GUILD STRUCTURE OF THE HUBBARD BROOK BIRD COMMUNITY: A MULTIVARIATE APPROACH[1]

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Abstract. We examined the similarities and differences in the foraging patterns of 22 insectivorous bird species during their breeding season in the Hubbard Brook Experimental Forest, New Hampshire, USA. Using multivariate techniques (clustering of hyperdimensional Euclidean distances, principal components analysis, and Varimax rotated factor analysis), we distinguish 4 groups of species or guilds, each of which exploits food resources in a distinctly different way. Partitioning occurs primarily by (1) foraging height and height-related characters, (2) foraging locations within the forest canopy, and (3) differential use of tree species, foraging substrates and foraging maneuvers. The results indicate that the importance of vegetation height to bird species diversity is related (1) to foraging opportunities which differ along a gradient from ground level to the upper canopy and which are roughly indexed by measures of foliage height diversity (FHD), and (2) to the presence of the supporting branch and bole framework which provides a major distinct foraging region. We suggest that foraging opportunities vary with height in a forest and are influenced by the physical and chemical characteristics of the plant species, which in turn affect the kinds and distributions of foraging substrates, the ways in which birds search for and find food, and the abundances of food resources. The implications of these findings for understanding the structure of forest bird communities are discussed.

Key words: bird foraging; community structure; guilds; Hubbard Brook; multivariate analysis; New Hampshire; plant diversity; resource partitioning; vegetation structure.

INTRODUCTION

The structure and functioning of a biological community are affected by the characteristics, life histories and interactions of its constituent species. Which species actually co-occur in a particular place at a given time is determined by a variety of historical and ecological factors. Chief among the latter is the necessity for coexisting species to partition limiting resources. Assuming that food is an important limiting resource (e.g., Lack 1954, 1966, Cody 1974), we propose that communities should be structured on the basis of how food is partitioned, and that syntopic species should differ in physical or behavioral characteristics resulting in differential food utilization. Further, if the factors that determine the "partitions" can be identified, then one can predict with greater accuracy how many and which kinds of species should occur at a particular site.

How can an animal community be analyzed so that the factors determining its structure may be identified? In many ecological studies, communities have been divided into guilds (Root 1967) or other groupings which contain ≥1 species that seem to exploit the same kinds of resources in similar ways. For bird communities, foraging similarities or differences among species have been inferred from 1 to several sets of morphological, behavioral or ecological data (e.g., Twomey 1945, Salt 1953, Root 1967, Willson 1974), which have often been combined on subjective or arbitrary scales (e.g., Cody 1974). Such procedures do not identify objectively the foraging characteristics that are most relevant in establishing differences between species, nor do they quantify how closely correlated the measured characters are.

Multivariate techniques weight variables by their relative contributions to the total community pattern, and reduce a large number of correlated variables into a smaller number of identifiable factors that determine similarities and differences among the species (Cooley and Lohnes 1971, Green 1971). They can also be used to position the species in an *n*-dimensional "community space" so that similarities and differences among the species can be visualized. Although multivariate techniques have been used to determine and analyze ecological relationships (e.g., James 1971, Anderson and Shugart 1974, Whitmore 1975, 1977, Findley 1976, Harner and Whitmore 1977, Inger and Colwell 1977, Smith 1977), only Karr and James (1975) have applied them to analyses of bird foraging characteristics.

In this study, we use multivariate techniques to examine the foraging behavior of 22 species of insectivorous birds breeding in a northern hardwoods forest. Our goals are to provide an objective classification of the similarities and differences among syntopic bird species in terms of how they exploit food resources, and to identify those measured parameters associated with feeding that are most important in determining the structure of this forest bird community. The results are then related to current thinking about bird species diversity, resource partitioning, and community structure.

TABLE 1. Characteristics of the 22 bird species* breeding in the Hubbard Brook Experimental Forest, New Hampshire

Species	Code	$\bar{x}$ live wt (g)†	Foraging height (M) $\bar{x} \pm$ SD	Foraging maneuver sample size‡
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	YbS	48.3	10.3 ± 4.2	169
Hairy Woodpecker (*Dendrocopus villosus*)	HW	66.9	9.8 ± 3.4	121
Downy Woodpecker (*Dendrocopus pubescens*)	DW	26.7	10.8 ± 4.8	189
Least Flycatcher (*Empidonax minimus*)	LF	10.5	11.1 ± 5.2	609
Black-capped Chickadee (*Parus atricapillus*)	BcC	11.5	12.7 ± 5.3	451
White-breasted Nuthatch (*Sitta carolinensis*)	WbN	21.0	12.0 ± 4.8	285
Winter Wren (*Troglodytes troglodytes*)	WW	9.2	1.7 ± 1.1	243
Wood Thrush (*Hylocichla mustelina*)	WT	49.0	0.2 ± 1.0	193
Hermit Thrush (*Catharus guttatus*)	HT	30.0	2.5 ± 3.9	177
Swainson's Thrush (*Catharus ustulatus*)	SwT	30.1	2.7 ± 5.2	344
Veery (*Catharus fuscescens*)	Ve	31.9	0.6 ± 1.4	106
Solitary Vireo (*Vireo solitarius*)	SV	17.0	10.5 ± 4.5	114
Red-eyed Vireo (*Vireo olivaceus*)	RV	17.6	11.5 ± 4.8	1719
Philadelphia Vireo (*Vireo philadelphicus*)	PV	12.1	14.4 ± 6.5	628
Black-throated Blue Warbler (*Dendroica caerulescens*)	BW	9.9	5.8 ± 4.1	193
Black-throated Green Warbler (*Dendroica virens*)	GW	9.0	13.9 ± 4.8	587
Blackburnian Warbler (*Dendroica fusca*)	BbW	10.4	15.0 ± 4.2	570
Ovenbird (*Seiurus aurocapillus*)	OB	19.5	0.2 ± 0.9	404
American Redstart (*Setophaga ruticilla*)	AR	8.9	11.0 ± 4.8	1223
Scarlet Tanager (*Piranga olivacea*)	ScT	28.1	12.8 ± 4.9	207
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	RbG	43.9	11.4 ± 5.4	378
Dark-eyed Junco (*Junco hyemalis*)	DJ	19.0	1.9 ± 3.2	375

* Other species (including some that breed occasionally, raptors, etc.) also occur (see Holmes and Sturges 1975) but are not included in the present analyses because of low sample sizes of their foraging behavior.
† Mean wt of summer birds captured in the Hubbard Brook Forest, from Holmes and Sturges (1975).
‡ Sample size for number of foraging maneuvers used in the multivariate analyses.

STUDY SITE AND METHODS

Study area

This investigation was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, on the 10-ha study plot described by Holmes and Sturges (1975). The forest is an uneven-aged, well-stocked stand of northern hardwoods, dominated by American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula allegheniensis* Britt.), with a few scattered white ash (*Fraxinus americana* L.), white birch (*Betula papyrifera* Marsh.), and red spruce (*Picea rubens* Sarg.). The canopy height averages ≈25 m. The forest understory consists of saplings of the dominant tree species, plus striped and mountain maples (*Acer pensylvanicum* L. and *Acer spicatum* Lam.), a fern (*Dryopteris spinulosa* Fern.), hobblebush (*Viburnum alnifolium* Marsh.), and various herbs. Detailed descriptions of and references to the Hubbard Brook Forest, its climate and vegetation are given by Likens and Bormann (1972).

Bird foraging patterns

The foraging behavior of 22 insectivorous bird species that regularly breed in the Hubbard Brook Forest (Table 1) was quantified during June and July, 1974 through 1976.

Each time a bird was seen to make a foraging maneuver (defined below), we recorded the following information: its species and sex, the time of d, type of foraging maneuver employed, substrate to which it was directed, height at which it took place, the plant species, and if in a tree, whether it was in the region proximal to the main axis of the trunk or distal, along the outer halves of the branches. Bird foraging maneuvers were defined as follows: (1) glean, a maneuver in which a stationary prey item was picked from the surface of a substrate by a standing or hopping bird; (2) hover, a maneuver in which a stationary prey was picked from the surface of a substrate by a hovering (or flying) bird; (3) hawk, a sally into the air in pursuit of a flying prey; and (4) probe/drill, a maneuver in which the bird's beak penetrated the substrate in pursuit of subsurface prey. Heights were estimated to the nearest 1.5 m (5 ft).

To obtain the foraging observations, we moved about the study plot on a systematic basis, observing as many different birds at various times of d as possible. Individuals were followed as long as they remained in sight, which in this dense forest habitat was usually not > a few s. In some cases, however, birds

TABLE 2. List, of foraging characters used in multivariate analyses. See text for definitions

Character	Code
1. Hover at leaf	HV LF
2. Glean from leaf	GL LF
3. Hover at branch	HV BR
4. Glean from branch	GL BR
5. Probe (or drill) into branch	PR BR
6. Hover at twig	HV TW
7. Glean from twig	GL TW
8. Hawk (sally) in air	HAWK
9. Glean from ground (litter)	GL GR
10. Probe into ground (litter)	PR GR
11. Hover at trunk	HV TR
12. Glean from trunk	GL TR
13. Probe (or drill) into trunk	PR TR
14. Probe into fallen dead wood	PR FDW
15. Maneuver proximal to trunk	PROX
16. Maneuver distal to trunk	DIST
17. Maneuver on beech	BEECH
18. Maneuver on sugar maple	SMA
19. Maneuver on *Betula* sp.	BIRCH
20. Maneuver on ash	ASH
21. Maneuver on other maple (mountain or striped)	OMA
22. Maneuver on *Viburnum*	VIB
23. Maneuver on conifer	CONIF
24. Maneuver on herbs or ferns	HERBS
25. Mean foraging height	HT
26. Standard deviation of foraging height	HTSD
27. $\bar{x}$ body wt of species	BRDSZ
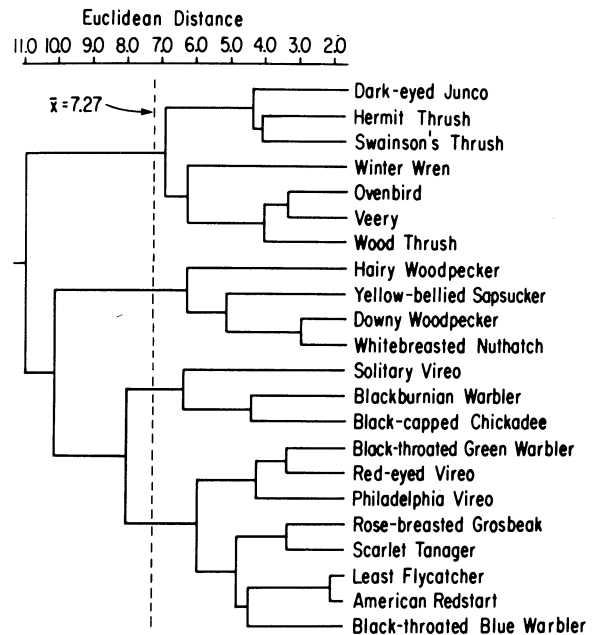
FIG. 1. Community dendrogram of Euclidean distances between all species, indicating foraging relationships. Dashed line indicates the $\bar{x}$ Euclidean distance between all combinations of species pairs in the Hubbard Brook bird community.

were observed for several min, and a sequence of foraging maneuvers was obtained. Analyses of the foraging data in subsets of these sequences (e.g., 1st observations only) indicate that they do not differ significantly (<.05, G test) from those of all observations in the sequences. We therefore include here data for each foraging maneuver (and its associated information) observed during the study period.

The data consist of measures of 27 foraging "characters" (Table 2). Twenty-four are related to foraging behavior and to the types and locations of substrates to which foraging maneuvers were directed. An additional 2 are mean foraging heights and their standard deviations, the latter providing an index to the vertical spread of foraging. The 27th character included in the analysis is bird size, specifically average body wt, which we include as an approximate index of prey size (Hespenheide 1975).

Although some intraspecific differences occur in foraging patterns between yr, between phases of the nesting season and between sexes (Holmes et al. 1978), the data in this analysis are those pooled for all individuals of each species collected during the field seasons.

Multivariate analyses

For these analyses, we follow the general nomenclature of Cooley and Lohnes (1971). Multivariate sta-

tistical analyses were performed on the data matrix consisting of 22 bird species (rows) by 27 foraging characters (columns). The first 24 characters (Appendix), representing utilization frequencies of foraging categories, were log-transformed to reduce skewness. The last 3 columns did not require transformation. All 27 columns were standardized to bring the means to 0 and the variances to 1.0, with the result that each measurement was expressed in standard deviation units from its column mean.

Dartmouth Time Sharing System computer programs (McGee 1978) were used in the analyses. The 22 × 27 character matrix (R-technique, Sneath and Sokal 1973) was used for the factor analysis. The matrix of correlations between all of the 27 characters was obtained, and eigen roots and vectors of this matrix were calculated. Principal components were obtained by multiplying these eigen vectors by the standardized 22 × 27 data matrix (Harman 1967). Eigen roots >1.0 were used to calculate a Varimax orthogonally rotated factor pattern, following the procedures of Cooley and Lohnes (1971).

The transposed (27 × 22) species matrix (Q-technique, Sneath and Sokal 1973) was used to calculate Euclidean distances between all of the 22 species in the hyperspace defined by the 27 foraging characters. This distance matrix was subjected to a hierarchical clustering analysis (maximum method, Johnson 1967) for purposes of illustrating species relationships.
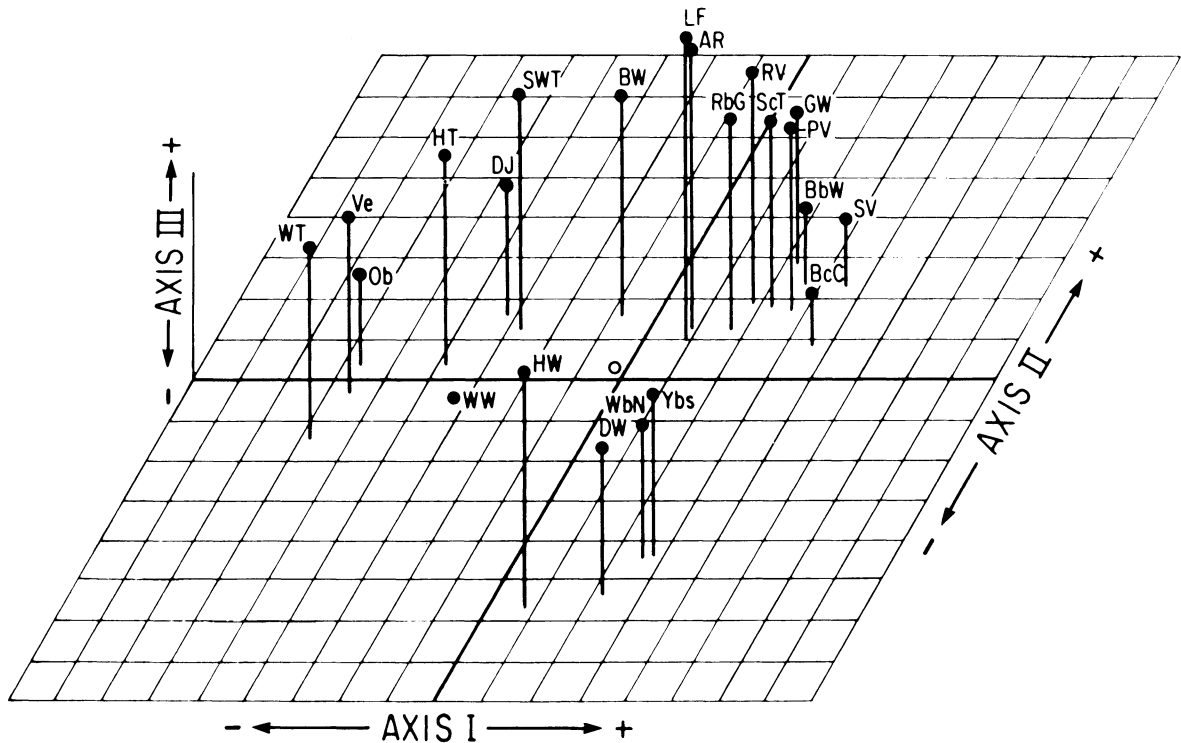
FIG. 2. Projection of 22 bird species along the first 3 principal component axes. Axes I, II, and III account for 36.7, 24.2 and 9.9% of total variance, respectively. See text for interpretation and Table 1 for species symbols.

RESULTS

During this study we collected observations on 9285 foraging maneuvers by 22 bird species occurring in the Hubbard Brook study area. The bird species included in the analyses, their scientific names, body wt, and the sample sizes of foraging observations for each are given in Table 1. The matrix containing the data for the remaining 24 foraging categories for each of the 22 bird species is given in the Appendix. The correlation and Euclidean distance matrices are available from the authors upon request.

Guild structure: cluster analysis of Euclidean distances

The cluster diagram of Euclidean distances is a 2-dimensional representation of the positions of the 22 bird species in the 27-dimensional hyperspace (Fig. 1). In this diagram, the species in the Hubbard Brook bird community are separated into a number of distinct groupings which we consider as foraging guilds (cf. Root 1967) because they contain species that exploit food in similar ways.

No precedents exist for quantitative separations of guilds. For the purposes of this paper, we define guilds as those species or groups of species that are separated from one another by Euclidean distances which are > the mean distance between all species ($\bar{r} = 7.27$, in this example). Using this criterion, we identify 4 guilds

or major patterns of food resource exploitation in the Hubbard Brook bird community (Fig. 1).

Guild I consists of the 4 species of thrushes, the Winter Wren, Ovenbird and Dark-eyed Junco, all primarily ground foragers. The 2nd group (guild II) contains those species that feed mainly along tree trunks and branches: the 3 species of woodpeckers and the White-breasted Nuthatch. Guild III contains the Solitary Vireo, Blackburnian Warbler and Black-capped Chickadee, while the 4th guild consists of 8 species including 2 vireos, 1 grosbeak, 1 tanager, a flycatcher and 3 warblers. The parameters separating these groupings will be considered in the factor analysis below.

Guild structure: principal components analysis

The 22 species are plotted along the 1st 3 principal component axes in Fig. 2. The guild pattern that emerges is very similar to that from the cluster analysis (Fig. 1). The 1st axis, accounting for 36.7% of the total community variance (Table 3) isolates the ground foragers (negative values) from all but 1 of the canopy feeders (positive values), and therefore appears to be height-related. The 1 exception is the Black-throated Blue Warbler which, although a foliage forager, occurs primarily in the low understory. Axis II, which accounts for an additional 24.18% of the variance, seg-

TABLE 3. The rotated factor pattern showing the most heavily weighted factors, either positive or negative, for each of the 27 characters

	Factors					
	I	II	III	IV	V	
Eigen roots	9.92	6.53	2.67	1.48	1.17	
Factor contribution to community variance (%)	36.73	24.18	9.88	5.50	4.35	
Cumulative %	36.73	60.91	70.79	76.29	80.64	ROW SS*
1 HV LF†		0.938				0.912
2 GL LF		0.772				0.822
3 HV BR				−0.768		0.909
4 GL BR	0.640					0.769
5 PR BR		−0.885				0.913
6 HV TW		0.417				0.503
7 GL TW			−0.570			0.741
8 HAWK		0.695				0.663
9 GL GR	−0.909					0.839
10 PR GR	−0.917					0.848
11 HV TR				−0.846		0.860
12 GL TR		−0.630				0.820
13 PR TR		−0.891				0.915
14 PR FDW	−0.891					0.856
15 PROX	0.723					0.800
16 DIST		0.847				0.968
17 BEECH					0.551	0.531
18 SMA			0.812			0.808
19 BIRCH	0.919					0.892
20 ASH	0.708					0.728
21 OMA	−0.719					0.736
22 VIB	−0.936					0.911
23 CONIF			−0.687			0.657
24 HERBS	−0.930					0.915
25 HT	0.961					0.951
26 HT SD	0.831					0.857
27 BRDSZ		−0.578				0.647

* Represents % of the variance of each character explained in 6-space (see text).
† Abbreviations for characters given in Table 2.

regates the bark foragers (negative values) from those species feeding in other parts of the canopy (positive values), suggesting the distinctiveness of bark as a foraging substrate. The 3rd axis takes into consideration an additional 9.9% of the variance, and shows the uniqueness of the Winter Wren among the ground foragers and of the Solitary Vireo, Black-capped Chickadee and Blackburnian Warbler (guild III, Fig. 1) among the canopy foragers.

Determinants of guild structure: Varimax factor rotation

The 2 multivariate methods used above have identified guilds within the Hubbard Brook bird community. However, the factors causing the guild separations have only been inferred. More direct and precise determinations of the characters that are important in segregating these bird species and guilds can be obtained from a Varimax rotated factor pattern of the foraging characters. For a clear, readable account of factor analysis, see Aspey and Blankenship (1977).

The 1st 5 eigen vectors extracted from the correlation matrix have values >1.0 and account for 80.6% of the community variance. These 5 orthogonal vectors are rotated in the original 27-space by the Varimax procedure until "simple structure" (Cooley and Lohnes 1971) is obtained. The vectors are now factors, and each contains combinations of correlated characters that largely account for the variance in foraging patterns among the bird species in the community. The factor loadings may be thought of as correlations between the original characters and the factor; each factor has high loadings for only a few characters (Table 3) which represent those that are most likely to be important in explaining the community patterns. Following the guidelines of Comrey (1973) and Aspey and Blankenship (1977), we list factor loadings of ≥0.45 only because lower values share <20% of the variance with the factor.

Factor I is considered height-related (Table 3). It contains high positive loadings for foraging height and the standard deviation of foraging height; birds which

forage higher tend to forage over a wide range of heights. Foraging actions directed toward substrates on birch and ash are positively correlated with this factor, because these plant species occur almost exclusively in the forest canopy and are essentially absent from the forest understory in the study area. The relatively high positive values for proximal and glean on branch probably occur because these are associated most strongly with feeding activities taking place high above the ground. The high negative loadings on this factor are associated either with plant types found on or near the forest floor (herbs, striped and mountain maples, *Viburnum*) or with foraging maneuvers directed toward forest floor substrates (probe and glean on ground and on fallen dead wood). Therefore, the heights at which birds forage are of prime importance in determining the plant species and the substrates from which they can obtain food.

Factor II has high positive loadings for gleaning and hovering on leaves in the distal sections of trees and for hawking insects from the airspace; high negative values represent probing and drilling maneuvers on trunks and branches, and gleaning on trunks (Table 3). This indicates that, in general, trunk and branch foraging is mutually exclusive from leaf and aerial foraging. Bird size as measured here by body wt is related to bark foraging activities (Table 3) probably because of the larger average size of the bark-feeding (woodpecker) species in this community (Table 1). This correlation may not be found in other regions where more small bark foragers occur.

Factor III has a high positive loading for sugar maple, and high negative loadings for glean on twig, and for feeding on conifers. Three species, the Blackburnian Warbler, Solitary Vireo, and Black-capped Chickadee, feed less often from sugar maple than most other bird species in the forest canopy (Appendix); both the warbler and the vireo utilize conifers more frequently than any other bird species, while the chickadee is the most frequent gleaner of twigs. This combination of characters then groups these 3 species into the same guild (Figs. 1 and 2). The heavy loadings for hover on branch and for hover on trunk on Factor IV are the characters that differentiate the solitary vireo from the other 2 species in guild III (Appendix).

Although Factor V is not easily interpreted or informative by itself, the heavy loading for beech indicates again the importance of tree species in resource partitioning among the bird species. In this case, 6 of the 8 species in guild IV use beech more frequently than any of the species in guild III (Appendix).

The 1st 2 factors account for 61% of the variance in bird foraging patterns, and define the major foraging locations and patterns of birds in this forest. The other factors indicate the importance of certain plant species and foraging substrates and methods in determining differences among the bird species.

These multivariate techniques provide an objective classification of the guild structure of a bird community, and can be useful in analyzing the parameters that may be important in determining that structure. It should be noted, however, that the results of such techniques are influenced by the choice of parameters to be included. For example, if a large number of the characters chosen are highly redundant or intercorrelated, the 1st several principal components may explain a larger proportion of the variance than if other uncorrelated variables had been selected (Cooley and Lohnes 1971). Likewise, the inclusion of other potentially important but not easily quantified characters, such as foraging rate or angle of foraging attack (cf. Root 1967), might also alter the results. Such potential biases do exist and must be kept in mind when using and interpreting multivariate results.

DISCUSSION

In recent years, discussions of bird community structure have been strongly influenced by MacArthur's discovery that foliage height diversity (FHD) was a good predictor of bird species diversity (BSD) in a series of habitats (MacArthur and MacArthur 1961, Recher 1969, Karr and Roth 1971, Willson 1974). These studies have implied a causal, although thus far undetermined, relationship between the vertical distribution of foliage and the number of bird species in a given habitat.

Other investigators, however, have failed to find such clear correlations (e.g., Balda 1969, Lovejoy 1972, Tomoff 1974, Pearson 1975, Roth 1976), but instead show that plant species diversity (Lovejoy), plant physiognomy (Tomoff) or habitat heterogeneity (Roth) were better predictors of BSD. Among forest habitats with similar FHD, Willson (1974) found that BSD varied widely, leading her to suggest the need for a broader search for the important determining factors.

The results of this study explain in a quantitative way why BSD is often correlated with FHD along vegetational gradients, and why BSD may vary within habitat types, particularly forests. As shown by the array of species-typical foraging patterns, several major food exploitation systems or guilds exist within the Hubbard Brook bird community.

The most important factors dividing the bird community into foraging guilds relate to the physical structure of the Hubbard Brook Forest. First, height and height-related characteristics separate the ground foragers (guild I) from all other species. Then, the location of foraging relative to tree trunks and the correlated behavioral characteristics of bark-probing and bark-gleaning divide the canopy species into those that forage mainly on bark (guild II) from those feeding along the outer parts of branches and among foliage (guilds III and IV). There are, therefore, 3 distinct foraging environments at Hubbard Brook: the forest floor, the trunks of trees, and the outer branches and

foliage. Each of these regions is exploited by bird species which have the specialized morphology and behavior necessary for feeding there; no species at Hubbard Brook exploits all 3 regions and only a few utilize 2 (e.g., Swainson's Thrush, Solitary Vireo, Black-capped Chickadee).

We propose that measures of FHD provide a general index to the presence and development of these major foraging regions and thus to the presence and size of the guilds that exploit them. We have shown that nearly 40% of the variance in foraging behavior among Hubbard Brook bird species is attributable to foraging height, emphasizing the important distinction between foraging opportunities on the ground and in the trees. Another 25% of the variance is related to bark foraging. Bark can only become an important foraging substrate when trees are large and well developed. Thus, adding shrubs and then trees along a vegetational gradient from grassland to forest not only increases the vertical habitat dimension and, as a consequence, the foliage layering and complexity (Karr and Roth 1971), but also provides supporting structures (e.g., the tree boles and branches) as foraging regions. Because the proportion of foliage at different heights is also a function of the branching structure of the trees, the 2 components are closely linked. The resulting increases in foraging opportunities explain both the general increase in BSD and FHD along such a gradient and Willson's (1974) finding that the presence of trees has a disproportionate effect on increasing BSD.

But, specifically, how do height and its associated characteristics of foliage and branch structure affect BSD? And why do some forest stands with similar FHD have different BSD? From our multivariate analyses of the 27 foraging characters chosen for this study, we have shown that although foraging height is important in separating bird species, partitioning on a finer level is achieved by the birds' differential use of plant species, foraging substrates, and foraging maneuvers. This suggests to us that different foraging opportunities exist within each major foraging region of the forest and that these depend on the kinds and distribution of available substrates, on the ways in which birds can search for and capture prey, and on the relative abundances of certain food resources. We propose that these characteristics or opportunities vary with height in a forest and between forest stands at least in part because of the physical and perhaps chemical characteristics of different plant species. Our reasons for suggesting this are as follows.

First, plant species frequently differ in branching patterns (Whitney 1976) or in leaf arrangements and densities (Horn 1971). Such differing physical structures provide different arrays, combinations, and abundances of substrates and their associated insect faunas, which vary with height and which may require specialized search strategies for optimal utilization by foraging birds. Also, the physical array of branches and leaves may place constraints on birds' movements or on how they search for suitable prey. Thus, hawking for insects may be difficult for birds in dense foliage; birds exploiting caterpillars on the undersides of leaves must use energy-expensive hovering techniques compared to birds that glean similar prey from upper leaf surfaces (Holmes et al. 1979 in press). The latter technique is only possible if the leaves can be reached by birds standing on the twig or branches, and thus depends on the leaf and branch arrangements of the plants. The changing patterns of sunflecks, which are also dependent on the leaf and branch structure of a forest canopy, will likewise affect insect activity and visibility, and as a consequence, the ability of birds to capture prey (Pearson 1975, 1977). Such differences in physical structure among plant species may influence where birds forage and how they forage. Therefore, we suggest that different foraging opportunities for birds exist where plant morphologies or plant species differ either with height in a forest or between forest stands. In this way, plant species can contribute to the differential partitioning of food resources by species in the bird community.

Plant species may also differ in the types and abundances of food resources available to birds. For instance, at Hubbard Brook, yellow birch has the highest densities of larval Lepidoptera among the major tree species (J. C. Schultz, personal communication), and several bird species feed more frequently from yellow birch than would be expected by the frequency of occurrence of this tree species alone. Such variation among plant species in insect fauna or abundance may be caused by differences in plant chemistry (Feeny 1976, Rhoades and Cates 1976), by differences in morphological complexity which provide different types and qualities of hiding places for insects (Orians et al. 1977), by historical factors (Southwood 1961) or by combinations of these.

We believe, therefore, that the bird community composition within and between forest habitats is largely dependent on the physical structure of the vegetation, the kinds and distribution of foraging substrates, and the availability and abundances of insect resources, all of which are influenced by the species composition of the plant community. The change in species composition and growth form of plants along a height gradient within a forest provides differing combinations of foraging opportunities that ultimately determine how many bird species can occupy that environment. Furthermore, because plant species associations and growth forms of forest change geographically and topographically, differences in this habitat component may explain the variation in BSD (bird species diversity) between forest habitats noted by Willson (1974).

Because these relationships are complex, it is clear that no single numerical index, such as FHD (foliage height diversity) or PSD (plant species diversity) will

adequately characterize these important environmental features. Karr (1976) and Whittaker (1977) consider other difficulties with these predictive measures and likewise conclude that more detailed knowledge of niche relationships, especially of food types, foraging substrates and physical factors, are needed to explain patterns of avian diversity. To this we would add plant species composition.

We suggest that an understanding of bird community structure and resource partitioning, especially in forest habitats, will come from intensive studies of 1 or a few bird species or guilds in habitats with contrasting plant life forms or plant species composition. Comparisons of the foraging patterns of birds in forests with similar FHD but with either similar or different tree species composition would provide a natural experiment for testing these hypotheses. Direct manipulation of habitat structure, if accomplished without affecting too many parameters, might also provide a fruitful approach.

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Appendix Percent utilization of foraging categories by 22 bird species in the Hubbard Brook Forest. Numbers 1–14 represent maneuver-substrate combinations, numbers 15–16 position in trees, and numbers 17–24 use of plant species. See Tables 1 and 2 for keys to abbreviations.

	DJ	HT	SwT	WW	OB	Ve	WT	HW	YbS	DW	WbN	SV	BbW	BcC	GW	RV	PV	RbG	ScT	LF	AR	BW
1. HV LF	22.9	19.2	27.9	5.8	16.3	32.1	4.1	0.0	4.7	0.5	0.0	22.8	23.0	7.6	31.0	52.6	64.6	31.2	41.5	74.4	51.6	47.2
2. GL LF	24.8	10.2	6.1	20.2	12.4	6.6	4.7	0.0	1.8	0.0	0.0	8.8	54.0	30.6	42.9	30.8	18.6	44.7	13.5	1.8	14.1	31.6
3. HV BR	0.0	0.0	0.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.0	0.4	1.1	0.9	1.1	1.9	0.8	2.9	0.5	0.2	0.5
4. GL BR	1.3	0.0	0.3	5.8	0.5	0.9	0.0	0.8	8.9	12.2	14.0	10.5	2.5	16.3	1.4	2.6	3.8	2.9	8.7	0.2	2.6	1.6
5. PR BR	0.0	0.0	0.0	4.5	0.0	0.0	0.0	20.0	16.6	24.9	8.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6. HV TW	0.5	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.2	0.2	1.7	1.6	1.0	0.3	0.0	0.0	0.1	0.0
7. GL TW	0.3	0.0	0.9	1.7	0.7	0.0	0.0	0.0	0.0	0.0	0.4	1.8	5.3	13.4	4.3	1.3	1.8	2.1	1.4	0.5	0.3	0.0
8. HAWK	7.7	10.2	4.1	6.6	1.5	0.0	1.6	0.0	8.9	0.0	2.8	2.6	8.8	2.9	11.4	7.0	5.9	6.6	24.2	21.7	29.4	10.9
9. GL GR	32.0	27.1	31.4	12.8	44.6	46.2	10.4	0.0	0.0	0.5	0.0	0.0	0.0	0.7	1.0	0.0	0.3	1.1	0.5	0.0	0.3	0.0
10. PR GR	6.7	21.5	21.5	6.6	19.1	7.5	72.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11. HV TR	0.5	1.7	5.5	1.2	0.7	2.8	1.6	0.0	1.2	0.0	0.0	28.9	1.4	1.1	2.2	1.7	1.4	5.3	5.3	0.5	0.6	3.6
12. GL TR	1.3	2.8	0.3	14.9	1.7	0.9	1.0	2.5	27.8	15.9	51.9	9.6	4.6	25.9	3.1	1.2	0.6	5.0	1.9	0.5	0.7	2.6
13. PR TR	0.0	0.6	0.0	9.1	0.0	0.0	0.0	76.7	30.2	46.0	22.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14. PR FDW	1.9	6.8	1.7	9.9	2.5	2.8	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	2.1
15. PROX	73.9	77.3	71.4	0.0	0.0	0.0	0.0	100.0	99.2	100.0	99.1	84.1	21.5	57.0	32.4	43.6	42.1	48.5	59.2	19.6	33.0	78.0
16. DIST	26.1	22.7	28.6	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.9	15.9	78.5	43.0	67.6	56.4	57.9	51.5	40.8	80.4	67.0	22.0
17. BEECH	13.4	25.3	27.5	27.9	12.1	19.0	28.6	23.8	1.7	17.5	23.4	15.7	10.8	5.8	8.1	29.5	9.2	24.3	29.5	21.9	21.5	26.4
18. SMA	9.1	16.5	26.8	11.7	15.0	19.0	28.6	34.4	45.8	23.7	38.5	16.5	7.4	13.5	28.7	41.0	26.8	29.2	16.9	35.7	38.3	19.7
19. BIRCH	17.4	6.3	19.6	18.8	3.7	4.8	4.8	41.0	38.4	56.2	29.4	50.4	58.3	75.5	53.0	23.8	40.4	36.6	47.3	37.9	33.4	29.5
20. ASH	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.8	12.4	2.6	5.9	3.1	5.0	4.1	0.6	2.3	19.3	4.2	1.3	0.5	0.5	0.0
21. OMA	8.3	0.0	7.8	8.4	18.7	31.0	9.5	0.0	1.7	0.0	0.7	0.0	0.6	0.0	2.0	1.9	2.7	4.2	2.1	3.3	3.7	10.4
22. VIB	15.9	32.9	9.2	14.3	15.0	21.4	9.5	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.1	0.5	1.0	0.0	0.2	0.2	9.3
23. CONIF	4.3	0.0	2.0	3.9	5.6	0.0	0.0	0.0	0.0	0.0	2.1	14.2	17.9	0.9	7.4	1.3	0.6	0.5	3.0	0.3	0.5	1.6
24. HERBS	31.5	19.0	7.2	13.0	29.9	4.8	19.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.2	1.9	3.1