacting factors operating at different scales of resolution.

CONCLUSIONS AND SUMMARY

Our results show that many factors influence the structure of forest bird communities. The habitat at higher elevations is a low, largely coniferous subalpine forest and the climate is cold and harsh. Compared to the northern hardwoods bird community, the subalpine community has fewer species, less diverse phylogenetic stock, generally lower and more variable population densities, lower niche diversity but greater niche overlap. These findings suggest that avian community structure is strongly affected by climatic severity in the subalpine zone, while other factors, such as competition, seem relatively more important in the northern hardwoods. Population and niche differences of the six species that occur in both communities are strongly associated with differences in habitat preferences and physiognomy, but competition is also implicated. The niche ordinations indicate that the organization of these communities can be largely understood in terms of where the species forage in relation to canopy height and substrate characteristics. Both communities are composed of (1) major species that tend to be most abundant and that clearly differ in their use of food resources by height and/or substrates, (2) minor species that may differ less clearly in these respects but coexist because of other differences in habitat use, and (3) incidental species that are present mainly as population overflow from other habitats.

In addition to the patterns of differentiation within communities, the structures of these bird communities reflect the biogeographic and phylogenetic origins of the avifaunas, the effects of Pleistocene events, and the species' wintering habits. Species derived from palearctic stock tend to be year-round residents and to exploit food resources that mainly reflect winter feeding, e.g., arthropods occurring on tree boles, twigs, and conifer foliage. In contrast, the migratory New World species that radiated in the American tropics occupy the more seasonal niches involving aerial, terrestrial, and foliage insectivory.

Each species responds to its habitat in a unique fashion. These response patterns have undoubtedly evolved as the life style of each incipient species adjusted in response to the different selective forces, including characteristics of the physical environment and the occurrence of other species as predators, competitors, and prey. Consequently, the mix of bird species in a particular habitat, and hence "community structure," depends on the abilities of those species to find, in both evolutionary and present time, that habitat and to exploit successfully its resources.

The purpose of studying the relationships among coexisting species is to help unravel how and why their patterns of habitat use have been determined or affected. We believe that community comparisons, such as ours, that consider quantitative differences in avian niche responses to the resource structure of the habitats, offer promise for accomplishing this goal. We caution, however, that our analyses were based on the patterns within one main study site in each habitat. In order to assess community variability and achieve more complete comparisons, several replicates within each habitat type are needed. To our knowledge, this has never been done for a study of bird foraging niches. This lack is understandable because such data are difficult and laborious to obtain, especially when the community consists of 20 to 30 species. Data obtained in such studies should be published in detail, including tables of foraging maneuvers, substrates used, habitat variables, etc., (see Holmes et al. 1979, Sabo 1980), which can be used for future syntheses. Moreover, future studies must be designed to include more rigorous and experimental approaches to gathering and analyzing the habitat responses and niche properties of birds. To do so will probably necessitate focusing on particular guilds, as was done by Root (1967), Morse (1976b), Rabenold (1978), Eckhardt (1979), and others, although none of these included replicated plots. As more of such studies are reported, it should become possible to understand more clearly how birds respond to their environments and to formulate models predicting community structure and habitat responses of forest birds.

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RECENT PUBLICATIONS

Fossil Vertebrates from the Bahamas.—Edited by Storrs L. Olson. 1982. Smithsonian Contributions to Paleobiology No. 48, Smithsonian Institution Press, Washington, DC. 65 p. Paper cover. This booklet comprises three articles that summarize the previous literature on fossil vertebrates from the Bahamas, revise some previously described specimens, and discuss changes in the late Pleistocene environment of the Bahaman archipelago. The article by Olson and William B. Hilgartner treats the fossil and subfossil birds, including several proposed changes in their nomenclature and a comparison of the late Pleistocene and modern avifaunas. Photographs, drawings, references, index.

Morphological Similarities between the Menurae and the Rhinocryptidae, Relict Passerine Birds of the Southern Hemisphere.—Alan Feduccia and Storrs L. Olson. 1982. Smithsonian Contributions to Zoology No. 366. Smithsonian Institution Press, Washington, DC. 22 p. Paper cover. The osteological studies reported here show that the Menuridae and Atrichornithidae differ markedly from the Ptilinorhynchidae and Paradisaeidae, whereas they share many peculiarities only with the Rhinocryptidae. These findings lead to the suggestion "that the Menurae and the Rhinocryptidae are among the most primitive of the Passeriformes and are representative of the ancestral stock that gave rise to the remainder of the passerines." Further stimulating ideas about the time, place, and pattern of early passeriform evolution are briefly discussed. An appendix proposes changes, based on skeletal characters, in the sequence of families within the superfamily Furnarioidea. Photographs, excellent drawings, references.

Prodromus of the Fossil Avifauna of the Hawaiian Islands.—Storrs L. Olson and Helen F. James. 1982. Smithsonian Contributions to Zoology No. 365. Smithsonian Institution Press, Washington, DC. 59 p. Paper cover. During the past decade, thousands of bones of extinct and living species of birds have been excavated from late Pleistocene and Holocene sites in the Hawaiian Islands. A preliminary report on these findings is given here, providing an overview and background information for future monographs. The fossil deposits, on five of the main islands, are described in detail. The species found so far, including forty that are extinct, are presented in an informal list since most of them remain to be worked out. Already, the fossils show that the land avifauna was much larger than previously suspected, and they point to the role of the early Polynesians in its extinction. These findings bear heavily upon the systematics of the endemic finches and on theories of Hawaiian biogeography. Maps, photographs, references.

Birds of Tropical America.—Alexander F. Skutch. 1983. University of Texas Press, Austin. 320 p. $29.95. Skutch's immense contribution to neotropical ornithology needs no introduction. This book is a collection of his life histories for 34 species of nonpasserines (Great Tinamou to Emerald Toucanet), previously published in several journals. It is intended to make the articles up to date and more readily accessible to the growing number of people interested in tropical nature. The author has "carefully revised the original accounts, in the process omitting details that no longer seem important and adding whatever new information has become available over the years." Skutch's style combines scientific facts with personal appreciation for the birds, and some of his experiences in studying them. The articles are illustrated with the author's photographs and full-page monochrome wash drawings by Dana Gardner. References, index.