

EFFECTS OF PLANT SPECIES AND FOLIAGE STRUCTURE ON THE FORAGING BEHAVIOR OF FOREST BIRDS

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ABSTRACT.—We quantified the behavior of four species of passerine birds foraging for arthropods among the foliage of different plant species and vertical strata of a northern hardwoods forest in New Hampshire (USA). Two species (*Vireo olivaceus* and *Setophaga ruticilla*) often changed their foraging patterns among strata but not among tree species, except in white ash. In the latter, both species flew more frequently between perches while searching for prey, which reflects the more open canopy and sparser distribution of ash foliage. A third species (*Vireo philadelphicus*) was stereotyped in its search and attack methods but had variable attack rates, indicating greater foraging success in some microhabitats than in others. The fourth species (*Dendroica caerulescens*), which inhabits the forest understory, showed few significant differences in its search or attack behavior, despite considerable variety in the sizes, shapes, and arrangements of leaves among available plant species. The foraging patterns of *S. ruticilla* were further influenced by differences among tree species in the abundance of a major prey type (leafhoppers, Cicadellidae: Homoptera) and by the active escape behavior of those prey.

We conclude that these four bird species, all of which search leaves at a distance and fly up to hover or snatch arthropod prey from leaf surfaces, are relatively unaffected by details of foliage structure such as leaf size, shape, petiole length, and arrangement on twigs. The distribution of foliage within a plant, however, and, in some cases, the abundance of certain food resources do differentially influence the foraging tactics and capture success of these species. Because foliage distribution and arthropod availability both vary with plant species, the floristics of a site will strongly influence the "foraging opportunities" available to birds and therefore their success in exploiting particular habitats. Received 20 July 1983, accepted 4 March 1984.

THE diversity of bird species occupying terrestrial habitats has often been shown to be correlated with various aspects of vegetation structure or composition, including foliage-height diversity (MacArthur and MacArthur 1961, Recher 1969), plant-species diversity (Tomoff 1974, James and Wamer 1982), habitat openness (Willson 1974, Probst 1976), and habitat patchiness (Karr and Roth 1971, Roth 1976). Few explicit explanations or even hypotheses have been advanced, however, to account for how or why these vegetation characteristics should affect birds in the ways observed. Several investigators have suggested that food resources are ultimately involved (Karr 1976, Terborgh 1980), but, because most temperate forest passerines are largely insectivorous, the relationship between vegetation structure and

food resources for such birds is likely to be indirect at best.

Some evidence suggests, however, that vegetation structure is important, because it strongly influences a bird's foraging behavior and success. Smith (1974a, b), Roth (1979), Eiserer (1980), and Power (1980) have demonstrated that grass height in open habitats has a major impact on both bird foraging tactics and foraging success. Maurer and Whitmore (1981) found differences in the foraging behavior of five species of forest-dwelling birds in two forests with contrasting structure. Likewise, in northern hardwoods, some bird species forage preferentially in certain kinds of trees, and their foraging tactics often change when the birds capture insects in different tree species (Holmes and Robinson 1981). We subsequently reported that the different ways forest birds search for and capture prey appear to be influenced by the spatial arrangement of leaves, branching patterns, and other parameters of foliage structure (Robinson and Holmes 1982). These find-

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ings have led us to the following generalization: the primary role of vegetation structure is to provide a set of opportunities and constraints that influence how and where birds perceive and obtain their arthropod prey (Holmes 1981, Robinson and Holmes 1982). These opportunities and constraints, in turn, are a function of the differences in architecture and in the types and abundances of available arthropods that occur between plant species. The resulting foraging environment ultimately determines which bird species can successfully exploit and survive in a particular habitat and, as a consequence, influences bird community structure and species diversity.

In this paper, we test part of this hypothesis by examining the behavior of four bird species foraging for arthropods among the different plant species and strata of a northern hardwoods forest. Specifically, we ask here whether or not the differences in foliage structure among the plant species in three vertical forest layers significantly affect the food-searching patterns, searching radii, attack rates, and foraging maneuvers of the four bird species: Red-eyed Vireo (*Vireo olivaceus*), Philadelphia Vireo (*V. philadelphicus*), American Redstart (*Setophaga ruticilla*), and Black-throated Blue Warbler (*Dendroica caerulescens*). All forage actively among foliage and capture most of their insect prey by flying up to leaves and plucking them from plant surfaces or the nearby airspace (Robinson and Holmes 1982).

STUDY SITE AND FOREST STRUCTURE

We conducted this study in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire on the 10-ha study plot described by Holmes and Sturges (1975). This forest consists of second-growth northern hardwoods, dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula allegheniensis*). The relative importance values (I.V., cf. Cottam et al. 1953) of these three tree species on the study area are 32, 31, and 23%, respectively. White ash (*Fraxinus americanus*) also occurs (I.V. = 3.2), along with scattered individuals of other tree species (I.V.s < 1) such as *Populus tremuloides*, *Picea rubens*, and *Abies balsamea* (Bormann et al. 1970).

For the purposes of this study, we consider the vegetation of this forest to be divided into several "foliage compartments." These consist of the foliage of the more common woody plant species in each of three vertical strata—the canopy (15–27 m above ground), the subcanopy (2–14 m) and the shrub layer

(<2 m). The foliage in the canopy stratum is relatively dense and evenly scattered (for foliage profile, see Sherry 1979), although the arrangement and dispersion of leaves within each tree species differ markedly (see below). Foliage density in the subcanopy is lower and more variable than that of the canopy (Sherry 1979), indicating a more open and patchy distribution. Shrub-layer foliage is denser than that in either canopy or subcanopy and consists of a mixture of plant species, principally the young saplings of two dominants (sugar maple and beech), one shrub (hobblebush, *Viburnum alnifolium*) and one shrub/small understory tree (striped maple, *A. pensylvanicum*). Because of the mixture of plant species and the relatively small sizes of individual plants in the shrub layer, it was possible to obtain foraging rates for only the Black-throated Blue Warbler within individual plant species in this stratum. For the other three bird species, which forage mainly in the canopy, the shrub stratum is treated here as a single foliage type.

The structure and arrangement of foliage differ among tree species. Sugar maple and beech are shade-tolerant "climax" species that have monolayered foliage distributions (cf. Horn 1971). Beech leaves are distributed in more-or-less flat sprays, with medium-sized leaves ($50.9 \pm 2.7 \text{ mm}^2$, $n = 40$) attached close to the branchlets by short petioles ($7.0 \pm 2.4 \text{ mm}$, $n = 50$). Sugar maple leaves average slightly larger ($54.5 \pm 2.5 \text{ mm}^2$, $n = 40$) and are clumped towards the ends of branches on longer ($42.7 \pm 15.0 \text{ mm}$, $n = 50$) petioles. (All leaf measurements are $\bar{x} \pm \text{SE}$; areas were measured with a LiCor™ leaf area meter.)

In contrast, yellow birch and white ash are shade-intolerant mid-successional species that have multi-layered foliage distributions (Horn 1971). White ash is the most distinctive, with pinnately compound leaves evenly distributed throughout its relatively sparse canopy. In this forest, most ash individuals are canopy emergents, their tops often surpassing those of the canopy dominants by 2–6 m. Yellow birch foliage also appears to be evenly distributed throughout its canopy, with small leaves ($35.3 \pm 2.0 \text{ mm}^2$, $n = 40$) attached by short petioles ($12.7 \pm 2.5 \text{ mm}$, $n = 50$). Ash is essentially absent from the subcanopy and shrub layer and birch from the shrub layer except in disturbed areas or near tree-fall gaps.

Striped maple occurs as saplings in the shrub layer and as small trees in the subcanopy. It has large lobed leaves ($188.4 \pm 5.6 \text{ mm}^2$, $n = 50$) connected to branches by relatively long petioles ($44.9 \pm 1.9 \text{ mm}$, $n = 50$). Hobblebush rarely attains a height of more than 1 m and is the only common woody shrub in this forest; its relatively large leaves ($134.1 \pm 4.4 \text{ mm}^2$, $n = 50$) are positioned on short petioles ($32.1 \pm 1.1 \text{ mm}$, $n = 50$) along clumped single stems projecting up from the ground. It often occurs in dense, irregularly distributed patches throughout the forest. In addition to these woody plants, there are various ferns, forbs, and other low-growing herbaceous plants

(see Siccama et al. 1970); these are rarely used as foraging substrates by the bird species considered in this paper (Holmes et al. 1979).

METHODS

Bird foraging behavior was observed during the breeding seasons, approximately late May to mid-July, in the years 1974–1979; most intensive sampling efforts were in 1975, 1976, and 1978. Foraging rates were quantified only during the nestling and early fledgling stages of the nesting cycles (mid-June to mid-July), when birds were feeding intensively. In each year, we systematically walked through the study plot and observed as many different birds as possible, many of which were individually color-marked. We observed at least 20–25 individual adults of the more common species (Red-eyed Vireo, redstart and Black-throated Blue Warbler) each year and 4–6 of the less abundant Philadelphia Vireo. Whenever an actively foraging bird was encountered, we followed it for as long as possible (which, because of the dense foliage, was usually <60 s) and recorded its locomotor and foraging patterns on a portable tape recorder. We specifically noted the number of perch changes (either hops or flights) made by the bird while searching for prey, the frequency of attacks it directed toward prey, the plant species, and height above ground. This information was transcribed from the tapes by means of a stopwatch. Because individual birds seldom remained long in the same stratum or tree species, many of the sequences obtained were very short (<30 s). For this reason, rather than calculating a separate rate for each sequence, as we did in a previous paper (Robinson and Holmes 1982), here we have added together the sequences occurring within each foliage compartment to obtain a single composite sequence, for which we then calculate overall flight, hop, and prey attack rates. In this procedure we follow Moermond (1979a, b) and Eckhardt (1979).

For statistical comparisons of locomotor patterns, we summed the number of originally observed foraging sequences of 10 s or more in which the hop/flight (H/F) ratio was greater than 1 or less than or equal to 1. Using Chi-square tests, we then compared frequencies of each bird species among the foliage compartments. With this method, we avoided the problem of serial dependence of flights and hops within a sequence (Williamson 1971; Smith 1974a, b).

We used the attack rate as an index to how often suitable prey were encountered in a particular foliage compartment. Because the goal of food-searching behavior is to find prey, the attack rate reflects "searching success." We recognize that this is not the same as "foraging success," which would require precise information on the percentage of successful attacks and the size, kinds, and nutritional value of prey taken.

Attacks were categorized as follows (see Holmes et

al. 1979 and Robinson and Holmes 1982, for more detailed definitions): (1) Glean—a perched bird attempts to capture prey from a nearby substrate; no flight is involved for either bird or prey. (2) Hover—a bird flies out to catch prey from a more distant substrate; the bird may pause and hover momentarily at the substrate or may snatch the prey from the substrate as it passes. (3) Hang—a modified glean in which the bird hangs, usually upside down, and often tears apart or in some way manipulates the substrate (e.g. a curled leaf). (4) Hawk—a bird flies out from a perch to catch flying prey. (5) Flush-chase or tumble—a bird chases elusive or evasive prey flushed from foliage, often in a long downward flight. Statistical differences among frequency distributions of the prey-attack categories were determined by Chi-square tests.

Lengths of hover flights were used as an index of the bird's maximum effective search radius (cf. Robinson and Holmes 1982); because of their skewed distributions, hover lengths were compared statistically with a median test. For tests involving many multiple pairwise comparisons (H/F ratios, hover-flight lengths), we adjusted alpha levels, accepting <0.001 as our minimum level of significance. This was necessary, because repeated pairwise use of the same statistical test invalidates the assumption of independence and raises the likelihood of Type I error. For other tests, statistical significance was accepted at $P < 0.05$.

RESULTS

Red-eyed Vireo.—At Hubbard Brook, the Red-eyed Vireo breeds commonly throughout the forest. Its diet consists primarily of Lepidoptera larvae and beetles, which it captures by hovering or sometimes by gleaning from leaf surfaces (Robinson and Holmes 1982). It forages mostly in the subcanopy and lower portions of the canopy (Robinson 1981) and shows little preference for foraging in any particular tree species (Holmes and Robinson 1981). When foraging, it searches foliage within about a 0.5–1-m radius and then flies at an average rate of about 9/min to a new perch. These search flights average 1.1 m in length. Between flights, this vireo hops along branches and twigs at a rate of 7/min while it visually searches nearby foliage (Robinson and Holmes 1982).

These foraging patterns of the Red-eyed Vireo, however, vary in specific ways among the different foliage compartments of this forest (Table 1). In white ash and the shrub layer, it flies frequently but seldom hops; in the canopy of the three dominant tree species, it hops and flies at intermediate rates, whereas in the sub-

TABLE 1. Foraging rates and search radii of Red-eyed Vireos in each of the major tree species and strata of the Hubbard Brook Forest. The flight rate is for search flights only and does not include flights used in attacking prey. The search radius is indicated by the mean length of prey-attacking hover flights.

Stratum	Tree species	(t) ^a	Foraging rate (number/min)			Search radius (in cm) $\bar{x} \pm SD$ (n) ^b
			Prey attacks	Search flights (F)	Hops (H)	
Canopy	White ash	(764)	2.1	14.5	3.4	58 ± 30 (22)
	Yellow birch	(2,330)	2.4	8.5	6.4	72 ± 36 (59)
	American beech	(721)	2.2	7.4	5.7	68 ± 36 (45)
	Sugar maple	(1,523)	2.6	6.2	6.1	73 ± 66 (104)
Subcanopy	Yellow birch	(2,934)	2.2	5.2	12.3	74 ± 71 (90)
	American beech	(2,631)	2.4	5.9	11.3	73 ± 35 (158)
	Sugar maple	(2,013)	2.5	6.0	12.5	74 ± 40 (154)
Shrub	All	(523)	2.4	13.7	2.8	68 ± 33 (47)

^a t = cumulative number of seconds that actively foraging birds were observed.

^b n = number of hover flights observed.

canopy of those same tree species, it hops more often and flies less frequently (Table 1). Statistical comparisons of the hop/flight (H/F) ratios in each tree species and stratum (Table 2) substantiate these trends. The patterns in ash and in the shrub layer are similar and often statistically distinct from those in other foliage compartments. Although there are no significant differences in the H/F ratios among the three dominant tree species within layers, 7 of the 9 possible comparisons between layers are statistically different (Table 2). Thus, within a stratum, the searching patterns of this vireo appear

to be unaffected by differences in foliage structure among trees (except for ash). Between strata, however, their behavior often changes, even within a particular tree species.

The maneuvers used by the Red-eyed Vireo to capture prey from foliage differ only slightly among tree species or strata (Fig. 1). The only statistically significant difference is that they hover more often in canopy than in subcanopy yellow birch ($P < 0.001$, Fig. 1a). Mean lengths of hovering attacks range from 58 cm in ash to 74 cm in subcanopy birch and maple (Table 1), but there are no statistically significant differ-

TABLE 2. Results of pairwise statistical (χ^2) comparisons of hop/flight (H/F) ratios of Red-eyed Vireos among tree species and strata [$* = P < 0.001$ (see Methods)].

	Canopy				Subcanopy			Shrub	H/F ≤ 1 ^a (%)	(n) ^b
	Ash	Birch	Beech	Maple	Birch	Beech	Maple	All		
Canopy										
Ash	—	*	NS	*	*	*	*	NS	97	(32)
Birch		—	NS	NS	*	*	*	NS	67	(89)
Beech			—	NS	NS	*	NS	NS	70	(27)
Maple				—	NS	NS	NS	NS	59	(64)
Subcanopy										
Birch					—	NS	NS	*	30	(37)
Beech						—	NS	*	40	(143)
Maple							—	*	40	(105)
Shrub										
All								—	100	(12)

^a Percentage of foraging sequences in which search flights were more numerous than hops.

^b n = number of observed foraging sequences.

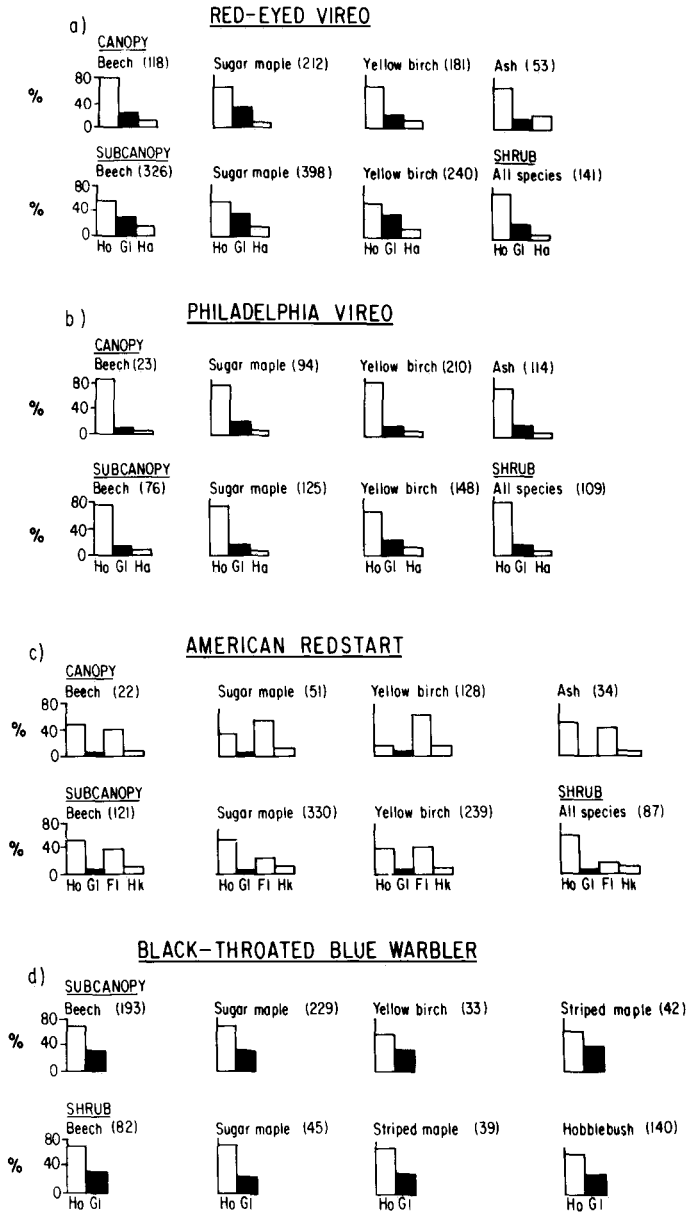


Fig. 1. Foraging maneuvers used by four passerine birds in attacking prey in each of the major tree species and strata of the Hubbard Brook Forest. Numbers of observed prey attacks in each foliage compartment are given in parentheses. See text for definitions of strata and prey-attack maneuvers. Ho = hover, Gl = glean, Ha = hang, Fl = flush-chase, Hk = hawk.

ences in these hover lengths among foliage compartments.

We conclude that the Red-eyed Vireo is relatively consistent in its use of attack maneuvers, has a constant search radius, but responds

to different strata and to white ash by changing its hop and flight rates. Perhaps as a result of these adjustments, the vireo's overall prey attack rate remains nearly constant among these foliage compartments (Table 1).

TABLE 3. Foraging rates and search radii of Philadelphia Vireos in each of the major tree species and strata of the Hubbard Brook Forest. The flight rate is for search flights only and does not include flights used in attacking prey. The search radius is indicated by the mean length of prey-attacking hover flights.

Stratum	Tree species	(t) ^a	Foraging rate (number/min)			Search radius (in cm) $\bar{x} \pm SD$ (n) ^b
			Prey attacks	Search flights (F)	Hops (H)	
Canopy	White ash	(721)	3.6	13.5	2.2	56 ± 24 (34)
	Yellow birch	(1,874)	3.6	12.4	3.1	63 ± 29 (89)
	American beech	(441)	1.6	9.3	3.9	78 ± 16 (7)
	Sugar maple	(825)	2.3	11.6	2.4	67 ± 22 (22)
Subcanopy	Yellow birch	(688)	3.8	9.2	3.7	65 ± 33 (47)
	American beech	(1,276)	2.8	10.5	5.2	68 ± 29 (59)
	Sugar maple	(701)	4.6	9.9	5.1	68 ± 34 (71)
Shrubs	All	(742)	3.2	12.3	2.8	71 ± 38 (44)

^a t = cumulative number of seconds that actively foraging birds were observed.

^b n = number of hover flights observed.

Philadelphia Vireo.—At Hubbard Brook, the Philadelphia Vireo is patchily distributed in the forest, occurring in areas where white ash and yellow birch are well represented in the canopy (Robinson 1981). In addition, it exhibits strong preferences for foraging and nesting high in the canopy, particularly in ash and yellow birch (Holmes and Robinson 1981, Robinson 1981). Its foraging behavior and diet are otherwise very similar to those of its congener, except that it tends to fly more often while foraging (Robinson and Holmes 1982).

Hopping and flight rates of the Philadelphia Vireo while searching for prey are similar in the various foliage compartments (Table 3), especially when they are contrasted with those of the Red-eyed Vireo (see Table 1). In each tree species and stratum, the Philadelphia flies 2–5 times more frequently than it hops. Like the red-eye, the Philadelphia Vireo tends to hop more frequently in the subcanopy than in the canopy, although the differences are slight (Table 3), and the H/F ratios between foliage compartments are not significantly different.

Unlike its congener, however, the Philadelphia's attack rates vary among foliage compartments (Table 3). Within the canopy, it attacks prey almost three times more often in ash and yellow birch than in beech. In fact, in 11 of the 18 times that we observed a Philadelphia Vireo feeding in a beech canopy, it left without making a single attack. This contrasts with 12 of 71 visits in canopy yellow birch ($P < 0.001$) and 8 of 31 in ash ($P < 0.01$). In the subcanopy

layer, the Philadelphia's attack rate is higher in sugar maple and yellow birch than in beech. Likewise, attack rates are higher in the subcanopies of sugar maple and beech compared with those in the canopies of these same tree species (Table 3). Thus, in contrast to the Red-eyed Vireo, the Philadelphia appears to find prey more often in some foliage compartments than in others.

The Philadelphia Vireo at Hubbard Brook primarily hovers for prey, gleans never accounting for more than 22% of the leaf-directed attacks (Fig. 1b). There are no statistically significant differences ($P > 0.10$) in the frequencies of maneuvers used among the foliage compartments. Likewise, hover distances of the Philadelphia Vireo do not vary significantly among foliage compartments (Table 3), indicating that this species, like its congener, has a relatively constant search radius.

Thus, the Philadelphia Vireo is relatively stereotyped in its foraging patterns; it searches for and attacks prey in the same manner regardless of tree species and strata. Its rate of prey encounter varies among foliage compartments, however, being highest in canopy ash and yellow birch and in subcanopy yellow birch and sugar maple.

American Redstart.—The redstart forages at all heights, from on or near the ground to the top of the canopy (Holmes et al. 1978, 1979). It searches the different tree species approximately in proportion to their occurrence (Holmes and Robinson 1981). While foraging, it hops

TABLE 4. Foraging rates and search radii of American Redstarts in each of the major tree species and strata of the Hubbard Brook Forest. The flight rate is for search flights only and does not include flights used in attacking prey. The search radius is indicated by the mean length of prey-attacking hover flights.

Stratum	Tree species	(t) ^a	Foraging rate (number/min)			Search radius (in cm) $\bar{x} \pm SD$ (n) ^b
			Prey attacks	Search flights (F)	Hops (H)	
Canopy	White ash	(332)	5.1	19.7	9.4	50 \pm 23 (10)
	Yellow birch	(1,098)	5.9	11.5	16.9	47 \pm 26 (50)
	American beech	(449)	3.2	13.5	16.2	46 \pm 29 (26)
	Sugar maple	(494)	4.9	10.2	18.0	51 \pm 30 (19)
Subcanopy	Yellow birch	(1,829)	6.2	10.1	14.9	48 \pm 42 (71)
	American beech	(1,423)	4.1	11.2	15.4	56 \pm 34 (75)
	Sugar maple	(3,832)	4.6	10.7	13.9	43 \pm 24 (158)
Shrub	All	(800)	4.1	18.2	9.6	47 \pm 26 (144)

^a t = cumulative number of seconds that actively foraging birds were observed.

^b n = number of hover flights observed.

and flies rapidly between perches, makes short hovering maneuvers to attack prey on leaves, and often chases prey it flushes (Robinson and Holmes 1982). It frequently fans and pumps its contrastingly patterned tail from side to side and flicks its wings while hopping through foliage, a behavior that appears to flush prey (Root 1967, Robinson and Holmes 1982). It also hawks insects from the air more often than any other common bird species at Hubbard Brook (Holmes et al. 1979).

When searching for prey, the redstart hops and flies at similar rates in all foliage compartments, except in white ash and the shrub layer, where the flight rates are elevated and greater than the hop rates (Table 4). Its H/F ratios are statistically indistinguishable in canopy and subcanopy foliage of the dominant tree species, but, in the comparisons involving ash and the shrub-layer data, there are significant differences in 3 of 7 cases (more flights in both ash and shrubs compared with canopy birch and subcanopy birch and beech). Thus, as in the Red-eyed Vireo, the redstart changes locomotor patterns when searching for prey in white ash and the understory.

The rate at which redstarts attack prey is similar in the different foliage compartments, except in yellow birch, in which prey were encountered slightly more often (Table 4). Its use of specific attack maneuvers, however, often varies among foliage compartments (Fig. 1c). In the subcanopy, there is a significant difference in maneuver use between birch and sugar ma-

ple ($P < 0.001$). In the canopy, the patterns in yellow birch differ significantly from those in both beech ($P < 0.001$) and sugar maple ($P < 0.001$). These differences occur largely because redstarts use the flush-chase maneuver more often in yellow birch than in the other tree species (Fig. 1c). There are also statistically significant differences ($P < 0.001$) in maneuver frequencies between canopy and subcanopy within both birch and sugar maple (Fig. 1c). Although the lengths of redstart hovers vary from 43 to 56 cm among the foliage compartments (Table 4), the differences are not statistically significant. Hence, again, as with the vireos, the redstart's searching radius seems relatively fixed.

We also quantified the occurrence of tail-fanning behavior by redstarts in each foliage compartment. The data indicate that redstarts fan their tails more often in yellow birch canopy and subcanopy than in any other foliage unit (Table 5). Yellow birch also hosts significantly more insect prey than any other tree species (Holmes and Schultz MS), especially leafhoppers (Homoptera: Cicadellidae). These often hop from their substrates when disturbed and appear to be the prey chased most often by redstarts in the tumble-maneuver (Robinson and Holmes pers. obs.). Hence, the tree species in which the redstart fans its tail most, yellow birch, is also that in which it encounters prey at the highest rate (as indicated by attack rates) and in which it uses the flush-chase maneuver most often.

TABLE 5. Frequency of tail-fanning by American Redstarts in the Hubbard Brook Forest in the major tree species and strata. Data are from the post-fledging period (late June to mid-July).

Stratum	Tree species	<i>n</i> ^a	Hops with tail fanned (%)
Canopy	White ash	65	55.4
	Yellow birch	309	86.0
	American beech	121	67.8
	Sugar maple	151	55.0
Subcanopy	Yellow birch	455	74.4
	American beech	381	58.0
	Sugar maple	888	61.3
Shrub	All plant species	298	46.6

^a *n* = number of hops observed.

In summary, the foraging behavior of the redstart is more variable than that of either vireo species. Its locomotion patterns, attack rates, use of foraging maneuvers, and searching tactics often differ among tree species and strata. Some of these changes are related to foliage structure, others to differences in prey availability.

Black-throated Blue Warbler.—The Black-throated Blue Warbler forages almost entirely in the shrub and lower subcanopy layers (Black 1975). While searching for prey, it hops more

often than it flies and searches nearby substrates while rapidly moving from perch to perch. Its primary prey-attacking maneuver is the hover (Robinson and Holmes 1982).

Hop and flight rates of the Black-throated Blue Warbler vary among plant species, fewer flights occurring in subcanopy sugar and striped maple and more hops in shrub-layer hobblebush (Table 6). None of the differences in H/F ratios among foliage compartments, however, is significant. The locomotory patterns used by foraging Black-throated Blue Warblers, therefore, seem largely unaffected by differences in foliage structure among understory or subcanopy plant species.

Attack rates of the black-throated blue are similar among plant species but generally higher in the shrub layer than the subcanopy (Table 6). Its foraging maneuvers are not significantly different among any of the foliage compartments; it consistently hovers about 65% and gleans about 35% of the time in each tree species and stratum (Fig. 1d). Mean lengths of hovers made by black-throated blues vary little among foliage compartments (Table 6). The only significant difference in hover lengths is between subcanopy beech and hobblebush.

In summary, the foraging rates, locomotor patterns, search radius, and prey-attacking maneuvers exhibited by the Black-throated Blue Warbler are relatively similar among the different plant species and layers.

TABLE 6. Foraging rates and search radii of Black-throated Blue Warblers in each of the major tree species and strata of the Hubbard Brook Forest. The flight rate is for search flights only and does not include flights used in attacking prey. The search radius is indicated by the mean length of prey-attacking hover flights.

Stratum	Tree species	<i>t</i> ^a	Foraging rate (number/min)			Search radius (in cm) $\bar{x} \pm SD$ (<i>n</i>) ^b
			Prey attacks	Search flights (F)	Hops (H)	
Subcanopy	American beech	(4,587)	1.7	10.1	6.2	62 ± 45 (121)
	Sugar maple	(5,219)	1.8	8.8	6.5	47 ± 30 (146)
	Yellow birch	(451)	2.4	12.0	5.9	59 ± 47 (23)
	Striped maple	(645)	2.0	9.2	5.5	45 ± 28 (24)
Shrub	American beech	(1,561)	2.1	11.8	8.9	50 ± 35 (45)
	Sugar maple	(482)	3.0	12.1	8.5	57 ± 40 (26)
	Hobblebush	(1,568)	2.5	12.1	11.0	40 ± 25 (72)
	Striped maple	(562)	1.8	11.9	7.3	37 ± 24 (22)
	All shrubs	(4,173)	2.3	12.0	9.4	45 ± 32 (165)

^a *t* = cumulative number of seconds that actively foraging birds were observed.

^b *n* = number of hover flights observed.

TABLE 7. Summary of changes in foraging tactics by tree species and strata for four passerine bird species at Hubbard Brook.

	Parameter	Species			
		Red-eyed Vireo	Philadelphia Vireo	American Redstart	Black-throated Blue Warbler
Vertical layers	Locomotion patterns	Flies more in shrubs, hops more in subcanopy	None	Flies more and hops less in shrubs	None
	Search radius	None	None	None	None
	Attack maneuvers	None	None	Fewer flush-chases in shrubs	None
	Attack rates	None	None	None	None
Tree species	Locomotion patterns	Flies more in white ash	None	Flies more in white ash	None
	Search radius	None	None	None	None
	Attack maneuvers	None	None	Flush-chases more in yellow birch	None
	Attack rates	None	Lower in beech	Higher in birch	None

DISCUSSION

Vegetation structure as a determinant of avian foraging behavior.—Holmes and Robinson (1981) suggested that leaf morphology and arrangement (e.g. size, shape, petiole length, distribution along branches, and elevation above twig) strongly affect the foraging behavior of those bird species that glean prey from nearby substrates. They reported, however, that bird species that hover to catch prey do not seem to change their use of foraging tactics among tree species. Thus, hovering might be viewed as a tactic that reduces the effect of habitat structure on bird foraging behavior. Results from the present study, which are summarized in Table 7, are only partly consistent with these conclusions. In support, Black-throated Blue Warblers, which search nearby substrates but primarily hover to catch prey, use the same foraging tactics in most understory shrubs in spite of their widely differing foliage structures. Likewise, the searching rates, locomotion patterns, and attack maneuvers of the Philadelphia Vireo, Red-eyed Vireo, and American Redstart change very little among dominant tree species within strata.

The distributions and densities of leaves, however, do influence the searching tactics of

these hovering species. The Red-eyed Vireo changes its locomotion pattern when it searches for prey in the sparser and more clumped foliage of the subcanopy as compared with its pattern in the canopy (Table 2). Similarly, the three bird species that forage in white ash converge on remarkably similar searching tactics in this tree species. The hop and flight rates of the two vireos, which are different in most foliage compartments, are nearly identical in white ash (Tables 1 and 3), and the redstart, likewise, flies more and hops less in white ash than in any other tree species. Because vireos and redstarts catch different kinds of prey (Robinson and Holmes 1982), it seems unlikely that the abundance or rarity of one kind of insect is responsible for these shifts in foraging behavior. Instead, the low density and more even distribution of leaves within ash canopies probably necessitate birds flying more often while searching for prey there.

The fact that redstarts and both vireo species respond in much the same way to the foliage of the shrub layer as they do to white ash is more difficult to understand. At least superficially, the vegetation structure of ash and the shrub layer is very different. Perhaps the small size and low foliage volume of each shrub or sapling and the narrow vertical distribution of

foliage require the birds to make frequent flights between individual plants in order to search enough leaves per unit time to meet foraging needs.

Taken together, these findings suggest that the locomotion patterns of birds that hover to catch prey and probably other birds that search substrates at a distance are affected to varying degrees by the general distribution of foliage (e.g. clumped vs. scattered, sparse vs. dense). Because most birds seem to have a relatively fixed search radius, these parameters influence how many leaves can be searched from a perch and, in turn, affect how often a bird will have to move between perches. Thus, for a Red-eyed Vireo to maintain a constant rate of prey capture, it seems to adjust its flight and hop rates among foliage compartments (Table 1).

Birds might be expected to increase their search radii in sparse, scattered foliage. That this does not seem to happen, as evidenced by the patterns observed in ash, may be due to inherent limitations in these birds' perceptual capabilities, as Fitzpatrick (1981) suggested. An increase in search radius could involve a trade-off between searching more leaves and experiencing greater difficulty in spotting small or cryptic prey at a distance.

Microhabitat selection and foliage structure.—Vegetation structure may also determine many of the preferences shown by species for particular foliage compartments and habitats. The primary reason for this is that the success of a particular searching tactic may vary with vegetation structure, at least for some species. For ground-foraging birds in open habitats, grass length has been shown to affect foraging success significantly (Smith 1974b, Eiserer 1980). In our study, we find that the Philadelphia Vireo, which uses a relatively inflexible searching behavior, is more successful in certain foliage compartments than in others. Within the canopy, this species locates and attacks more prey per unit time in ash and yellow birch than it does in sugar maple or beech. Throughout its breeding range, this vireo is associated with successional tree species such as quaking aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and alder (*Alnus* spp.) as well as yellow birch and white ash (Barlow and Rice 1977). The Philadelphia's active, flight-oriented, searching behavior seems better adjusted to the characteristic "multilayered" leaf distribution

of these successional tree species (Horn 1971) than to the "monolayered" leaf distribution of beech and sugar maple. Thus, the Philadelphia Vireo's greater foraging success in ash and yellow birch may be a result of its ability to forage in tree species with particular foliage structures.

Differences in prey-attack rates do not explain why the Philadelphia Vireo forages more frequently in the upper canopy than the sub-canopy; it attacks prey with equal frequencies in both strata. The reason probably involves interspecific aggression from the socially dominant Red-eyed Vireo, which occurs primarily at mid-heights in this forest (Robinson 1981). The upper canopy, especially the emergent white ashes, therefore seems to provide a refuge from red-eye aggression (Robinson 1981).

The preference of the Black-throated Blue Warbler for the forest understory may be a result of differences in vegetation structure between the canopy and understory. The plant-species composition and foliage distribution of the understory differs considerably from that of the canopy. The Black-throated Blue Warbler hops less, flies more, and hovers more than its canopy-foraging congeners, *D. virens* and *D. fusca*, which are syntopic at Hubbard Brook (Robinson and Holmes 1982). The Black-throated Blue Warbler may have morphological and/or perceptual characteristics that make it more efficient at exploiting the understory than its congeners. Alternatively, the Black-throated Blue Warbler's preference for the understory may result from competitive interactions or from physiological adaptations to the cooler, more humid microhabitat of the understory (cf. Karr and Freemark 1983).

Insect abundance as a determinant of foraging behavior.—Until now, we have treated the distribution of leaves as the crucial variable in determining bird-locomotion patterns. Because virtually all insects taken by these birds are found on leaf surfaces, this may be justifiable, if we assume that insects are randomly distributed throughout trees and strata. Differences in the abundances, distribution, and kinds of prey available in each foliage compartment, however, also play a role in causing shifts in bird foraging behavior (cf. Paszkowski 1982). This is especially true for the redstart, which both fans its tail and chases after flushed prey more often in yellow birch than in other tree species.

Because these attack maneuvers are strongly associated with the capture of homopterans (Robinson and Holmes 1982; Root 1967; Sherry 1982, in press), it may be either that yellow birch foliage is arranged in such a way that tail fanning is more effective there or that homopterans are more abundant in yellow birch. The latter is supported by insect-density data from Hubbard Brook (Holmes and Schultz MS). This higher density of homopterans in yellow birch, therefore, helps to explain the redstarts' higher attack rate, more frequent use of tail fanning, and higher frequency of flush-chases in this tree species. It is also possible that the variable attack rate of the Philadelphia Vireo reflects differences in the abundance of some preferred prey items (e.g. certain leaf-rolling or background matching types of Lepidoptera larvae) between foliage compartments.

Role of vegetation structure in determining bird-community structure.—In general, the number of bird species in a habitat increases with the addition of vertical layers (MacArthur and MacArthur 1961, Willson 1974) because of the addition of major supporting structures, such as boles and branches, above a distinct ground layer. These vertical layers provide foraging opportunities for guilds of species that are morphologically adapted for exploiting prey on bark, twigs, leaves, and on the ground (Holmes et al. 1979). Results from this latter study suggest that the addition of well-developed vertical layers to a habitat may provide further opportunities for new species, especially within guilds. The Red-eyed Vireo's flexible searching behavior may be most efficient in the more clumped foliage of the subcanopy, where it does the majority of its foraging (Robinson 1981). This, in turn, provides an opportunity for the subordinate Philadelphia Vireo, which is well-adapted for foraging in at least some of the tree species of the upper canopy. Similarly, the distinct foliage structure of the shrub layer may require specific foraging adaptations. The shrub-foraging Black-throated Blue Warbler, for instance, uses more hover maneuvers to catch prey than do its two sympatric congeners at Hubbard Brook that forage in the canopy (Robinson and Holmes 1982). Franzreb (1978), Hunter (1980), and Wiens and Rotenberry (1981) also report close associations between birds and particular plant species.

Holmes et al. (1979) found that the guild patterns among the arboreal birds at Hubbard

Brook were influenced by their preferences for certain plant species, particularly yellow birch and conifers as opposed to beech and maple. Conifers, although rare in this forest, represent a contrasting life form from the dominant hardwoods and, as such, provide opportunities for specialized species. Yellow birch may be preferred, because it generally has higher insect densities (Holmes and Schultz MS), and its physiognomy (small leaves on short petioles) makes leaf surfaces easily accessible to birds that glean (Holmes and Robinson 1981).

The distinctive foliage structure of trees such as white ash may greatly limit the number of bird species that can effectively forage in them. A woodland dominated by ash would probably contain very few species of foliage-searching birds. James and Wamer (1982) found that forests dominated by one tree species tended to have fewer bird species. We predict, however, that a forest consisting only of a single tree species (yellow birch, for example) that can be searched in many different ways and has higher insect densities might have a nearly full complement of species. Thus, the number and abundance of birds in forests with few tree species could depend greatly upon which tree species are present.

In conclusion, the number of bird species found in a particular habitat is influenced by a complex of factors including foliage structure, species composition of the vegetation, and types and abundances of available foods. A more complete understanding of the determinants of bird-community structure will require carefully designed comparative and quantitative studies on how bird species respond to the vegetation structure and food resources available in their habitats. Additionally, experimental manipulations of both forest structure and insect distributions are necessary to test predictions about the relationships between bird-species diversity and its correlates.

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