

NICHE AND HABITAT RELATIONS IN SUBALPINE BIRD COMMUNITIES OF THE WHITE MOUNTAINS OF NEW HAMPSHIRE¹

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Abstract. The populations, foraging behavior, and habitat selection of 20 insectivorous species of subalpine birds were studied during three breeding seasons in the White Mountains, New Hampshire, USA. The object was to clarify how an elevation gradient of environmental adversity affected diversity, dominance, niche, habitat, and species biology.

Population densities and territory sizes were measured from census plots. Territory sizes correlated with species body mass, probably in response to size-related food requirements. Lower elevations had more even distributions of densities among species and less steep dominance-diversity curves than did higher elevations.

To show habitat selection patterns in the subalpine vegetation, principal components analysis (PCA) was used to develop a model that emphasized elevation and broadleaf-to-coniferous foliage as the two major gradients. Bird species diversity (BSD) reached a maximum in well-developed preclimax red spruce-balsam fir forests with some broadleaf crowns present. Individual species responses were mapped using the model as a base chart, grouping together: (1) five species living at altitudes above 1100 m with small differences in their specific patterns, (2) five other species widely distributed through the mid-subalpine zone (800–1100 m), (3) six more mid-subalpine species segregating along the broadleaf/conifer foliage gradient, and (4) three species found near water.

Niche relations were studied using detrended correspondence analysis, a modified version of reciprocal averaging. Resource use was divided by (1) terrestrial vs. arboreal position, (2) a gradient from fine distal (leaves) to coarse proximal (trunk) substrates, and (3) different specializations for food acquisition. BSD was greater in the resource categories requiring less energy and less specialized morphological adaptations to exploit, or having greater insect resource bases.

To investigate the relations between habitat and niche, a matrix of the correlations between the niche and habitat variables, using species means for data, was analyzed by PCA. Three relations emerged: (1) the elevation/forest structure gradient was correlated with the terrestrial/arboreal foraging segregation, (2) the niche substrate gradient responded to vegetation structure along the broadleaf/conifer gradient, and (3) in both cases the response of foraging behavior to habitat structure involved many variables acting together. Niche and habitat were thus closely linked as aspects of species ecotopes; species responses were illustrated for the Blackpoll Warbler and other wood warblers. Food was inferred to limit populations occasionally, so that interspecific competition plausibly underlies niche differentiation. Thermoregulation is hypothesized to affect habitat selection.

Key words: bird community; ecotope; elevation gradient; foraging behavior; habitat selection; ordination; species diversity; subalpine zone; White Mountains; wood warbler.

INTRODUCTION

Complex webs of interacting historical and ecological factors surround the species of a biological community and influence their evolution (Whittaker 1975). This study attempts to interpret community patterns of resource division among subalpine birds. Limiting resources may be partitioned by populations to reduce interspecific competition (Park 1962, Connell 1975, Diamond 1975), although need not always be critical for summer breeding birds (Wiens 1974). If, however, food limits breeding success, long-term selective pressures should enhance species differences in use of food resources. Competition (or resource use overlap) would be ultimately minimized by evolutionary coadjustments of species morphology, physiology, and behavior.

The subalpine zone has a simpler resource spectrum than tropical and warm temperate communities (cf. MacArthur 1969, 1972, Orians 1969, Karr 1971, 1976, Lovejoy 1974), and for its relatively small species pool interspecific relations are easier to study. Differences among the birds' physical and behavioral characteristics may partition resources by (1) habitat selection—preference for different environments or communities, and/or (2) niche relations—differences in use of food or other resources in a given community.

Niche and habitat responses occur simultaneously in the communities of a landscape. Communities are formed of guilds (Root 1967), and foraging behavior of birds can be used in conjunction with morphological and natural history data to infer the resource partitioning mechanisms within these guilds (MacArthur 1958, Root 1967, Holmes et al. 1979b, Sabo and Whittaker 1979). The habitat responses of species to major environmental gradients (and historical and ecological factors) may be inferred from a landscape-wide sampling and analysis (Whittaker 1967, James 1971, Terborgh 1971).

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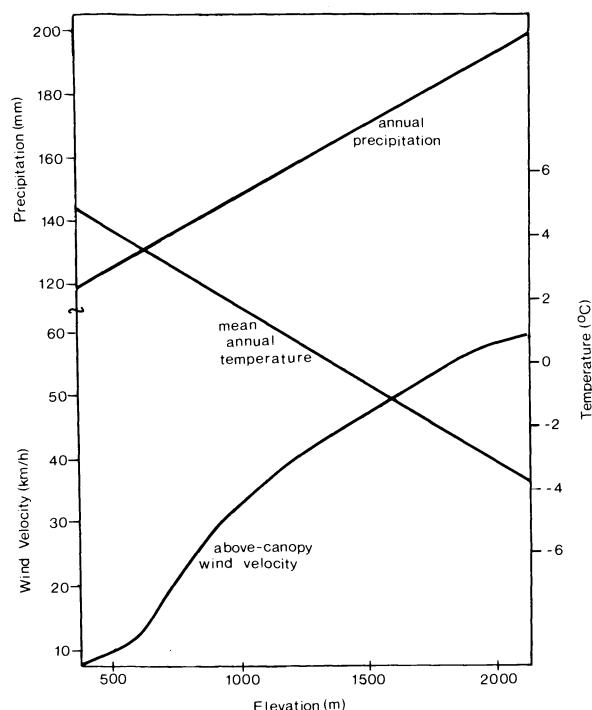


FIG. 1. Macroclimate in the White Mountains of New Hampshire becomes progressively colder, wetter, and windier with elevation. Determined from regressions on weather stations, United States Forest Service data.

Rather overwhelming masses of data can result from studies of community structure. Multivariate techniques can summarize and present the major relationships in the data set as Karr and James (1975), Holmes et al. (1979b), Sabo and Whittaker (1979) have done for niches, and James (1971), Anderson and Shugart (1974), Whitmore (1975, 1977) for habitats. Ecological determinants of community structure may then be inferred (Cody 1974, 1978, Karr and James 1975, Smith 1977). In this study the structure and interrelationships of niche responses and habitat selection are explored.

STUDY AREA

The habitat data were gathered over a wide area of the White Mountains in northern New Hampshire. The White Mountains lie in the Androscoggin, Connecticut, Merrimack, and Saco River watersheds. They rise to 1917 m elevation in the Presidential Range, and 30 peaks rise above 1300 m. The subalpine zone, an extension of the taiga or boreal forest, forms a continuum of similar intergrading communities from 750 m to tree line near 1450 m. Below 750 m, northern hardwood forests predominate, consisting mainly of sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), and yellow birch (*Betula lutea*) (Bormann et al. 1970); the bird communities of these have been described by Holmes and Sturges (1975) and Holmes et al. (1979b).

From 750 to 850 m elevation, a steeper transition from northern hardwood to subalpine forests occurs in a belt of communities where neither type dominates (Siccama 1974). From 850 to 1100 m deciduous trees occur locally to form a mosaic with the dominant coniferous species. Above 1100 m this deciduous element rapidly declines, partly because of snowshoe hare browsing (Siccama 1974). Most of these areas have been logged, so dead boles are few, and perhaps this explains the few woodpeckers found. Fire is rare. Krummholz is the usual physiognomy from 1275 m to tree line. Above tree line, herb and dwarf-shrub alpine tundra communities occur (cf. Bliss 1963). Dominant trees of the subalpine are balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), paper birch (*Betula papyrifera*), and mountain ash (*Sorbus americana*); black spruce (*Picea mariana*) and tamarack (*Larix laricina*) occur in swamps and bogs. Paper birch and the short-lived pin cherry (*Prunus pensylvanica*) occur early in successional sequences, followed by mountain ash and fir. Fir occasionally forms a self-perpetuating community that cycles between senescent and vigorous phases (Sprugel 1976). Red spruce with some fir and broadleaf species is the typical climax. Important understory shrubs include hobblebush (*Viburnum alnifolium*) and mountain maple (*Acer spicatum*). Abundant herbs are shield fern (*Dryopteris spinulosa*), bladder sedge (*Carex intumescens*), clintonia (*Clintonia borealis*), wood sorrel (*Oxalis montana*), bunchberry (*Cornus canadensis*), and whorled wood aster (*Aster acuminatus*).

Niche and population studies were restricted to Mount Moosilauke, 44°01'N, 71°50'W, the western great peak of the White Mountains. The summit rises to 1467 m, and the 41-km² subalpine zone is fairly typical for this area. It includes a protected ravine along the Baker River headwaters. One additional plot was censused in a climax red spruce community in the Nancy Pond area, 44°02'N, 71°24'W, elevation 950 m. Table 1 lists the species analyzed, their mass, density, and territory size. Mass data were obtained from specimens in the Cornell University Museum collected during the breeding season, representing dead wet mass. Values are in close accord with previously published data for live-trapped individuals (Holmes and Sturges 1975, Clench and Leberman 1978). The sexes were averaged together.

Similar but less well-developed subalpine areas with similar bird communities occur in the Chic-chocs of the Gaspé (Godfrey 1966), the Green Mountains of Vermont (Wallace 1939), the Adirondacks and Catskills of New York (Bull 1974, Able and Noon 1976), and around Mount Katahdin in Maine (Palmer 1949).

With increasing elevation, climate becomes wetter, cooler, and windier (Fig. 1, cf. Reiners and Lang 1979). Snow cover lingers to June at high elevations, with occasional midsummer snowfalls. The coniferous growth form, limited to compact trees in adverse cli-

TABLE 1. Principal subalpine insectivorous birds of the White Mountains. *N* is sample size; *S* is weighted average of six 5-ha plots on Mt. Moosilauke representing average subalpine densities; *V* refers to Nancy Pond site in virgin spruce grove.

		Body mass g		Population density (pairs/km ²)		Territory size		Habitat stands <i>N</i>	For- aging maneu- vers <i>N</i>
		$\bar{x} \pm SD$	(<i>N</i>)	$\bar{x} \pm SE$	<i>V</i>	ha	(<i>N</i>)		
YF	Yellow-bellied Flycatcher <i>Empidonax flaviventris</i>	11.8 ± 1.0	(6)	33 ± 2	21	1.8	(13)	88	361
BC	Boreal Chickadee <i>Parus hudsonicus littoralis</i>	10.2 ± 0.4	(2)	1 ± 1	14	1.2	(2)	13	272
RN	Red-breasted Nuthatch <i>Sitta canadensis</i>	11.0 ± 0.8	(6)	2 ± 1	4	=10	(2)	11	640
WW	Winter Wren <i>Troglodytes troglodytes hiemalis</i>	9.2 ± 0.5	(6)	9 ± 5	4	1.6	(2)	29	286
ST	Swainson's Thrush <i>Catharus ustulatus swainsoni</i>	30.8 ± 2.2	(16)	22 ± 3	29	2.1	(12)	77	282
GT	Gray-cheeked Thrush <i>Catharus minimus bicknelli</i>	27.5 ± 2.0	(5)	9 ± 2	7	2.1	(8)	79	140
GK	Golden-crowned Kinglet <i>Regulus satrapa satrapa</i>	6.8 ± 0.8	(12)	11 ± 6	60	0.6	(9)	30	1217
RK	Ruby-crowned Kinglet <i>Regulus calendula calendula</i>	7.0 ± 0.6	(9)	1 ± 2	16	0.6	(2)	21	272
SV	Solitary Vireo <i>Vireo solitarius solitarius</i>	16.4 ± 1.5	(7)	2 ± 1	1	=5	(2)	25	179
NV	Nashville Warbler <i>Vermivora ruficapilla ruficapilla</i>	9.0 ± 0.9	(14)	9 ± 3	24	1.1	(7)	39	211
MG	Magnolia Warbler <i>Dendroica magnolia</i>	9.2 ± 1.7	(12)	30 ± 8	16	0.7	(9)	49	682
YR	Yellow-rumped Warbler <i>Dendroica coronata coronata</i>	12.1 ± 1.1	(29)	31 ± 5	16	1.0	(11)	86	1043
GW	Black-throated Green Warbler <i>Dendroica virens virens</i>	9.1 ± 1.0	(13)	21 ± 2	19	1.2	(8)	56	1242
BA	Bay-breasted Warbler <i>Dendroica castanea</i>	13.0 ± 1.2	(20)	2 ± 2	14	1.5	(2)	8	753
BP	Blackpoll Warbler <i>Dendroica striata</i>	12.8 ± 1.2	(19)	154 ± 7	74	0.4	(63)	329	2160
CW	Canada Warbler <i>Wilsonia canadensis</i>	10.5 ± 0.3	(6)	24 ± 9	10	0.7	(9)	33	884
AR	American Redstart <i>Setophaga ruticilla</i>	8.2 ± 0.7	(15)	40 ± 2	9	0.6	(14)	86	1024
PF	Purple Finch <i>Carpodacus purpureus purpureus</i>	26.8 ± 2.7	(39)	12 ± 5	13	2.1	(7)	25	228
J	Dark-eyed Junco <i>Junco hyemalis hyemalis</i>	19.8 ± 1.3	(37)	19 ± 2	20	1.1	(10)	79	684
WT	White-throated Sparrow <i>Zonotrichia albicollis</i>	26.8 ± 2.5	(24)	64 ± 6	41	0.6	(33)	112	1058

mate, is dense and twig-rich at higher elevations. Insectivorous birds begin breeding in late May and early June, with most species single brooded and approximately synchronous due to the short season. No evidence for polygyny was observed.

METHODS

Census plots

In 1977 six 5-ha census plots were studied on Mount Moosilauke. Five of these represented the elevation

gradient 850 m, 975 m, 1100 m, 1250 m, 1375 m, while the sixth at 1040 m represented sheltered areas. Using six to eight standardized time censuses (Holmes and Sturges 1975) modified from the spot-map technique (Williams 1936, Kendigh 1944), bird populations were estimated from the numbers of singing males. The six census plots were then taken as measures of bird densities in elevational and edaphic belts whose area was planimetrically determined from the United States Geological Survey Mount Moosilauke 2.2-m quad-

rangle. The census densities were weighted by the area they represented to yield estimates of the average subalpine population densities.

Data analyzed for the habitat selection study provided estimates of the variation in species densities in stands of similar elevation and topographic position. Two 5-ha census plots from the six were censused in 1976 and 1978 to observe population changes. Also, in 1977 a 7-ha plot was studied near Nancy Pond in the virgin spruce grove. Territory sizes were measured from the species spot-maps; partly because of small sample size, territories did not usually differ in size between plots. Determining territory sizes from spot-maps is imprecise, although less so when many pairs are present (as for the Blackpoll Warbler). Estimates of territory size were also made by tracking a given singing male for up to 1 h, and these estimates generally agreed with the spot-map values. Singing-male counts differ in the extent of bias among various species. In 1977 on one 5-ha census plot, birds were color banded and mist netted to ascertain the bias among the species. Because censuses included not only the early morning period of greatest activity, but also twilight periods for thrush choruses, species were censused more or less evenly.

Habitat characterization

Habitat selection may be quantified by recording descriptive data for topography and vegetation structure; the former (with modification by the latter) affects abiotic factors such as mean temperature, precipitation, and wind velocity. To take a sample, a singing territorial male was observed for ≈ 15 min so that an approximate extrapolation of the pair's territory could be made. Frequently the territory lay in a homogeneous forest stand with other species pairs present, so that data for these could be gathered simultaneously. Measurements were made of 5 topographic and 22 vegetation physiognomic variables. Observations of 1286 subalpine bird territories in 496 stands listed in the Appendix were made during the 1977 (148 stands) and 1978 (348 stands) breeding seasons. From these data, I developed a model of the subalpine habitats, to use as a base map to illustrate species responses.

In the analysis, a species' abundance was given by the percent habitat occupied. The percent habitat occupied is, ideally, the number of stands a species nests in out of 100 identical stands. In practice this percent is figured from ≈ 20 fairly similar stands. Stands with relatively identical topography and vegetation physiognomy cluster in one area of a base map derived from an ecological ordination of all 496 stands. The percent habitat occupied is thus the fraction of those stands in a small area on this base map in which a given species occurs. Since some species, such as thrushes, tend to be overlooked because of infrequent song choruses, the value computed for the percent habitat occupied

is lower than the actual value. This bias should be relatively constant for a given species, however, and not distort the indicated habitat distribution.

Comparing results of the percent habitat occupied with the spot-map procedure, values of percent habitat occupied are $\approx 10\%$ lower for a given area than those of the spot-map. Thrushes and Solitary Vireos, which sing infrequently, and Red-breasted Nuthatches, with large home ranges, had values more typically 25%–40% lower than spot-map "percents" for similar areas. The percent habitat occupied procedure neglects the role of nest site limitation, but seems effective in expressing population responses to habitat gradients. Population measures by the spot-map procedure would require enormous time investment to collect data over a comparable diversity of habitats. Disadvantages of the percent habitat occupied procedure include (1) day-to-day variability in sampling efficiency because of weather, (2) the lack of representation from areas devoid of birds, and (3) unrecorded shifts in habitat selection from year to year. The importance of these disadvantages was kept low by (1) field work done mainly in fair weather before noon, (2) the infrequency and marginal ecological significance of barren areas in habitat selection, and (3) field observation and plot censuses in 1976 and 1978 for comparison.

For each stand, field measurements were made of (1) elevation from the United States Geological Survey topographic quadrangle; (2) aspect; (3) slope using a clinometer; (4) exposure using the decimal scale, 0 = ravine, 2 = sheltered valley, 4 = midslope, 6 = exposed upper slope, 8 = exposed ridge, 10 = pronounced summit; (5) water using the scale, 0 = no surface water, 2 = wet depressions present, 4 = small water body present, as along a stream, 6 = an extensive swamp, 8 = along lake; (6) canopy height read from a clinometer; (8–17) the foliage height profile (five strata were delimited at 0.7-, 2-, 5-, and 8-m heights to correspond to strata of ferns and herbs, shrubs, and three canopy divisions; each stratum rated on a 10-point scale for broadleaf and for coniferous foliage density; this score ideally standardized as the percent divided by 10 of the circumference of a ≈ 20 -m diameter circle that is obscured by broadleaf or coniferous foliage); (18–27) the tree diameter profile (the number of live and of dead trees in five size classes demarcated at 7.5-, 15-, 22-, and 30-cm diameter at breast height [DBH] within a ≈ 20 -m diameter circle). Some of these procedures are only semiquantitative but have sufficient accuracy and greater efficiency compared to more detailed measurements (cf. techniques of Braun-Blanquet 1932, Moore et al. 1970, Mueller-Dombois and Ellenberg 1974).

To develop the subalpine habitat model, 23 analytical variables were derived from the field measurements to characterize the habitat stands as thoroughly as possible (Table 2). Vegetation responses to elevation seem most pronounced towards tree line, so ele-

TABLE 2. Habitat variables used for a principal components analysis of vegetation physiognomy. Weighting factor records degree of bird response to a variable. First PCA axis describes an elevation gradient, the second a coniferous to deciduous gradient. $n = 496$ stands. * $P < .001$.

Habitat variable	Weighting factor	Axis I		Axis II	
		Eigenvector	Correlation	Eigenvector	Correlation
Elevation	.965	-.518	-.863*	-.091	-.082
Aspect	.052	-.003	-.084	.004	.070
Slope	.093	-.007	-.121	-.002	-.019
Exposure	.667	-.265	-.652*	-.073	-.098
Water	.311	.066	.348*	.013	.036
Canopy height (log-scaled)	.853	.466	.871*	-.299	.303*
Canopy coverage (%)	.502	.177	.574*	.120	.209*
Half height of vegetation	.660	.324	.805*	-.253	-.339*
Conifer percentage of foliage volume	.650	-.187	-.475*	-.596	-.816*
Total foliage volume low, 0-2 m	.216	-.033	-.255*	.038	.157*
Total foliage volume mid, 2-5 m	.179	.008	.072	.037	.180*
Total foliage volume high, >5 m	.711	.355	.820*	-.155	-.194*
Conifer foliage volume low, 0-2 m	.443	-.147	-.545*	.011	.021
Conifer foliage volume mid, 2-5 m	.286	-.026	-.147*	-.100	-.309*
Conifer foliage volume high, >5 m	.292	.082	.464*	-.251	-.764*
Broadleaf foliage volume low, 0-2 m	.282	.062	.358*	.070	.220*
Broadleaf foliage volume mid, 2-5 m	.341	.060	.289*	.754	.657*
Broadleaf foliage volume high, >5 m	.702	.248	.590*	.485	.622*
Live trees, mean DBH	.379	.146	.633*	-.169	-.394*
Live trees, standard deviation DBH	.360	.135	.616*	-.151	-.372*
Dead trees, mean DBH	.071	.010	.200*	-.033	-.370*
Dead trees, standard deviation DBH	.102	.013	.203*	-.053	-.462*
Dead trees, basal area percentage	.278	-.060	-.354*	-.051	-.162*

vation values were transformed by logarithmic scaling from tree line (1420 m). Aspect values were entered as degrees from southwest (225°) to represent the effect of greater insolation; flat areas were given the mean value (90° from southwest). Vegetation half height is the height above which half the foliage volume occurs. Foliage volume of a stratum is estimated as the stratum height range multiplied by the coniferous (and/or deciduous) foliage density score. The DBH of trees is used as a measure of stand development, while the standard deviation of DBH is used to show the range of sizes available (how even-aged or heterogeneous a particular stand is). Dead-tree percentage is the basal area percentage of dead trees in a stand. Exposure and water were recorded on semi-qualitative scales, and there is no particular biological or physiographic justification for the chosen intervals.

These variables are given weights commensurate with their importance in determining species distributions. The 23 variables differ in how strongly the species respond to them. All species respond strongly to elevation; some respond to water; a few respond to aspect, albeit weakly. The correlation coefficient r estimates the magnitude and direction of this response; its square gives the variation in species distribution accounted for by a particular habitat variable. The formula for calculating the weighting factor

WF for variable j is $WF_j = \sum_{i=1}^{20} r_{ij}^2$, where i is one of

20 species. Because habitat variables have essentially arbitrary units, some scaling is necessary. Two scalings were tested; the first standardized the variables

to a mean of 0.0 and standard deviation of 1.0. A more biological scaling results if the standard deviation of a variable is scaled to how strongly the variable influences species distributions. So instead of setting all standard deviations to 1.0, the squared correlation coefficient offers an alternate biological scaling (the squares are summed over 20 equally weighted species to represent the focus on individual species, cf. Noy-Meir et al. 1975). The ordinations using standardized and biologically scaled habitat variables were highly correlated ($r = .89$, $P \ll .001$, $n = 23$ habitat variable positions on the first eigenvector). The biological scaling has been used, with variable j 's value x_{ij} for stand i scaled to its new value x'_{ij} by

$$x'_{ij} = (x_{ij} - \bar{x}_j) \cdot \sum_{j=1}^{20} r_{ij}^2 / SD_j,$$

where \bar{x}_j is the 496-stand mean for variable j , $\sum_{j=1}^{20} r_{ij}^2$ the sum over 20 subalpine species of the squares of their correlation of occurrence with j ($n = 496$), and SD_j the standard deviation of j . The habitat axes were judged to be monotonic variables (James 1971); and principal components analysis (PCA) from the ORDIFLEX program (Gauch 1977) was performed on the 496 stand by a 23 scaled-variable matrix to obtain axes expressing the major underlying relations of the data set.

Niche observations

Foraging behavior was observed almost exclusively in the Mount Moosilauke subalpine zone, from late

May to early July 1976–1978, encompassing the incubation, nestling, and fledging periods. All daylight hours were sampled, with 75% of the data collected between 0500 and 1100 eastern daylight time, the period of greatest activity. The early morning feeding pulse compensates for thermoregulation during the quite cool night, a major energy expenditure for woodland passerines in the White Mountains (Holmes et al. 1979a). Food limitation and interspecific competition would therefore be most significant during the morning. Uncommon species, females, and nonsinging males were consciously sought to avoid bias toward conspicuous individuals; also, concealing habitats such as the upper canopy, dense fir groves, underbrush, and small ravines, were diligently searched. Data recorded on 13 618 maneuvers were foraging height, tree or herb species, distance from trunk, substrate, and maneuver type. Twelve original maneuver types were condensed for analysis so that peck = a thrust into the substrate; glean = a picking maneuver while the bird is on a substrate; hawk = a short, moving flight associated with a substrate; hover = a suspended flight while the bird picks from a substrate; and flycatch = an energetic sally to capture an airborne prey.

The data were compiled into a 20 species by 24 variable matrix (Table 4). The bird species diversity (BSD) for resource categories was also computed (Table 4), using the formula $H' = -\sum_i^{20} q_i \cdot \log_e q_i$, where

$q_i = p_i / \sum_i^{20} p_i$, and p_i is the fractional use by species i of the resource category.

Several multivariate approaches to niche ordination were tried. Species responses to niche variables are often ditonic or bell shaped. Many techniques (e.g., principal components analysis, factor analysis, discriminant function analysis) assume linear relationships; when applied to ecological data with ditonic distributions, they give distorted and even uninterpretable results (Noy-Meir and Austin 1970, Kessell and Whittaker 1976, Austin 1977a, Gauch et al. 1977). Techniques least vulnerable to distortion by ditonically distributed data include polar ordination, reciprocal averaging, and nonmetric multidimensional scaling (Austin 1977b, Fasham 1977, Gauch et al. 1977). Ordination techniques compared for niche variables were reciprocal averaging and several of its variants (detrended correspondence analysis, secondary reciprocal averaging, and reciprocal averaging followed by PCA—cf. Sabo and Whittaker 1979), polar ordination, and multidimensional scaling (ALSCAL program).

Detrended correspondence analysis (DCA) produced the best ordination. It was superior in presenting clear well-defined niche gradients. Most of the other techniques involved axes (folding the axis back onto itself) or yielded weak axes defined by a single

datum. Individualistic species (e.g., Red-breasted Nuthatch, Winter Wren) were well integrated into the community pattern by DCA. This paper presents results obtained from DCA.

DCA is an improved version of reciprocal averaging that reduces distortion on higher axes and is more tolerant of outliers (Hill 1979). Like reciprocal averaging, DCA is, in one of its algorithms, a weighted-average ordination effected by iterative approximations (Hill 1973). Species are scored by positions along an initial arbitrary gradient from 0 to 100, and their scores determine the sample scores by multiplying through the data matrix. These sample scores are then used as weights to recalculate the species scores. After each calibration, scores are rescaled from 0 to 100. The new scores allow recalculation of the sample scores, and this back-and-forth iteration (cross-calibration) continues, stabilizing in a unique one-dimensional ordination. The design is a dual ordination of species and samples, with neither paramount, and with the ordination expressing an optimal correspondence of species and sample scores. Multidimensional analogues of the first axis can be obtained with matrix algebra (Hill 1973). Like PCA, reciprocal averaging and DCA are eigenvector techniques, but differ in simultaneous double standardization, an additional division step, and use of chi-square rather than covariance or correlation distance (Chardy et al. 1976, Gauch et al. 1977). DCA differs from reciprocal averaging by breaking an axis into a series of strips, then ordinating within each strip. It also tends to equalize the species' variances along each axis. Axis length is expressed as standard deviations of species response, with 4 SD indicating a complete turnover of species. Technical details are given by Hill (1979). DCA was recently developed by M. O. Hill, and in tests on numerous sets of ecological and artificial data appeared to be the most adept technique yet for indirect ordination (H. G. Gauch, M. O. Hill, *personal communication*).

Niche and habitat relations

Each of the 20 species has a characteristic mean value for every niche and habitat variable. An expression for the relation between a particular pair of niche and habitat variables would be their correlation, computed from the 20 species' mean values for these variables. This correlation is, of course, a rougher estimate than if one were to evaluate the niche variable in a series of different habitats for each species, at great sampling effort. To demonstrate the general community relations between niche and habitat variables, a matrix giving the correlations between the 24 niche and 23 habitat variables was computed from the species mean values for these variables. This 24-by-23 matrix was submitted to centered, nonstandardized PCA to show the interrelated groups of variables. A

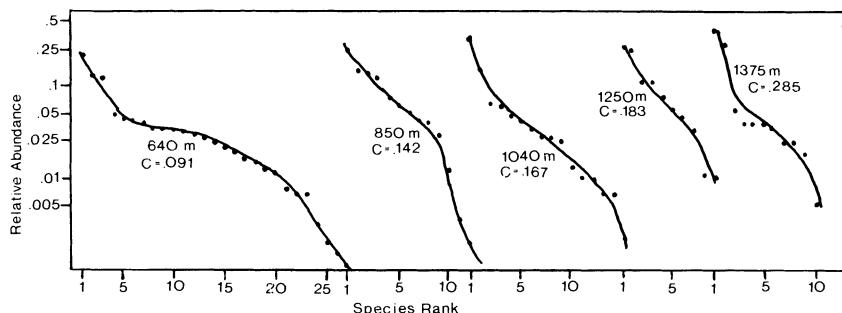


FIG. 2. Dominance-diversity curves along an elevational transect in the subalpine zone. Curves progress from log-normal to broken-stick and geometric-series distributions at higher elevations. Simpson index of dominance: $C = \Sigma p^2$.

similar procedure has been used by Barkham and Norris (1970) for vegetation and soil variables. Canonical correlation analysis (CCA), occasionally used for this kind of problem (Karr and James 1975), is generally ineffective for ecological data sets, and offers no additional information beyond a PCA or reciprocal averaging ordination (Gauch and Wentworth 1976). Further, CCA cannot handle matrix singularities, i.e., when some row or column of the data matrix is a linear compound of one or more others (Barkham and Norris 1970); the current data set contains nine matrix singularities. Thus, a straightforward PCA of the correlation matrix was preferred to a CCA.

RESULTS

Species populations and territories

Table 1 gives the territory sizes and densities calculated. The Blackpoll Warbler is the most abundant species (31% relative abundance in the subalpine zone, 18% in the climax forest). The virgin forest has a more even distribution of densities ($H' = -\Sigma p \cdot \log p = 2.68$) than the subalpine zone ($H' = 2.38$); this is discussed under habitat relations. The 1977 census was similar to those in 1976 and 1978 with one noticeable trend: following the bitter winter of 1976–1977, several species with wintering grounds in the southern “snow belt” (Pennsylvania and south) decreased greatly—the Winter Wren (down 54%), Golden-crowned Kinglet (down 56%), and Dark-eyed Junco (down 43%). The similarly bitter winter of 1977–1978 was followed by an additional slight reduction.

Territory size averages 1.6 ha ($n = 20$ species), but is much larger in two species with specialized requirements. Red-breasted Nuthatches (10 ha) rely on dead trees (20% of all maneuvers) which are quite scarce (7% of all trees in nuthatch territories), and may be limited by holes for nest sites because woodpeckers are rare (Bent 1948). Solitary Vireos (5 ha) often have narrow territories in the subalpine, as long as 300 m along streams. Considering the remaining 18 species as using more finely grained resources, territory sizes are moderately correlated with body mass ($r = .58$,

$P = .01$), paralleling resource requirements and energetic expenditures respectively (McNab 1963, Schoener 1968, Harestad and Bunnell 1979). Territoriality's primary adaptive function in insectivorous birds has been inferred to be defense of the food resource base (Stenger 1958, Verner and Engelsen 1970, Williams and Batzli 1979). The subalpine correlation supports food as a determinant of territory size, and suggests food limitation.

Along an elevation transect from the northern hardwood forests to krummholz (Fig. 2), dominance diversity curves (Whittaker 1965, 1972, May 1975) become increasingly steep. From broken-stick distributions in the low-elevation forests (640 m+), the curves pass through intermediate forms toward geometric series distributions at high elevations (1375 m). Able and Noon (1976) found a similar trend in the Adirondack and Green Mountains for subalpine birds, and attributed it to effects of environmental severity. Dominance, measured by the Simpson index ($C = \Sigma p^2$, for relative abundance p), correlated with elevation ($r = .80, P < .05, n = 6$ census tracts), indicating simpler communities at higher altitudes. Total population was uncorrelated with elevation ($r = .46, P > .20, n = 6$); this suggests that the stressful environments at higher elevations may still provide adequate resources for well-adapted species. With Blackpoll Warbler densities subtracted, the remaining population density varies irregularly without elevation trends at 360 ± 70 SD pairs/km². This suggests that an overall carrying capacity (based perhaps on food levels) may exist. No trend was found relating the diversity (generalist/specialist) of foraging for the species present to elevation ($r = .35, P > .20$); any such trend within species would be obscured, however, since the niche data are pooled from all elevations.

Habitat relations

A principal components analysis (PCA) of 23 habitat variables for 496 stands produced a model of subalpine vegetation in which elevation and coniferous/deciduous foliage were the primary vegetation gradients. Ta-

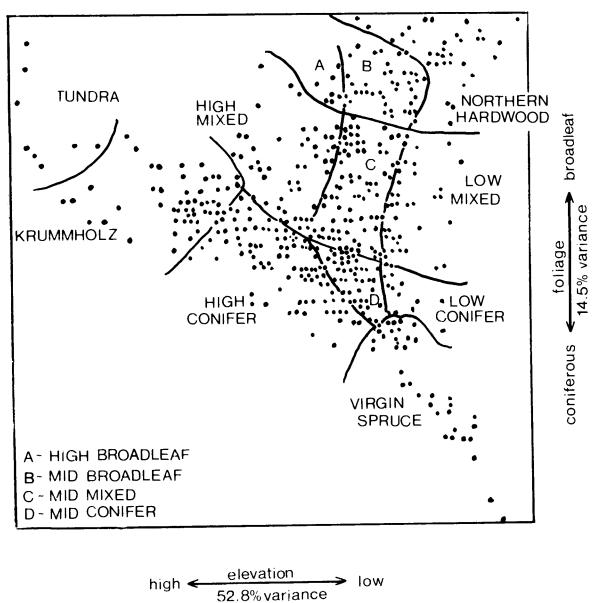


FIG. 3. Vegetation model of subalpine habitats from principal components analysis with points representing stand samples. Details of axis significance in Table 2. Divisions are by elevation—low (<750 m), mid (750–975 m), high (>975 m); by percent conifer foliage volume—broadleaf (<30%), mixed (30%–70%), conifer (>70%); and by physiognomy. Low broadleaf stands are classified as northern hardwood forests.

ble 2 shows the relations of the 23 habitat variables to the first two PCA axes and the weighting factor Σr^2 . The weighting factor shows great species response to elevation and exposure and to other variables correlated with the first component. Variables involved with the secondary coniferous/deciduous foliage gradient, such as broadleaf foliage volume, generally had lower weight factors. Some variables, aspect and slope in particular, had little effect on bird species distributions. The eigenvectors of Table 2 give the PCA ordination of habitat variables. Because eigenvectors characterize relative, not absolute, relations of the variables to the PCA axes, partial correlation coefficients (Table 2) better show the strength of these relations.

The corresponding ordination for 496 stands (Fig. 3) presents an organized description of subalpine vegetation. When each stand is classified as to elevation (low <750 m, mid 750–975 m, high >975 m), foliage type (broadleaf type with >70% broadleaf foliage volume, mixed 30%–70%, conifer <30%), and stature (typical second-growth forests, virgin forests, krummholz, tundra), the various groups form intergrading clusters whose halfway boundaries are demarcated in Fig. 3. The PCA ordination of stands is then used as a model of subalpine vegetation, and as a base map to plot bird species responses.

Fig. 4 locates the population centers for the 20 sub-

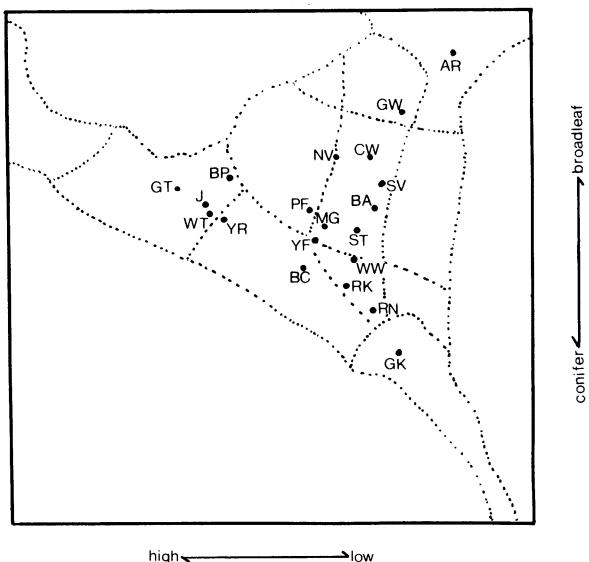


FIG. 4. Population centers of 20 subalpine species plotted on the vegetation chart of Fig. 3. See Table 1 for species abbreviations.

alpine species on the vegetation base map. Although each species has different mean values for characteristic habitat variables (Table 3), a species may occur over a wide range of habitats. Fig. 5 illustrates differential habitat selection by five wood warblers, and suggests the evolution of a krummholz habitat selection pattern in the warblers by this sequence: (1) extension of range from northern hardwoods center into subalpine, American Redstart; (2) population center moves up into subalpine, while the species is still common in the northern hardwoods, Black-throated Green Warbler; (3) species spreads more into subalpine, no longer found throughout northern hardwoods, Canada Warbler; (4) species found throughout the subalpine, population center moves to higher elevations, Yellow-rumped Warbler; (5) population concentrated in krummholz, less common at lower elevations, Blackpoll Warbler.

The primary environmental gradient is elevation. As elevation increases and conditions become colder, wetter, and windier (Fig. 1), the forest structure changes to a more coniferous, less-developed forest of smaller, more even-aged trees with a greater proportion of these dead. Bird species diversity begins a steep decline at 1100–1200 m elevation, with a marked drop in the krummholz as the increasing environmental stress and decreasing habitat variety selectively filter bird species (Fig. 6). At 1100–1200 m, with stands generally more exposed, broadleaf trees become much scarcer as fir increases in abundance; and at tree line the firs themselves give way to alpine dwarf-shrub communities.

A number of species appear adapted to the high end

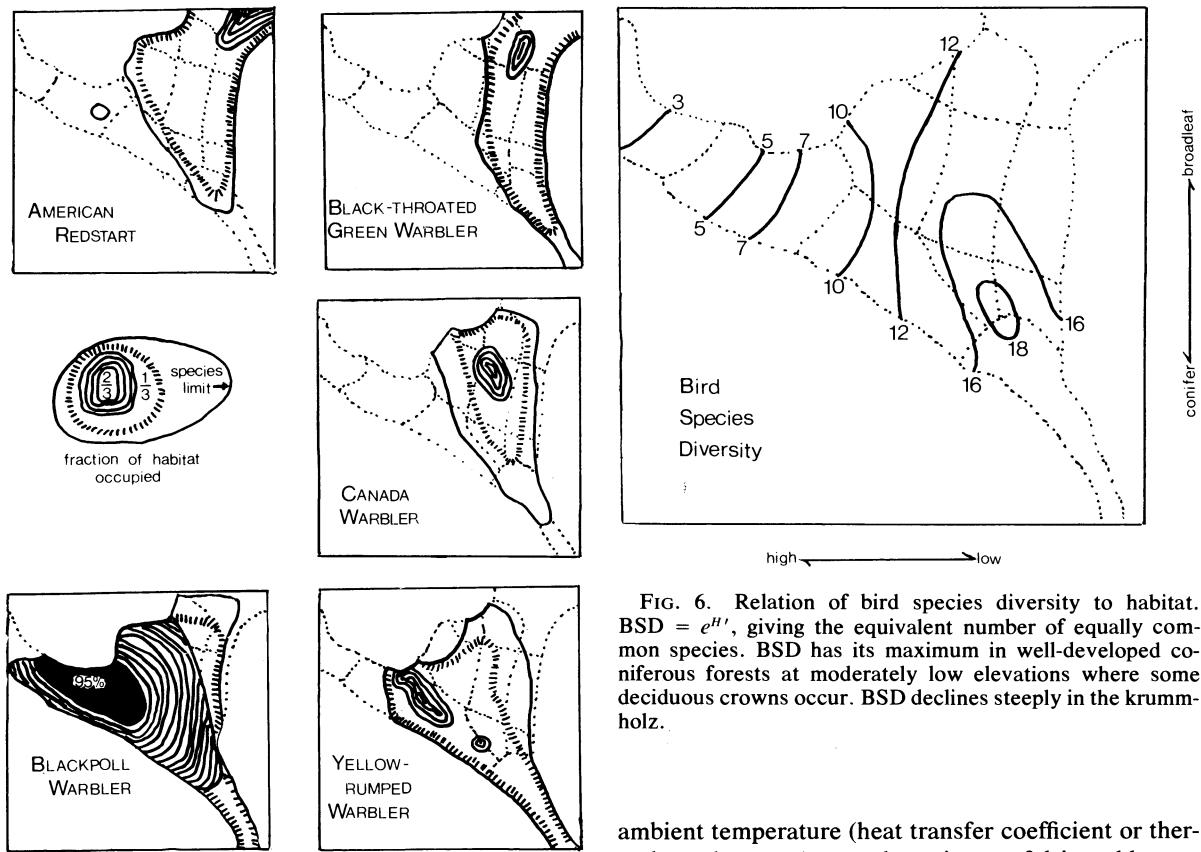


FIG. 5. Habitat selection patterns of five warbler species, differentiated along the elevation gradient. Graphed on the vegetation chart of Fig. 3.

of the elevation gradient. Among the warblers, the Blackpoll numerically dominates the krummholz community. The Yellow-rumped Warbler, whose geographic range overlaps the Blackpoll's except in the far north, is centered in high-elevation conifer forests, and abruptly declines in the mid-krummholz. The Dark-eyed Junco and White-throated Sparrow extend beyond the Blackpoll into tundra communities; larger size and ground feeding are advantageous for very high elevations. The two sparrows have different nest site requirements that may aid ecological separation. The White-throat uses a clearing edge with a lookout and the Junco uses a dense shrub clump with a rock outcrop or exposed bank (Eaton 1968, Lowther and Falls 1968). These four species have similar patterns of decreasing occurrence toward lower elevations.

Habitat selection by the Gray-cheeked Thrush resembles that of the four previous species; but this species has a narrower range into lower elevations, where it may compete with the morphologically and behaviorally similar Swainson's Thrush. The Gray-cheeked Thrush has a significantly flatter slope than Swainson's Thrush of standard metabolism against

FIG. 6. Relation of bird species diversity to habitat. $BSD = e^{H''}$, giving the equivalent number of equally common species. BSD has its maximum in well-developed coniferous forests at moderately low elevations where some deciduous crowns occur. BSD declines steeply in the krummholz.

ambient temperature (heat transfer coefficient or thermal conductance), an adaptation useful in colder environments (Holmes and Sawyer 1975).

At elevations below 750 m, northern hardwood forests predominate, from which a number of species range into the subalpine, in order of decreasing subalpine extent: American Redstart, Red-eyed Vireo (*Vireo olivaceus*), Black-throated Blue Warbler (*Dendroica caerulea*), and Ovenbird (*Seiurus aurocapillus*).

A second important gradient, from broadleaf to coniferous foliage, represents both paper birch to climax red spruce succession in the subalpine zone, and habitat gradients from northern hardwood forests toward pine forests on drier sites below 750 m and toward spruce forests at higher elevations. Below 1100 m habitat selection is salient along this gradient. The Golden-crowned Kinglet is most abundant in the old spruce forests with their great coniferous foliage volume, leading to a well-spaced sequence through the Red-breasted Nuthatch and Bay-breasted Warbler in developed coniferous and mixed forests, the Canada and Black-throated Green Warblers in ecotonal mixed forests, to the American Redstart in early seral and northern hardwood forests (Figs. 4 and 5). Several species are widely distributed through the mid-subalpine zone, 800–1100 m, with graphs similar to the Yellow-rumped Warbler's: Yellow-bellied Flycatcher, Swainson's Thrush, Nashville Warbler, Magnolia Warbler, and Purple Finch. Although higher axes add little to the

TABLE 3. Species means for habitat selection parameters. Sample sizes and abbreviations in Table 1. On the exposure scale, 2 = sheltered valley, 4 = midslope, 6 = exposed upper slope. On the water scale, 0 = no surface water, 2 = wet depressions present, 4 = small water body present (e.g., stream or swamp). Foliage volume is a linear index to amount of foliage present (see text).

Species	Elevation mean (m)	Elevation standard deviation	Exposure	Water	Canopy height (m)	Canopy coverage	% Conifer foliage volume	Conifer foliage volume low, 0–2 m	Broadleaf foliage volume high, >5 m	Live trees DBH (cm)
YF	1090	180	4.1	0.9	9.0	65	64	32	35	10
BC	1210	240	4.9	1.2	8.8	63	80	42	7	11
RN	960	290	3.2	1.5	11.1	70	54	10	55	13
WW	950	200	2.9	3.0	10.4	69	56	29	47	12
ST	1020	240	3.8	1.8	9.0	64	61	28	45	12
GT	1290	190	5.1	0.6	4.8	47	75	45	13	7
GK	850	200	3.3	1.9	13.1	66	64	20	50	13
RK	1010	200	3.4	3.2	9.5	65	77	28	16	12
SV	680	240	2.8	3.0	12.2	73	41	20	90	12
NV	1030	210	3.7	1.9	9.0	60	53	33	36	10
MG	1080	270	3.8	1.3	8.8	59	68	37	34	10
YR	1140	190	4.5	1.0	7.9	59	72	33	17	10
GW	820	180	3.4	1.6	12.5	79	37	15	113	13
BA	880	160	3.4	2.5	11.3	75	59	19	44	13
BP	1210	260	4.4	1.0	6.4	57	69	39	25	9
CW	870	250	3.2	1.7	10.4	76	44	27	68	11
AR	830	280	3.2	1.9	10.4	74	38	20	92	11
PF	1100	370	4.1	1.2	7.5	64	64	30	45	10
J	1340	270	5.4	0.5	4.0	42	72	38	15	7
WT	1300	250	5.0	0.8	5.0	45	75	41	12	8

PCA ordination, several species depending on water are not emphasized until axis V. Streams are a key component of Winter Wren and Solitary Vireo territories, and swamps the most likely sites for Ruby-crowned Kinglets (Table 3, column 5).

Bird species diversity (BSD) also exhibits patterns in the subalpine vegetation (Fig. 6). BSD was calculated from cells of 20–25 stands in the same area of the base map, using percent habitat occupied for species entries in the formula $BSD = \exp(-\sum p \cdot \log_e p)$. BSD increases along the broadleaf/conifer succession gradient, reaching a maximum in well-developed pre-climax fir-spruce forests where the deciduous element constitutes ≈15% of the foliage volume, such as those in Jobidunk Ravine east of Mount Moosilauke and along Desolation Trail northwest of Mount Carrigain. Since deglaciation 10 000 yr ago, such preclimax forests may have predominated in the White Mountains because old climax stands are susceptible to wind-toppling. They were thus spatially and temporally extensive communities where species would have had sufficient opportunity to coadjust resource use patterns for coexistence.

Niche relations

Foraging behavior involves insect resources that differ in their taxa, size, behavior, macroscopic and microsite locations. Gleaning insectivorous birds consume taxa of suitable size proportional to their encounter (McAtee 1932, Root 1967), although during

the fledging period lepidopteran larvae are preferred (Morse 1976).

Foraging height, foliage type, and crown position (proximal/distal to trunk) are the main macroscopic resource variables. Substrate-maneuver combinations that describe different methods for food acquisition are microsite variables. A substrate gradient is represented from airborne insects through those on leaves to increasingly coarse substrates, with litter and fallen logs appended as distinct resources. Maneuver types for access to these substrates form a sequence from generally low energy expense, stationary maneuvers (peck, glean) to active, energetic ones (hover, flycatch).

The major divisions of community resource use are terrestrial vs. arboreal position and a canopy substrate gradient. The first detrended correspondence analysis (DCA) axis accounts for 77% of the variance, and mainly segregates five forest-floor species (Fig. 7, Table 5). These five further separate by the Winter Wren's specialty of fallen logs, the Dark-eyed Junco's use of twig pecks and the understory; the White-throated Sparrow use both twig and litter pecks; the thrushes are elevation replacements that peck and glean litter and also feed in the understory. This first gradient is ≈3.74 SD of species response in length, indicating nearly complete turnover of species.

The second DCA axis (16% of the variance) represents a gradient from heavy coarse substrates proximal to the trunk (boles, branches) to finer light sub-

TABLE 4. Niche variables used for an ordination of foraging behavior by detrended correspondence analysis. Fractional use (and bird species diversity) of 24 resource categories by 20 subalpine birds. Rows 1–14 represent maneuver-substrate combinations adding to 1.000 for each species, 15–16 positions in live and dead trees, 17–20 live tree and stratum classes, 20–24 foraging height strata adding to 1.000. Sample sizes and abbreviations in Table 1.

	YF	BC	RN	WW	ST	GT	GK	RK	SV	NV	MG	YR	GW	BA	BP	CW	AR	PF	J	WT	(H') BSD	
1. Aerial flycatch	.191	.004004002003	.008	.005	.001	.005	.009	.016	1.01	
2. Leaf glean	.285	.390	.332	.052	.216	.101	.491	.537	.369	.575	.521	.395	.388	.484	.446	.290	.269	.683	.172	.092	2.87	
3. Leaf hawk	.296	.026	.029	.010	.067	.050	.196	.261	.073	.156	.131	.152	.140	.035	.109	.099	.124	.115	.050	.007	2.74	
4. Leaf hover	.136	.037	.035067	.122	.076	.118	.006	.054	.047	.096	.155	.036	.043	.086	.335	.072	.003	.002	2.58	
5. Twig peck	.008	.125	.018	.028	.014	.029	.019	.011	.017	.016	.007	.051	.017	.006	.004	.025	.010	.010	.202	.192	2.29	
6. Twig glean	.053	.154	.023	.003	.071	.043	.113	.055	.391	.156	.217	.179	.185	.324	.300	.360	.174	.024	.215	.213	2.73	
7. Twig hawk and hover	.055002046	.014	.060	.011	.073	.032	.057	.065	.078	.034	.080	.104	.058	.010	.057	.020	2.69	
8. Branch peck037	.097007015006005	.011	.001	.004003	.001	.024	.015	.014	1.98	
9. Branch glean044	.027011014067	.011	.006	.019	.019	.064	.009	.018	.007	.063	.017	.018	2.49	
10. Bole peck118	.342004	.007005	.019	.001	.012	.003	.001003	.004	1.08	
11. Bole glean	.003	.066	.095	.014006001	.010	.011002	.005002	...	1.56	
12. Litter peck115	.188	.396	.002001002	.214	.363	1.54	
13. Litter glean143	.270	.237	.002004038	.062	1.44	
14. Fallen log maneuvers633	.039	.007014	.014	0.46
15. Distal to trunk	.598	.414	.344	.030	.176	.179	.516	.614	.567	.312	.413	.496	.570	.509	.564	.437	.514	.618	.230	.188	2.89	
16. Proximal to trunk	.391	.586	.657	.102	.200	.100	.480	.386	.433	.688	.588	.504	.430	.505	.436	.563	.476	.382	.481	.349	2.92	
17. Conifer tree foliage	.421	.820	.491	.063	.124	.264	.941	.993	.575	.450	.720	.604	.431	.402	.540	.363	.090	.224	.579	.372	2.84	
18. Broadleaf tree foliage	.568	.118	.306	.045	.252	.014	.055	.007	.425	.550	.280	.365	.569	.598	.451	.634	.900	.776	.136	.164	2.70	
19. Herb foliage149	.086002030	.024	1.18
20. Forest floor815	.486	.636	.004003001006257	.427	1.57	
21. Understory, 0.1–2 m	.011	.026	.025	.154	.223	.264	.033085	.126	.035042	.043	.004130	.094	2.34	
22. Midstory, 2–5 m	.476	.474	.233	.031	.199	.100	.349	.044	.140	.379	.424	.399	.238	.088	.387	.717	.672	.254	.357	.342	2.81	
23. Midcanopy, 5–8 m	.424	.313	.334092382	.522	.687	.436	.302	.373	.515	.665	.467	.224	.281	.548	.168	.134	2.79	
24. Upper canopy, >8 m	.089	.188	.409233	.434	.173	.100	.155	.191	.248	.247	.103	.018	.038	.197	.088	.003	2.58	

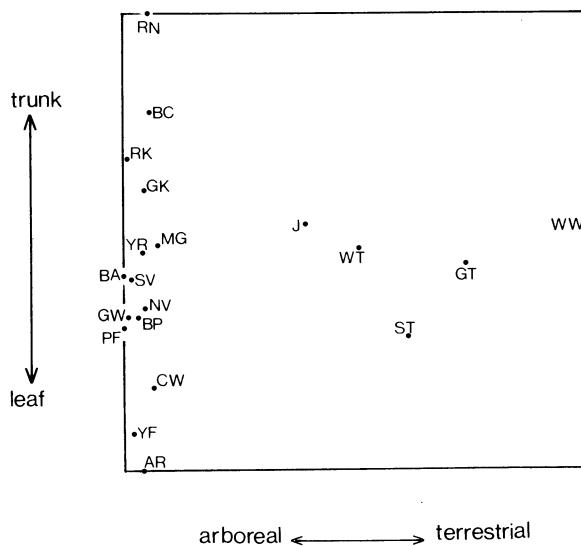


FIG. 7. Niche responses ordinated by detrended correspondence analysis. Axis I represents an arboreal to terrestrial gradient. Axis II represents a gradient from fine to heavy substrates, and is correlated with broadleaf to coniferous use. Axis significance detailed in Table 5. Axes I and II account for 77% and 16% of the variance, respectively.

strates exploited by active maneuvers in the distal crowns (leaf hovers, aerial sallies). Because coniferous trees generally have larger trunks and broadleaf foliage is more open, this gradient also goes from coniferous to deciduous use. The Red-breasted Nuthatch represents a bole-pecking guild. The two kinglets using fine substrates, and the Boreal Chickadee using larger ones, are both conifer specialists. The next two species along the gradient, the Magnolia and Yellow-rumped Warblers, form a transition from conifer and large substrate use to the more generalized species in the central cluster. These central species usually feature small specialties—the Solitary Vireo, Bay-breasted and Blackpoll Warblers favor twig gleans, the Nashville Warbler and Purple Finch use leaf gleans most, and the Black-throated Green and Bay-breasted Warblers forage at greater heights (see Table 4). After the central cluster, the Canada Warbler and Yellow-bellied Flycatcher, active aerial foragers on both deciduous and coniferous foliage, form a link to the American Redstart, the most energetic and broadleaf-dependent species. This second gradient is ≈ 3.18 SD of species response in length, indicating significant turnover of species.

The Purple Finch, a deciduous foliage specialist, prefers leaf gleaning and distal canopy positions, for which its chunky "grosbeak" morphology seems unadapted. Holmes et al. (1979b) recorded a similar niche for the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) in lower elevation northern hardwoods forests. Adaptations for winter granivory and frugivory probably select for their morphology.

TABLE 5. Relations among niche variables from an ordination by detrended correspondence analysis. Axis I describes a terrestrial-arboreal gradient. Axis II describes a gradient from fine to coarse substrates that correlates with deciduous to coniferous foliage. * $P < .05$, ** $P < .001$, $n = 20$ species.

Niche variable	Axis I		Axis II	
	Eigen-vector	Corre-lation	Eigen-vector	Corre-lation
Variance accounted for	77.0%		15.5%	
Aerial flycatch	0.5	-.158	0.0	-.417
Leaf glean	5.6	-.776**	41.5	.153
Leaf hawk	5.6	-.513*	34.6	-.318
Leaf hover	9.4	-.256	25.2	-.554*
Twig peck	30.5	.298	52.5	.276
Twig glean	9.1	-.366	35.5	-.260
Twig hawk and hover	9.1	-.362	29.6	-.581*
Branch peck	7.0	-.179	77.4	.711**
Branch glean	4.8	-.379	44.7	.160
Bole peck	0.0	-.185	100.0	.704**
Bole glean	7.2	-.139	86.8	.714**
Litter peck	63.6	.781**	43.1	.005
Litter glean	72.5	.848**	37.1	-.182
Fallen log maneuvers	100.0	.686**	51.3	.082
Distal to trunk	5.6	-.885**	38.1	-.389
Proximal to trunk	8.3	-.789**	42.8	.376
Conifer tree foliage	8.6	-.508*	49.4	.662*
Broadleaf tree foliage	5.1	-.538*	26.4	-.782**
Herb foliage	63.1	.590*	32.7	-.172
Forest floor	74.6	.996**	43.4	-.002
Understory, 0.1–2 m	47.6	.834*	41.8	-.019
Midstory, 2–5 m	9.9	-.396	33.3	-.443
Midcanopy, 5–8 m	2.7	-.820**	39.9	-.016
Upper canopy, >8 m	0.8	-.610*	55.7	.790**

Higher DCA axes reflect compromises made on the first 2 axes—e.g., the kinglets' use of fine conifer substrates is itself an axis; the longest of these axes is 1.3 SD of species response long, accounts for 5% of the variance, and is not significant.

The pattern of BSD in the resource categories may be interpretable as a function of energetics, morphological adaptation, and insect productivity (see Table 4). BSD is lower for maneuvers more energetic than glean (hawk, hover, flycatch); few species rely on these maneuvers probably because search costs tend to be minimized when possible (Schoener 1971), and often a glean would suffice. Peck maneuvers depend on suitable bill adaptations; since relatively few species are thus specialized, pecks show a lower BSD than gleans—this principle may apply to specialization for hovers and flycatches as well. BSD is higher on leaves and twigs than on heavier substrates that require specialization to exploit and offer insects refugia from search. Although lepidopteran larvae generally feed on foliage, they frequently take refuge hidden in the bark or litter during daylight and feed nocturnally. Of course, these hidden resources may be less than those on foliage, which could lead to lower BSD for the heavier substrates. BSD increases in the complex foliage strata from the simpler ground layer, tracking the foliage's greater insect resources into the canopy.

TABLE 6. Principal components analysis of niche-habitat correlations. The matrix of correlations between niche and habitat variables, using species means as data, is submitted to PCA to establish groups of related variables. On axis I terrestrial foraging becomes more prominent at higher elevations. Axis II shows active maneuvers and lighter substrates correlated with the more open broadleaf foliage. Conifer trees, having greater height and DBH than broadleaf species, support woodpecking and high-canopy species. See also Fig. 8. * $P < .05$, ** $P < .001$, $n = 24$ niche, 23 habitat variables.

Variable	Axis I		Axis II	
	Eigenvector	Correlation	Eigenvector	Correlation
Variance accounted for		70.9%	15.9%	
Niche variables				
Aerial flycatch	-.043	-.314	.027	.220
Leaf glean	.171	.911**	-.092	-.180
Leaf hawk	.105	.820**	-.041	-.104
Leaf hover	.138	.723**	.249	.572*
Twig peck	-.394	-.935**	.016	-.058
Twig glean	.059	.486*	.299	.786**
Twig hawk and hover	.109	.654**	.332	.737**
Branch peck	.020	.203	-.274	-.753**
Branch glean	.156	.856**	.029	.047
Bole peck	.063	.410*	-.270	-.660**
Bole glean	.061	.402*	-.278	-.691**
Litter peck	-.436	-.990**	.064	-.002
Litter glean	-.217	-.971**	-.017	-.088
Fallen log maneuvers	.046	.369	-.130	-.314
Distal to trunk	.235	.954**	.042	.085
Proximal to trunk	.113	.869**	.022	.161
Conifer tree foliage	-.013	.015	-.326	-.755**
Broadleaf tree foliage	.205	.750**	.412	.661**
Herb foliage	-.221	-.980**	.027	-.015
Forest floor	-.254	-.965**	-.039	-.123
Understory, 0.1–2 m	-.359	-.991**	.003	-.038
Midstory, 2–5 m	-.070	-.280	.281	.796**
Midcanopy, 5–8 m	.286	.979**	.011	.036
Upper canopy, >8 m	.239	.816**	-.348	-.506*
Habitat variables				
Elevation	-.285	-.983**	-.069	-.114
Aspect	-.030	-.147	-.061	-.142
Slope	-.111	-.533**	.297	.688**
Exposure	-.231	-.962**	-.007	-.014
Water	.146	.735	-.107	-.260
Canopy height	.296	.987**	-.062	-.100
Canopy coverage	.298	.986**	.075	.119
Half height of vegetation	.288	.975**	-.108	-.176
Conifer % of foliage volume	-.174	-.735**	-.303	-.618*
Total foliage volume low	-.196	-.892**	.131	.286
Total foliage volume mid	.063	.549*	-.034	-.142
Total foliage volume high	.277	.992**	-.043	-.074
Conifer foliage volume low	-.268	-.988**	-.023	-.041
Conifer foliage volume mid	-.076	-.455*	-.257	-.746**
Conifer foliage volume high	.206	.695**	-.407	-.661**
Broadleaf foliage volume low	.191	.819**	.240	.496*
Broadleaf foliage volume mid	.138	.640**	.265	.591*
Broadleaf foliage volume high	.198	.832**	.258	.522*
Live trees, mean DBH	.253	.933**	-.192	-.342
Live trees, standard deviation DBH	.240	.968**	-.109	-.211
Dead trees, mean DBH	-.040	-.195	-.271	-.633*
Dead trees, standard deviation DBH	-.028	-.101	-.456	-.784**
Dead trees, % basal area	-.289	-.975**	-.050	-.081

Species ecotopes: niche and habitat interrelations

Table 6 groups the related niche and habitat variables using a PCA of the correlation matrix. In Fig. 8, the first two PCA axes have been used for an ordination of species ecotopes, using ecotope as the species' full range of environmental relations, includ-

ing both niche and habitat responses (Whittaker et al. 1973). The community is organized into three groups: (1) three ground-foraging species with populations centered at high elevations, (2) nine species, with a variety of niches occurring through most of the subalpine, forming a core assembly, (3) eight predominately lower elevation species differentiating along a coniferous to deciduous use gradient.

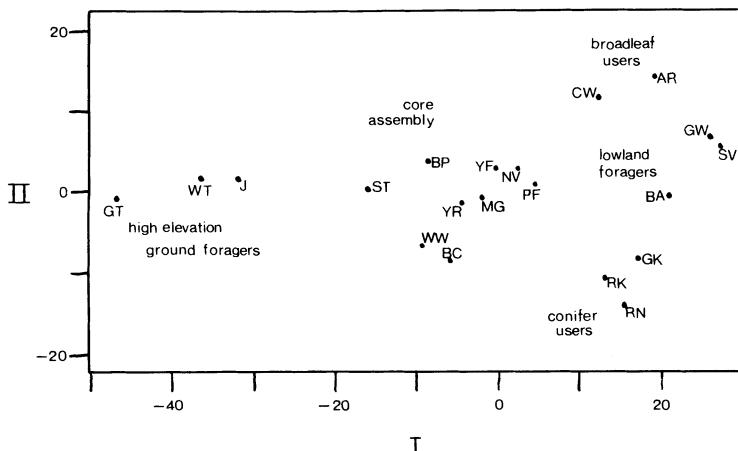


FIG. 8. Ordination of species ecotopes, using niche-habitat axes of Table 6.

The first PCA axis accounted for 71% of the variance, and correlated with both the first habitat axis ($r = .85, P < .001, n = 23$ habitat variables) and the first niche axis ($r = -.65, P < .001, n = 24$ niche variables); thus the elevation/forest structure gradient correlates with the terrestrial/arbooreal foraging segregation. Note the concentration of lower habitat features and ground-feeding niche characters at negative correlations vs. the concentration of canopy habitat features and foliage-feeding niche characters with strong positive correlations. At higher altitudes and greater exposures the forest shortens, and loses its deciduous element; also, underbrush begins to predominate and the conifers grow more compact. Hence, foraging moves to lower heights and to twigs, where rich lichen growths provide nocturnal insects with refuge. Twig pecking is particularly influenced by elevation ($r = .73, P < .001, n = 20$ species means) and exposure ($r = .69, P < .001$). Moreover, the decreased foliage volumes may act with colder climate to squeeze out the smaller foliage gleaning insectivores (all krummholz species exceed 12 g).

The second PCA axis accounted for 16% of the variance and correlated with both the second habitat axis ($r = .65, P < .001$), and the second niche axis ($r = -.67, P < .001$). The coniferous/broadleaf gradient is represented in both habitat and niche, and further explains the fine/coarse substrate gradient. Older forests, usually the only subalpine stands to exceed 8-m height and present a fair array of dead boles, are mainly coniferous. Broadleaf species form early successional stands that are often short lived; these species have open deliquescent branching patterns and on death their boles quickly rot and fall. Hence those birds foraging above 8 m on coniferous trees, or on boles and large branches, will favor coniferous stands. Birds in deciduous stands can better exploit the more open deciduous foliage with hover and glean maneuvers. Conifer foliage volume above 4.5 m especially correlated

with maneuvers in the upper canopy ($r = .71, P < .001$). The standard deviation of dead tree DBH correlated with bole pecking ($r = .69, P < .001$). The third PCA axis (6% variance) was not readily interpretable, and further axes rapidly declined in variance accounted for.

The loss of information by compacting so many niche and habitat variables into two axes is inevitable. However, among these many variables two major directions of species response have been recognized; these two directions represent a good share, though far from all, of the species' adaptive responses to the environment. Niche and habitat are intimately related, to be expected from the striking changes in vegetation along elevation and foliage gradients. Selection forces operating on habitat partitioning correspondingly affect the niche. The species ecotope is an evolutionary response to environmental constraints, available resource exploitation opportunities, and potential competitive interactions.

DISCUSSION

Food limitation, interspecific competition, and niche differentiation

Two assumptions underlie much of the interpretation of niche relationships: that species niches represent differentiation in the use of limited resources, which reduces competition between species, and that such differentiation is an evolved, selectively determined characteristic of species. Neither of these can be given formal proof. Summer food resources do not limit all communities (Wiens 1974) or in all breeding seasons. A few studies have shown conclusively, however, the role of food limitation and competition in community structure (Davis 1973, Samson and Lewis 1979, Williams and Batzli 1979; cf. also Lack 1954, 1966). Despite lack of proof, sufficient evidences are in accord with the two assumptions that these seem

reasonable (though incomplete) bases for interpreting subalpine bird community structure.

In the subalpine forest, the annual summer pulse of insect productivity is the major resource base for passerine breeding. Insect populations vary greatly year to year, so only in scarcer years will food limit breeding success. During a *Heterocampa* caterpillar outbreak in a nearby northern hardwoods forest, species abandoned their usual niches to exploit the superabundant resources—even woodpeckers hawked larvae from leaves (R. T. Holmes, *personal communication*). Aside from cases of resource superabundance, the relative roles of food limitation vs. opportunistic foraging optimization in determining the observed structure of a particular community may intergrade and be difficult to assess. Rabenold (1978) was able to evaluate the relative importance of limitation vs. optimization by studying geographically separate spruce-fir forests of very similar physiognomy.

The widespread occurrence of foliage gleaning in the subalpine (Table 4, rows 2 and 6), one of the energetically cheapest modes of foraging (Holmes et al. 1979a), represents foraging optimization. That species rely on other modes as well possibly results from food limitation as a selective pressure. In a northern hardwoods forest near Mount Moosilauke, bird predation reduced insect resource levels by 37% compared to foliage protected from bird predation, with the maximum reduction of 63% occurring during the fledging period (Holmes et al. 1979c). Depending how close to the carrying capacity the overall population density is, subalpine forests may have similar reductions of their insect levels. With such insect reductions, interspecific competition could select for niche differentiation. The correlation between territory size and body mass ($r = .58$, $P = .01$, $n = 18$ species) supports the occurrence of food limitation in the subalpine. The subalpine summer begins abruptly, with most species fledging within a short time at the end of June. Competition for food in scarce years is thus a plausible selection force in this community because of approximate synchrony of breeding. The observations in many studies (cf. Schoener 1974) of distinct patterns of species difference in foraging are best interpreted as resource use by niche-differentiated species for which interspecific competition is selectively significant during some years (Lack 1966).

The potential role of thermoregulation in habitat selection

The Blackpoll Warbler seems optimally adapted to the colder climates of higher elevations and latitudes. How might thermoregulation influence a bird's habitat selection pattern? Holmes et al. (1979a) studied passerine bioenergetics in a nearby hardwood forest at lower elevations and unexpectedly found energy expenditures during the cool night to be an important item in the budget. Thermoregulatory responses can

be characterized by critical temperatures (lower and upper bounds of thermoneutrality) and the heat transfer coefficient (thermal conductance) (Calder 1974). Holmes and Sawyer (1975) hypothesized the significantly lower heat transfer coefficient of the Gray-cheeked Thrush compared to Swainson's Thrush was an adaptation for colder temperatures. Several temperate, subarctic, and subalpine studies have indicated that adult birds with altricial young live near the limits of their energy reserves during the breeding season (Yarbrough 1970, 1971, Morton et al. 1973, Holmes 1976), possibly as a result of food limitation. Sheldford's law of tolerance, that when an organism nears one particular tolerance limit, its tolerance for other factors narrows, may further sensitize these birds to the climatic regime, with thermoregulatory parameters determining in which habitats reproductive success is possible.

Numerous studies have shown relations between body size and avian energetics (cf. Calder 1974), so that the absence in the krummholz of species with mean body masses below 12 g suggests thermodynamic constraints. Metabolic rate, lower critical temperature, and the heat transfer coefficient are power functions (with positive fractional exponents) of body mass, so the large size of the Blackpoll Warbler (12.8 g) compared to other warblers ($\bar{x} = 10.1$ g, $n = 7$ subalpine species) confers a thermoregulatory advantage (based on regression equations) in colder, wetter environments. Moreover, metabolic and thermoregulatory parameters of birds living in cold or hot climates have been found predictably to deviate from their predicted regression values on body mass (Trost 1972, Blem 1973, Dawson and Bennett 1973, Kendeigh and Blem 1974). Thus, bioenergetic parameters have the versatility beyond regression predictions to be adapted to a particular environmental regime. The subalpine climate seems so distinct from the climate of lower elevations that at least some of the subalpine species should accrue a competitive advantage from their greater energetic efficiency compared to other birds lacking bioenergetic adaptations specifically for cold, wet, windy regimes.

Ecotope of the Blackpoll Warbler

The Blackpoll Warbler prefers high-elevation communities (Fig. 5), and territory size decreases with elevation ($r = -.54$, $P < .001$, $n = 54$ territories on Mount Moosilauke) while population densities increase. If the Blackpoll is bioenergetically better adapted than other warblers to the colder climate at higher elevations, it would have a competitive edge through increased ecological efficiency in the krummholz, which may lead to its ecological dominance there. Primary, and presumably secondary, productivity decreases with elevation in the White Mountains based on stand characteristics and temperatures (Reiners and Lang 1979),

so insect levels should not be less at lower elevations. Blackpoll densities increase greatly with elevation, but the population density for the remaining species taken together shows no elevation trend. Hence, the larger territories at lower elevations are due to neither decreased food levels compared to the krummholz, nor probably to increased competition at lower subalpine elevations. The population density trend supports the hypothesis that the Blackpoll is bioenergetically more adapted to cold, wet climate than the other warblers.

The species also has a vast taiga and subarctic range from Alaska to Labrador (Clement and Gunn 1957), and bioenergetics may contribute to its great abundance there and in the similar, less extensive subalpine biome. Adaptations include relatively large body mass (12.8 g) and probably a lower critical temperature and heat transfer coefficient below regression predictions. Blackpoll Warblers have insulation, the most thickly developed semiplumes and down plumules among the warblers (comparing specimen series), and this is a typical adaptation to cold-climate thermoregulation by lowering thermal conductance (Scholander et al. 1950). The bird forages slowly and is stationary for a remarkably long time fraction (51% of the diurnal period in Morse 1979). This may be a behavioral adaptation to reduce heat loss by maintaining the boundary air layer. Unlike other warblers, the Blackpoll reaches highest densities in the upper krummholz and subarctic, never breeds in the lowland New Hampshire valleys (S. Sabo, personal observation), and rarely breeds in the low-elevation spruce forests covering most of Maine (Palmer 1949, Rabenold 1978). The species distribution may be restricted by lower energetic efficiencies in warmer areas. Also, the Blackpoll's advantages may give it a competitive advantage in subalpine and subarctic climate, leading to its ecological dominance. The success of this strategy is emphasized by its hazardous 5500-km migration, longest of the warblers. It can thus exploit its position as the terminal warbler on an ecological gradient into cold, wet, windy coniferous forests to preempt resources on a continental scale.

Like the Red-eyed Vireo of the northern hardwoods, the Blackpoll's numerical success is correlated with heavy use of foliage gleans (75% of maneuvers) and stereotyped feeding behavior, an indicator of foraging optimization and less sensitivity to interspecific competition (Holmes et al. 1979a). Blackpoll foraging changes with elevation. comparing high (>1200 m) and low (<900 m) elevation areas on Mount Moosilauke, average canopy heights are 7.6 and 13.1 m. The Blackpoll's mean foraging heights are 3.3 and 5.6 m, respectively, about the same relative height (44% vs. 43% canopy height). Similarly, the percent conifer foliage volume changes from 95% to 64% going down the mountain, and the warbler's use of conifer foliage follows this trend from 69% to 35% (intermediate elevations have correspondingly

intermediate values). Overall, the Blackpoll's behavior is a simple function of gross elevational changes in vegetation physiognomy, regardless of differing competitive environments, much as Morse (1979) found. The warbler also has a rigid pattern of substrate-maneuver use (percent similarity between low and high elevations, $PS_{LH} = \sum_j \min(p_{Lj}, p_{Hj}) = 90\%$) and tree position use ($PS_{LH} = 91\%$). Exploitation of these smaller scale resources may be restricted by specific morphological adaptations of bill, wing, tail, and legs (Schoener 1965, Karr and James 1975), and corroborates Morse (1979). Morse (1979) also observed that Bay-breasted Warblers, a sibling species to the Blackpoll, forage very similarly but rarely co-occur with Blackpools. Blackpoll strategy exploits the cold, wet subalpine, while usually Bay-breasts depend on lowland insect epidemics. Limiting ecological similarity may have provided impetus for evolving different ecological strategies, and with them thermoregulatory differences leading to distinct habitat selection patterns for the two species.

Niche and habitat interactions of other wood warblers

Because so many warbler species occur in northeast North America, their niche and habitat relations may be considered on a large scale. MacArthur (1958) studied two *Dendroica* warblers that were spruce budworm (*Choristoneura fumiferana*) epidemic specialists: the Cape May Warbler (*D. tigrina*) foraging 63% of the time in the top 3 m of 15–18 m spruce trees, and the Bay-breasted Warbler foraging at midheights (see also Hensley and Cope 1951, Stewart and Aldrich 1951, Morris et al. 1958). Since budworm epidemics are confined to lowland areas, both these species would be expected as scarce sporadic breeders in the mountains. Because subalpine forests have low stature, the Cape May's foraging zone is largely absent. The Cape May is thus a rare vagrant, the Bay-breast an uncommon breeder in the subalpine zone. Another bird, the Blackburnian Warbler (*D. fusca*), also forages quite high in trees (MacArthur 1958, Morse 1968, Holmes et al. 1979b), and is likewise barred from most of the subalpine zone by low tree stature. The species occurs up to the 750-m ecotone, and Morse (1971) inferred that it was an inflexible forager, as also has been found for the Black-throated Green Warbler (MacArthur 1958, Morse 1971). The Black-throated Green likewise has an elevation ceiling, but it forages lower in trees than the Blackburnian and occurs up to 1100 m, where increasing exposure further reduces forest stature (cf. Able and Noon 1976). The Black-throated Green is socially dominant over other warblers (Morse 1971). On the mapped census plots, it aggressively displaced Magnolia and Yellow-rumped Warblers, whose densities were greater in very similar habitats

lacking Black-throated Greens. Both the Magnolia and Yellow-rump have a wide range of occurrence (from elevation 250 m in the Pemigewasset River valley near Hubbard Brook, to 1400+ m krummholz), and have rather nondescript foraging strategies. Although both forage low in trees, they differ somewhat in habitat selection. Morse (1968, 1971) found their foraging behavior plastic. These adaptations may be a response to interspecific competition for food resources as a proximate limiting factor on the breeding ground. The Yellow-rump's wintering range is more northerly, and unlike other warblers, the Yellow-rump winters in flocks (A. F. Skutch in Bent 1953), perhaps to neutralize the social dominance of other species.

Two other warbler genera may be briefly discussed. The common breeding ground habitat of *Wilsonia* centers around low shrubs. Three warblers—in southeast United States mesophytic forest understories the Hooded Warbler (*W. citrina*), in northern hardwood-subalpine ecotone understories the Canada Warbler, and in boreal and subarctic willow thickets Wilson's Warbler (*W. pusilla*)—form a latitudinal gradient in eastern North America that may reflect an underlying niche "gestalt" (von Uexküll 1909, James 1971) and phylogenetic history. Through its preference for active low-height foraging in deciduous foliage, the Canada Warbler is bounded at higher elevations as suitable habitat disappears. It may suffer competition in the upper northern hardwood forests (below 700 m) from the Black-throated Blue Warbler with a similar niche gestalt (Holmes et al. 1979b).

Lastly, the American Redstart, sole member of *Seriphaga*, a distinct offshoot from *Dendroica* (Griscom and Sprunt 1957), is an extremely wide-ranging successful form (Arctic Circle to southeast United States) that modifies its aerial and leaf-hover specialty in response to habitat differences. Its behavior changes as it follows birch higher in elevation to shorter and denser stands; its foraging is then (comparing data of Holmes et al. 1979b to the subalpine) lower (11.0 to 4.1 m mean maneuver height) and less dominated by aerial and leaf-hover maneuvers (81% to 46%).

Foraging behavior of the warblers responds to habitat structure, but in those species with more rigid behavior patterns, behavior can influence habitat selection. Social dominance and thermoregulation may also influence habitat selection. The habitat reflects the environmental conditions of a site and the array of insect resources. Warblers typically exhibit some site tenacity, with population recruits nesting in similar nearby habitats. Selection will operate through breeding success in suitable habitats, so that gradually a gestalt might evolve from habitats where a species niche is most likely to succeed, to fit in relation to the resources, the climate, and the other species usually present. The bird's niche gestalt (James 1971) represents its perception of habitats that are fit for its morphological, physiological, and other adaptations for

exploiting a certain section of resource hyperspace. The gestalt, as perception and behavioral response, may then specify the bird's ecotope as regards both niche and habitat factors. Gestalt and ecotope express the evolutionary track of a bird species—a specialization adapted to survival in a range of environments occupied by coexisting species.

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APPENDIX

Location of habitat sites

Geographic area	Stands sampled
Hubbard Brook Experimental Forest	2
Mount Moosilauke	173
Cannon and Kinsman Mountains	23
Cherry Mountain	6
Franconia Ridge	41
Pemigewasset Basin	36
Mount Carrigain	15
Nancy Pond	48
Willey Range and Ethan Pond	35
Zealand and Twin Mountains	36
Presidential Range	48
Montalban Ridge	22
Carter-Moriah Range	11
Total	496