

FORAGING BEHAVIOR OF FOREST BIRDS: THE RELATIONSHIPS AMONG SEARCH TACTICS, DIET, AND HABITAT STRUCTURE¹

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Abstract. The different searching tactics of passerine birds foraging for arthropods among the foliage of a northern hardwoods forest result in the capture of different kinds of prey. Five major searching modes are employed by the 11 foliage-foraging bird species in the Hubbard Brook Experimental Forest, New Hampshire. These are distinguished primarily by the rates and distances moved by the searching birds and by the types and forms of their prey-attacking maneuvers. These in turn reflect how large an area is scanned, how thoroughly it is searched, and how the bird moves from perch to perch in its search for prey. Mean searching and prey-attacking flight distances are positively correlated, indicating that birds move just far enough on average to take them into areas they have not previously searched visually. Likewise, birds that move rapidly while searching make significantly more prey attacks per unit time and hence encounter prey more often. Slow searchers scrutinize substrates more thoroughly and seem to take more cryptic and often larger prey.

The results suggest that there are limitations on the ways that birds can search for and capture arthropod prey among foliage. We hypothesize that constraints imposed by the structure of the vegetation and by the types and abundances of prey determine the available foraging opportunities. Such habitat parameters may affect, in ecological or evolutionary time, the foraging traits of birds that can successfully exploit a particular habitat, and hence influence the patterns of bird habitat selection and community structure.

Key words: *bird foraging; community structure; diet; forest birds; Hubbard Brook; searching behavior; vegetation structure.*

INTRODUCTION

The methods by which animals search for food determine in large part how often and what kinds of prey they encounter. This relationship between searching behavior and diet has been studied intensively in certain invertebrate groups, particularly parasitic insects (Varley 1941, Bansch 1966, Dowell and Horn 1977, Waage 1979), predatory coccinellid beetles (Banks 1954, Dixon 1959) and some herbivorous caterpillars (e.g., Jones 1977a, b). Despite extensive interest in vertebrate foraging behavior, however, it is only recently that investigators have examined the ways in which these animals search for food and its significance for understanding patterns of resource exploitation and community structure (e.g., Cody 1968, 1974, Williamson 1971, Eckhardt 1979, Moermond 1979a, b, Morton 1980, Fitzpatrick 1981, Huey and Pianka 1981). Only the studies of Smith (1974a, b) on thrushes, Davies (1977) on flycatchers, and Morton (1980) on warblers have clearly demonstrated a relationship between the search paths of insectivorous birds and the kinds of prey taken.

In this paper, we examine the search tactics used by 11 species of passerine birds foraging for insects among the foliage of a northern hardwoods forest, and,

through dietary analysis, relate these to the prey obtained. We then discuss the factors, particularly vegetation structure and resource availability, that influence these patterns and consider the implications for understanding bird habitat selection and community structure.

STUDY AREA

This study was conducted on a 10-ha plot in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, USA. The forest consists of late successional northern hardwoods, dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*), with occasional scattered clumps or individuals of white ash (*Fraxinus americana*), white birch (*Betula papyrifera*), and red spruce (*Picea rubens*). The canopy averages 25–27 m in height. The shrub layer is a dense mixture of sugar maple and beech saplings, hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and mountain maple (*A. spicatum*). Detailed information on the vegetation, geology, and other features of the forest can be found in Bormann and Likens (1979) and references therein. Features of the vegetation and foliage structure relevant to this study are given below.

METHODS AND PROCEDURES

This study was conducted in the summers of 1974 through 1979. During this period, insect populations

¹ Manuscript received 29 July 1981; revised 22 February 1982; accepted 23 February 1982.

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TABLE 1. Characteristics of the 11 species of passerine birds that forage mostly on arthropod prey on plant surfaces in the Hubbard Brook Forest.

Families and species	Body size* (g)	Number/10 ha† ($\bar{x} \pm SD$)	Attacks on arthropods‡ (% of all prey)		
			On leaf	On bark	n
Tyrannidae					
Least Flycatcher, <i>Empidonax minimus</i>	10.3	27.0 \pm 4.7	76.2	2.2	609
Paridae					
Black-capped Chickadee, <i>Parus atricapillus</i>	11.1	0.7 \pm 0.8	38.2	58.0	451
Vireonidae					
Solitary Vireo, <i>Vireo solitarius</i>	15.9	1.5 \pm 1.7	31.6	55.2	114
Red-eyed Vireo, <i>Vireo olivaceus</i>	17.3	23.5 \pm 6.0	83.4	9.5	1719
Philadelphia Vireo, <i>Vireo philadelphicus</i>	11.5	3.0 \pm 0.8	83.2	10.5	628
Parulidae					
Black-throated Green Warbler, <i>Dendroica virens</i>	9.2	8.3 \pm 1.1	73.9	13.6	587
Black-throated Blue Warbler, <i>Dendroica caerulea</i>	10.0	11.8 \pm 1.4	78.8	8.3	193
Blackburnian Warbler, <i>Dendroica fusca</i>	10.0	3.2 \pm 2.3	77.0	14.4	570
American Redstart, <i>Setophaga ruticilla</i>	8.6	35.9 \pm 8.0	65.7	4.5	1223
Thraupidae					
Scarlet Tanager, <i>Piranga olivacea</i>	29.3	2.4 \pm 1.3	55.0	20.2	207
Fringillidae					
Rose-breasted Grosbeak, <i>Pheucticus ludovicianus</i>	45.9	5.9 \pm 1.8	75.9	16.4	378

* Mean live masses of adult birds (R. T. Holmes, *personal observation*).

† Mean densities of breeding adults for the summers 1974 to 1979 at Hubbard Brook (for census procedures, see Holmes and Sturges 1975).

‡ Percent of observed prey attacks directed at arthropod prey on leaf and bark substrates. Maneuvers directed at prey in or on other substrates (e.g., air, ground) are not listed. (Adapted from Holmes et al. 1979a.)

remained at relatively low levels; there were no outbreaks of defoliators or other major year-to-year differences in insect availability (J. C. Schultz, P. J. Nothnagle and R. T. Holmes, *personal observation*). The data were gathered between mid-June and mid-July, coinciding with nestling and early fledgling phases of the breeding cycle. At these times, demands for energy are greatest and birds spend most of their time foraging (Black 1975, Holmes et al. 1979b). Observations of foraging birds were made throughout the day, but mostly between 0600 and 1200 Eastern Standard Time (EST).

We quantified the behavior of adult birds that were actively foraging and not of those that were resting, primarily singing, or involved in other activities that might affect foraging rates (see Black 1975). To obtain the data, we regularly and repeatedly traversed the study plot, moving from one foraging bird to another. When a foraging individual was encountered, we followed it for as long as it could be kept in sight. The relatively dense foliage and high canopy of this forest made prolonged observations difficult; as a consequence, most sequences were relatively short, varying from a few seconds to rarely as long as 5 min (see below). The numbers of different individuals observed depended on the population density of each species (see Table 1). For rarer species, the data come from a minimum of 5 or 6 individuals each season. For the

others, at least 10 to 15 and often many more individuals were observed during the study.

We recorded on tape every movement directed at searching for and capturing prey, location (height above ground, position in tree, tree species), capture success, and the kinds of prey obtained. Foraging sequences were transcribed from the tapes, using a stopwatch. Associations between variables were assessed with product-moment correlation analyses, with significance levels determined by *t* tests (Sokal and Rohlf 1969).

Foraging rates

For each foraging sequence, we tallied the numbers of hops, flights, and prey-attacking maneuvers. These were divided by the number of seconds for that sequence to obtain the rates for each kind of search movement. Hop, flight, and maneuver rates were averaged over all sequences for each bird species and variances calculated (see also Morton 1980). We only used sequences in which the birds were continuously in sight for at least 20 s. This method of calculating foraging rates differs from Morse (1968), Eckhardt (1979), and others who used an overall rate for the total number of seconds accumulated for all foraging sequences recorded, a procedure that provides no information on the variability of the behaviors.

Kinds of searching movements

We define a searching movement as any change in position made by a bird that was searching for prey. This excludes movements directed towards prey, which are treated separately (see below). Searching movements were divided into flights, in which birds change perches by flying, and hops, in which they shift positions without extending their wings. For all flights, we estimated the angles (in increments of 45° from the horizontal) and distances moved. Only flights between perches within more-or-less continuous vegetation are considered in the analyses. The results therefore refer to within-patch searching.

The distances moved by birds while hopping were not recorded. Most hops were approximately 2–10 cm in length, and involved movement along a branch or between closely positioned twigs or branches.

Prey-attacking maneuvers

Whenever birds attempted to capture prey, we recorded what kind of foraging maneuver they used (e.g., glean, hawk, hover, etc.). Maneuvers are defined below. Whenever a maneuver involved a flight, we estimated the angle flown (in increments of 45° from the horizontal) and the distance moved.

Diets

Information on the foods taken by Hubbard Brook birds was gathered by observation of prey captured and from samples obtained by administering an emetic to wild-caught birds, following the methods of Prys-Jones et al. (1974). For the latter, birds were captured in mist nets in areas of comparable vegetation structure 1–2 km from the observation plots. Immediately after capture, birds were given 0.1 cm³ of a 1% solution (1 g/100 g H₂O) of antimony potassium tartrate per 10 g of body mass, and placed in a darkened container lined with wax paper. Within 2–3 min, most birds had regurgitated pellets of partially digested insects, which were then preserved in 70% alcohol. These were sorted and the prey identified to order or family and counted.

Like most techniques for obtaining dietary samples from birds (Hartley 1948), this emetic procedure has certain drawbacks and limitations (see Herrera 1975, Zach and Falls 1976, Lederer and Crane 1978). However, any biases apply more or less equally to samples from all species, at least among those that have roughly similar food requirements such as the 11 insectivorous species considered here. Hence, the data obtained in this study are used as a relative index to differences in diet among these bird species occupying the same forest environment.

RESULTS

The birds and the foraging environment

Of the 22 bird species that breed regularly in the Hubbard Brook Forest, 11 search for prey primarily on

the surfaces of vegetation, while the others specialize on prey in the forest litter or in bark (Holmes et al. 1979a). In this paper, we focus on the former group. Of these 11 species, 9 obtain more than half of their prey from leaf surfaces (Table 1), mostly in the forest canopy, although one, the Black-throated Blue Warbler, feeds among the understory vegetation. The two remaining species, Solitary Vireo and Black-capped Chickadee, take 30–40% of their prey from leaves (Table 1), but also search branches and trunks. The chickadee in particular forages in a different manner from the others and its behavior will be described separately in a later section. Population densities for these bird species and masses as indices of body sizes are given in Table 1; additional data about the bird community and the species' foraging relations, including foraging heights and substrates, are given in Holmes and Sturges (1975) and Holmes et al. (1979a).

The distribution of foliage in the Hubbard Brook Forest varies, but is most dense between 0 to 2 m and 15 to 25 m (see Sherry 1979). Leaves, with the exception of conifers, are two dimensional, which limits the number of hiding places and backgrounds on which insects can hide. Except for the occasional leaf-rolling or leaf-tying caterpillars, birds searching leaves do not usually have to contend with buried or hidden prey.

Most of the prey available to birds on the foliage at Hubbard Brook are larval and adult moths (Lepidoptera), adult flies (Diptera), wasps (Hymenoptera), and beetles (Coleoptera), nymphal and adult leafhoppers and froghoppers (Homoptera), and spiders (Arachnida). Within the foliage compartment of this forest, most arthropods are on leaf surfaces and not on twigs or small branches. Most important, all of these prey occurred at low densities in the years of this study (e.g., an average of 2.2 caterpillars per 1000 leaves in June 1978) and were widely scattered in distribution (J. C. Schultz, P. S. Nothnagle, and R. T. Holmes, *personal observation*). With such generally low densities, the probability that a bird will find a suitable prey item on any given leaf is exceedingly low. This has important implications for how birds search for prey.

Searching tactics

Foraging rates.—Small forest passernines move rapidly from perch to perch when searching for prey by hopping along or flying between branches and twigs (Table 2). Searching velocities, defined as the total number of perch changes per minute (=hop + flight rates, Table 2), range from 6.8 to 28.7 moves/min. Three broad groups are evident: (1) slow searchers (Least Flycatcher, Solitary Vireo, and Scarlet Tanager) which change perches less than 10 times/min, (2) intermediate-rate searchers (Rose-breasted Grosbeak, Red-eyed Vireo, and Philadelphia Vireo) which change perches 14–16 times/min, and (3) rapid searchers (the four parulid warblers) changing positions at rates >24 times/min. In a similar study Eckhardt (1979) classified the

TABLE 2. Searching and attack rates ($\bar{x} \pm \text{SE}$) of foraging insectivorous birds in the Hubbard Brook Forest.

Species	N (s)*	Hops/min (H)	Search flights/min (F)	Perch changes/min (H + F)	H/F ratio	Prey attacks/min
Least Flycatcher	53 (3033)	0.0	7.5 ± 0.4	7.5	0	3.4 ± 0.3
Solitary Vireo	31 (3852)	2.6 ± 0.6	5.9 ± 0.3	8.5	0.44	1.4 ± 0.2
Red-eyed Vireo	76 (7442)	6.7 ± 0.6	9.3 ± 0.4	16.0	0.73	2.1 ± 0.1
Philadelphia Vireo	64 (3876)	3.9 ± 0.4	12.4 ± 0.4	16.3	0.31	3.0 ± 0.2
Black-throated Blue Warbler	147 (9775)	16.0 ± 0.8	9.9 ± 0.4	25.9	1.62	2.2 ± 0.2
Black-throated Green Warbler	38 (4489)	16.2 ± 1.6	8.5 ± 0.7	24.7	1.91	4.5 ± 0.6
Blackburnian Warbler	32 (3485)	19.9 ± 1.6	8.8 ± 1.2	28.7	2.26	4.0 ± 0.5
American Redstart	130 (8816)	14.4 ± 0.8	12.3 ± 0.5	26.7	1.14	5.6 ± 0.3
Scarlet Tanager	42 (3059)	2.2 ± 0.5	4.6 ± 0.3	6.8	0.48	1.9 ± 0.2
Rose-breasted Grosbeak	43 (4022)	8.1 ± 1.1	5.8 ± 0.5	13.9	1.40	2.5 ± 0.3

* N = number of foraging sequences (cumulative number of seconds).

two major insectivorous bird guilds in a Colorado mountain community as "passive" (<4 moves/min) and "active" (>10 moves/min) searchers. These are roughly comparable to our first two categories, but the slow searchers at Hubbard Brook (6–8 times/min) move considerably more often than Eckhardt's "passive" searchers.

The rates of hopping and of flying also vary among species. The ratio between the hop rate and the flight rate (H/F ratio, Table 2) is a useful index to how species move while searching for prey. On the basis of H/F ratios, four groups of species can be distinguished: (1) the *Dendroica* warblers and the grosbeak, which hop more often than they fly (H/F > 1); (2) the vireos and the Scarlet Tanager, which fly more often than they hop (H/F < 1); (3) the American Redstart, which hops and flies about equally (H/F = 1); and (4) the Least Flycatcher, which practically never hops (H/F = 0).

The rates at which species attack prey vary from 1.4 times/min for the Solitary Vireo to 5.6 times/min for the redstart. These rates are significantly correlated with the number of perch changes per min ($r = +.63$, $P = .04$). This suggests that species which move rapidly while searching encounter more prey, as predicted by certain optimal foraging models (Schoener 1971, Norberg 1977). We found no significant correlations between bird size (measured as cube root of body mass) and either search rate ($r = -.53$, $P = .12$) or prey-attack rates ($r = -.49$, $P = .15$), contrary to the predictions of Fitzpatrick (1981).

Search flight characteristics.—When foraging within continuous patches of foliage, most birds made short flights in either horizontal or obliquely upward directions (Fig. 1). There are no discernible differences among the species in the vector components of search flights.

Differences do occur in the distances flown between perches while searching (Fig. 1). From the frequency distributions of search flight distances, we can distinguish three basic patterns (Fig. 1): (1) many short (<0.9 m) flights which skew the distributions to the left,

characteristic of the *Dendroica* warblers; (2) a more normally distributed pattern with few short flights, many of intermediate lengths (0.6–1.2 m), and a few long flights, shown by the vireos, the redstart, and grosbeak; and (3) flights of variable lengths, but including many that are relatively long (>2 m), characteristic of the tanager and Least Flycatcher.

The mean search flight lengths for these species are inversely correlated with the mean hop rates ($r = -.78$, $P = .01$). Species that make frequent hops move only short distances when they fly. Similarly, search flight rate is inversely related to search flight distance ($r = -.58$, $P = .08$). Although not significant, this latter relationship suggests that species which fly frequently in their search for prey tend to move short distances per flight.

Prey-attacking patterns

The searching movements of a bird often result in encounters with prey. The attack on prey therefore culminates the search and is an important component of foraging behavior. We distinguished five major prey-attacking actions used by the foliage-dwelling birds at Hubbard Brook (Table 3). This expands slightly the classification given by Holmes et al. (1979a). We use the terminology given previously (Holmes et al. 1979a) and whenever possible, give the equivalent terms recently proposed by Fitzpatrick (1980).

1. Gleaning.—This is a maneuver in which a standing or hopping bird takes a stationary prey item from a substrate. It is equivalent to the "perch-glean" of Fitzpatrick (1980), but includes gleans preceded by a flight (Fitzpatrick's "landing-and-gleaning"). In these cases, it was often difficult to tell whether the prey was seen before or immediately after the bird landed. Like Eckhardt (1979), we assume that gleaned prey are usually spotted nearby (<0.3 m) and the attack does not involve a flight component.

At Hubbard Brook, gleaning is the dominant attack maneuver for Rose-breasted Grosbeaks, Black-throated Green Warblers, Blackburnian Warblers, and

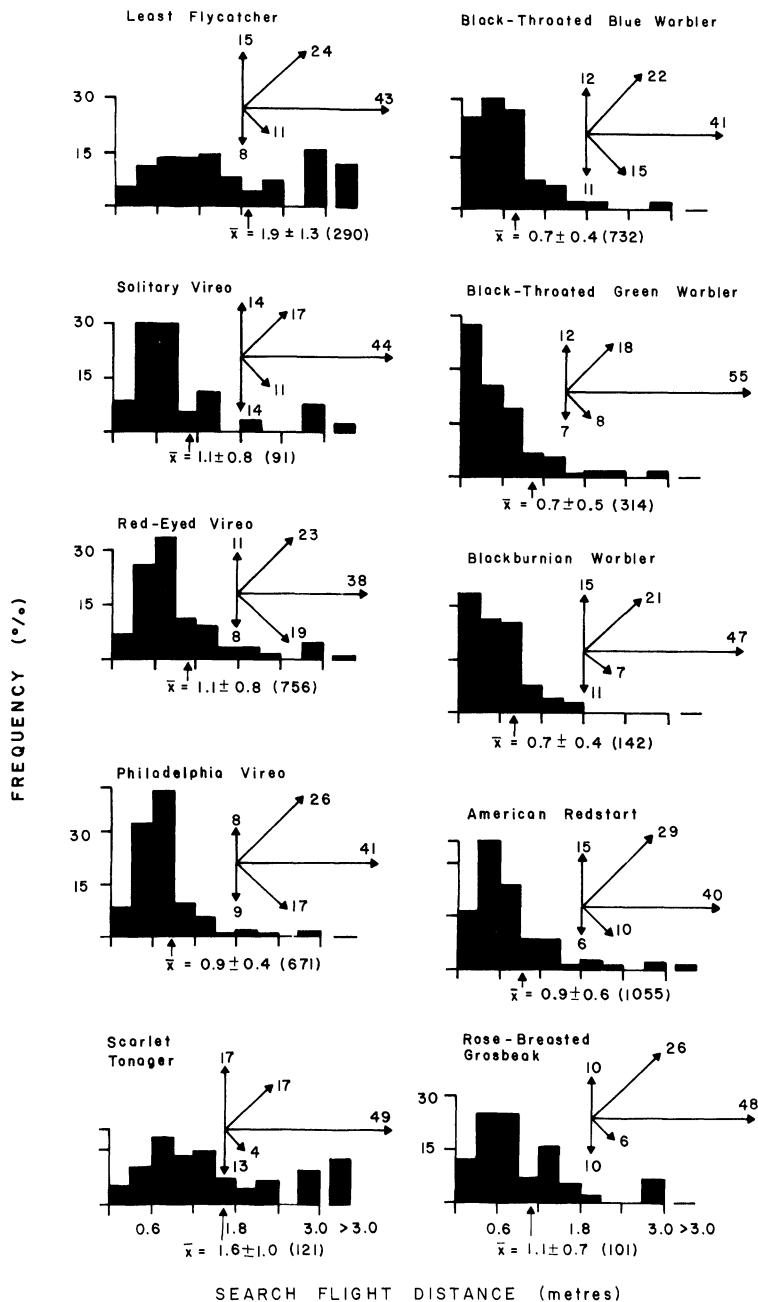


FIG. 1. Lengths ($\bar{x} \pm SD$) and angles of flights between perches used while searching for arthropod prey. Arrows indicate flights that are straight up, 45° upward, horizontal, 45° downward, and straight down. Vector length is proportional to the percentage of flights in the direction indicated.

chickadees (Table 3). Least Flycatchers seldom glean, while the remaining species are intermediate in their use of this maneuver.

2. Hovering.—Included in this category are all attacks in which the prey item is picked from a substrate while the bird is in flight ("sally-gleans," "hover-gleans," and "upward strikes" of Fitzpatrick 1980).

Hovering is a predominant maneuver of 7 of the 11

species of foliage-dwelling birds at Hubbard Brook (Table 3). The Least Flycatcher hovers extensively, in contrast to many of its congeners in other habitats that largely hawk prey from air (Eckhardt 1979, T. C. Moerman, personal communication). The Black-throated Blue Warbler also differs from its congeners in that it hovers more often than it gleans (Table 3). The same patterns observed among the species for

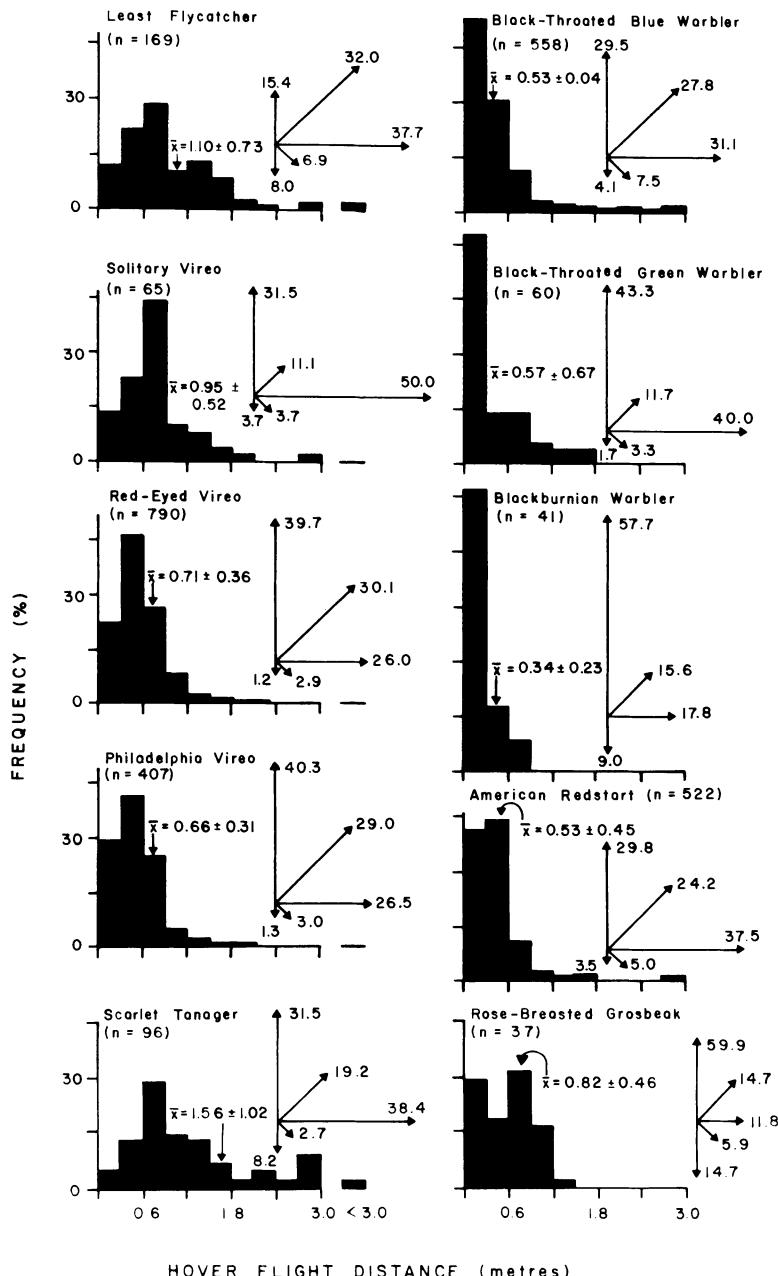


FIG. 2. Lengths ($\bar{x} \pm SD$) and angles of hover flights (distance travelled from perch to substrate on which prey was located). Arrows indicate flights that are straight up, 45° upward, horizontal, 45° downward, and straight down. Vector length is proportional to the percentage of flights in the direction indicated.

their search flight distances are evident in the frequency distributions of their hover flight distances (Figs. 1 and 2). Distances flown by these birds while searching are significantly correlated with their mean hover distances (Fig. 3). Thus, the *Dendroica* warblers fly short distances between perches and capture prey from nearby substrates, while the three vireos fly medium-length distances and attack prey at medium distances. A similar relationship has been reported for

Anolis lizards (Moermond 1979b) and for tyrannid flycatchers (Fitzpatrick 1981). Its significance is that these animals move just far enough to take them into new areas beyond their previous field of vision. As also reported by Moermond and Fitzpatrick for their animals, the search flights of these forest birds are slightly longer than their prey-attacking flights (Figs. 1 and 2). The latter represent average distances at which prey are spotted and not the outer limits of the "search

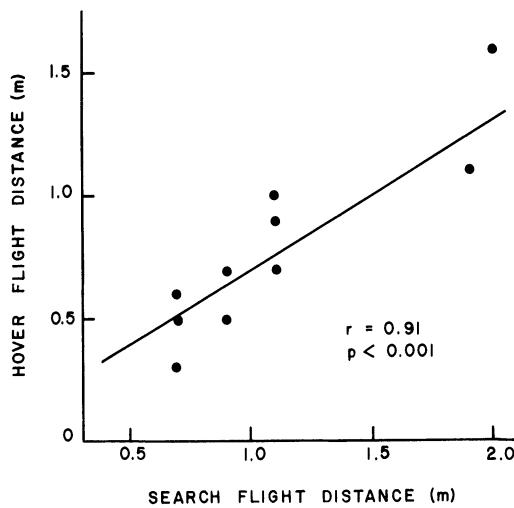


FIG. 3. Correlation of search flight and hover flight lengths for 10 species of foliage-dwelling birds at Hubbard Brook. No comparable data were available for the Black-capped Chickadee (see text).

radius" (see Eckhardt 1979). The Least Flycatcher is an exception. Its search flights (Fig. 1) are almost twice as long as its average prey-attacking distance (Fig. 2). Significantly, the flycatcher is the only foliage-dwelling bird in this forest that frequently turns around on its perch and therefore searches a 360° field.

The hovers of most species are directed vertically, although some species also show strong 45° upward and horizontal components (Fig. 2). The strong vertical component of these maneuvers probably reflects the fact that most insect prey are on the undersurfaces of leaves (R. T. Holmes et al., *personal observation*) and birds scan leaf surfaces above or in front of them. This same tendency for most hovering flights to be directed upward at insects on the undersides of leaves has been found for many birds in tropical forests where most insects also rest on the undersurfaces of leaves (Greenberg and Gradwohl 1980).

3. Hanging.—This maneuver is a combination of a hover and a glean in which a bird flies to a leaf or twig tip and hangs from it. In doing so, it may either pluck a large prey item from a leaf, or, more often, uncurl a leaf that has been rolled by a caterpillar or spider. Only the Black-capped Chickadee at Hubbard Brook hangs frequently, but the Red-eyed Vireo also uses this maneuver (Table 3). Uncurling leaves is a fundamentally different maneuver from the others described here because the birds must manipulate the substrate (e.g., unfold a leaf) to find a concealed prey. Also, the birds may not cue in on the prey itself but on the change in the shape or characteristics of the substrate caused by the prey.

4. Flush-chase.—This maneuver involves the chasing of prey flushed by the bird, usually in a long downward flight. Although most species in this forest occasionally chase large prey items that they flush while searching, the redstart is the only one that uses this flush-chase technique extensively. It moves actively along the branches and twigs, fanning its contrastingly patterned tail and flicking its wings, actions which appear to flush prey. The bird then chases, often tumbling after the prey as it drops off the foliage.

5. Hawking.—In this maneuver, flying prey are pursued and captured by birds in flight (Fitzpatrick 1980). This maneuver is not used frequently by any species at Hubbard Brook (Table 3). The Scarlet Tanager often searches outward from the inner crowns of large canopy trees and makes some long hawking maneuvers. The Least Flycatcher sits on relatively open perches, usually below the main canopy, and makes occasional sallies to hawk flying insects. Other species, such as the redstart, hawk facultatively, especially at midday when flying insects are more abundant (Holmes et al. 1978).

Diets

Emetic data.—Those species for which we have sufficient data tend to segregate by diet (Table 4). Caterpillars are important in the diets of four species: two

TABLE 3. Prey capturing (attack) maneuvers of the 11 foliage-dwelling insectivorous birds in the Hubbard Brook Forest.

	Percent						N
	Hover	Glean	Hang	Flush-chase	Hawk	Other*	
Least Flycatcher	81.1	3.1	...	6.2	9.6	...	993
Black-capped Chickadee	8.8	57.0	28.7	...	2.4	3.5	658
Solitary Vireo	60.8	34.5	0.4	0.9	3.3	...	153
Red-eyed Vireo	56.6	29.9	7.1	1.9	4.5	...	2187
Philadelphia Vireo	68.7	24.2	2.4	0.4	4.3	...	790
Black-throated Blue Warbler	60.7	33.4	...	1.1	4.0	0.8	1186
Black-throated Green Warbler	35.4	54.2	1.6	6.6	2.0	...	833
Blackburnian Warbler	24.6	61.9	0.7	6.0	1.8	...	803
American Redstart	53.1	22.8	0.4	17.4	6.3	...	1676
Scarlet Tanager	54.5	26.3	0.6	...	18.3	0.3	327
Rose-breasted Grosbeak	36.7	55.8	1.5	3.5	2.4	...	455

* Mostly probes, in which birds obtain hidden prey from within a substrate.

TABLE 4. Bird diets in the Hubbard Brook Forest, 1974–1976, based on the emetic technique. Values represent percent frequencies of each taxon in the sample of identifiable prey items.

Species (N)*	n†	Lepidoptera		Homoptera	Hymenoptera	Coleoptera	Diptera	Arachnida	Other
		Larval	Adult						
Least Flycatcher (48)	187	4.8	...	8.0	15.0	49.8	21.4	0.5	0.5
Red-eyed Vireo (71)	231	33.4	...	6.9	8.7	34.2	14.3	1.7	0.9
Philadelphia Vireo (5)	24	50.0	4.2	20.8	4.2	8.3	4.1	4.1	4.1
Black-throated Blue Warbler (19)	58	27.6	...	5.2	5.2	50.0	12.0
Black-throated Green Warbler (5)	23	47.8	4.3	34.8	...	13.1
American Redstart (44)	176	4.5	1.1	34.7	11.9	13.1	30.2	1.1	3.4
Scarlet Tanager (12)	41	7.3	34.1	41.5	4.9	2.4	9.8
Rose-breasted Grosbeak (16)	77	15.6	1.3	...	11.7	62.3	6.5	2.6	...

* N = Number of emetic samples.

† n = Number of identifiable prey items.

vireos (Philadelphia and Red-eyed) and two warblers (Black-throated Blue and Black-throated Green). The American Redstart, Black-throated Green Warbler, and probably the Blackburnian Warbler prey heavily on homopterans (principally leafhoppers, Cicadellidae). The Scarlet Tanager takes more Hymenoptera, especially wasps (Ichneumonidae), and Coleoptera. Five species have a high percentage of beetles in their diets (Table 4). Given the fact that coleopteran fragments are durable, it is important to point out that the stomach contents of three species, the Philadelphia Vireo, Black-throated Green Warbler, and American Redstart, contained few beetle fragments, suggesting that they seldom take this type of prey. Dipterans are taken most often by redstarts and Least Flycatchers, but also by Red-eyed Vireos and Black-throated Blue Warblers.

Field observations of prey captured.—Although it was often difficult to identify prey captured in the field, we did accumulate additional observational data on prey taken (Table 5). These records are used here to complement the emetic data given above by providing information on the larger types of prey eaten.

Lepidoptera larvae appear more frequently in the

observation records (Table 5) than in the emetic samples (Table 4) for all species, primarily because they are often large and require some handling before being swallowed. In addition, since these larvae are frequently fed to young (Royama 1970, R. T. Holmes, *personal observation*), they are often carried rather than swallowed by the adult birds and hence more readily observed. Adult Lepidoptera, mostly moths, were taken relatively more frequently by Solitary Vireos and American Redstarts, while Scarlet Tanagers took a higher percentage of Coleoptera and Hymenoptera (mainly *Megarhyssa* sp.), many of which were large and also required considerable handling time before being swallowed.

Because of the fragmented conditions of insects in the emetic samples and the difficulty of measuring prey observed in the field, we were unable to obtain a direct measure of prey size. However, the percentage of identifiable prey items caught (Table 5) can be used as a rough index to the relative size of prey captured by these 11 bird species. Only the Solitary Vireo, which moves slowly and methodically scans the vegetation, took a high proportion of observably large prey. The low frequency of large insects in the diets of most

TABLE 5. Field observations of prey taken by birds at Hubbard Brook, 1976–1979. Values are percent frequencies.

	Identified items		Lepidoptera		Coleoptera	Diptera	Hymenoptera	Arachnida
	Number	(%)*	Larval	Adult				
Least Flycatcher	5	(1.1)	60.0	40.0
Black-capped Chickadee	29	(4.4)	75.9	3.4	6.9	13.8
Solitary Vireo	58	(37.9)	73.2	19.6	5.4	1.8
Red-eyed Vireo	207	(9.5)	86.8	3.9	3.4	3.9	...	2.0
Philadelphia Vireo	63	(7.9)	87.3	4.8	...	7.9
Black-throated Blue Warbler	109	(9.2)	80.7	13.8	...	1.8	...	3.7
Black-throated Green Warbler	58	(6.9)	82.8	8.6	6.9	1.7
Blackburnian Warbler	48	(5.9)	75.0	16.6	2.1	4.2	...	2.1
American Redstart	55	(3.2)	67.3	25.5	1.8	1.8	1.8	1.8
Scarlet Tanager	19	(5.8)	63.1	5.3	15.8	...	15.8	...
Rose-breasted Grosbeak	41	(9.0)	82.9	...	7.3	...	7.3	...

* Identified prey items as percent of total number of foraging maneuvers observed in summers of 1976–1979.

TABLE 6. Characteristics of the searching patterns of insectivorous birds that seek prey primarily among foliage of the northern hardwoods forest at Hubbard Brook.

Searching pattern and bird species	Hop/flight ratio	Search flight distance	Search velocity	Primary prey-attack maneuver(s)	Attack maneuver distance	General search pattern	Prey-type obtained
Open-perch Searchers Least Flycatcher Scarlet Tanager	<1	medium-long (0.6–3 m)	slow (5–10)*	hover, hawk	medium-long (0.6–3 m)	perch in open, search medium-far substrates	active prey: wasps, flies
Variable-distance Searchers Solitary Vireo Red-eyed Vireo Philadelphia Vireo Rose-breasted Grosbeak	<1	medium (0.6–1.2 m)	medium (10–20)*	hover	medium (0.6–1.2 m)	search near and far substrates, while steadily moving slowly	medium to large insects, e.g., caterpillars
Flush-chasers American Redstart	≈1	short–medium (0.3–0.9 m)	fast (>20)*	tumble, hover	mostly short, some long (0.3 m to long chases)	move rapidly, chase flushed prey	active prey: flies, leaf hoppers
Near-surface Searchers Black-throated Blue Warbler Black-throated Green Warbler Blackburnian Warbler	>1	short (0.3–0.6 m)	fast (>20)*	glean	short (0.3–0.6 m)	move short distances at high rate; search nearby substrates	small to medium, often cryptic insects
Substrate-restricted Searchers Black-capped Chickadee	variable	variable	variable, usually slow	glean, hang, probe	short	search specific substrates	hidden or cryptic prey

* Searching moves or perch changes/min.

species probably reflects the fact that there were few large (>1 cm) foliage-dwelling insects in the northern hardwoods at Hubbard Brook during this study period (J. C. Schultz et al., *personal observation*).

Searching modes and diet

To synthesize from the data just presented, we can distinguish five major searching modes among these 11 species, each resulting in the capture of different kinds of prey (Table 6). These form a continuum from species that frequent open places and search for prey over long distances to those that forage among dense foliage and search for prey close by. These searching patterns are similar to the "foraging modes" described by Fitzpatrick (1980) for tyrannid flycatchers, although his groupings and nomenclature refer more to the prey-attack phase and not to overall search tactics.

1. *Open-perch Searchers*.—Birds that use this searching mode usually perch on twigs and branches in the more open areas below the main canopy and seldom hop among the foliage. They scan surrounding air space and vegetation and locate prey that are often far away. The prey taken are often active, either flying or moving about on vegetation. At Hubbard Brook, two species fit this category, the Least Flycatcher and Scarlet Tanager. The flycatcher typically perches on twigs in the more open areas below the main canopy, it rarely hops, seldom flies more than 2–2.5 m for prey,

and obtains mostly flying insects such as flies and beetles. Although this flycatcher does hawk some insects from the air, most of its prey attacks are hovers directed towards insects sitting on leaves. This searching mode is similar to "upward striking" foraging mode (Fitzpatrick 1980) used by many tropical flycatchers.

The other Open-perch Searcher is the Scarlet Tanager. It often sits in the open inner branches of large canopy trees and searches outward for insects, which are often actively flying wasps and beetles. The tanager takes some flying insects but more often waits for the insect to land before attacking. We have several observations of tanagers watching and then attacking large ichneumonid wasps that were themselves searching the foliage for insect larvae.

In some respects this searching mode is similar to what Eckhardt (1979) and Huey and Pianka (1981) called "passive searching," in that species utilizing both search tactics tend to perch in the open and search substrates at a considerable distance from the perch. However, both the Scarlet Tanager and the Least Flycatcher catch most of their prey from leaf surfaces rather than in the air and fly considerably more often than Eckhardt's "passive" searchers, two of which are in the same genus (*Empidonax*) as the Least Flycatcher. The lack of true "passive searchers" and the infrequent use of aerial hawking by most species at Hubbard Brook in general may be due to the closed,

even-aged canopy of this sector of forest. "Passive" searchers may need large open areas in which to spot actively moving prey and to have room in which to maneuver when chasing them. The only species in the Hubbard Brook area that would qualify as a "passive searcher" is the Eastern Pewee (*Contopus virens*), which is usually restricted to large treefall openings or occasionally along road cuts. The lack of large gaps in the canopy at Hubbard Brook may require the Least Flycatcher to change perches more often and search proportionately more leaf surfaces than its congeners in other, more open habitats.

2. *Variable-distance Searchers*.—This searching mode is characteristic of the three vireos and to a lesser extent of the Rose-breasted Grosbeak. These species hop and fly frequently and search substrates both nearby and far away. This searching mode results in the capture of a relatively high proportion of Lepidoptera larvae.

The Solitary Vireo slowly and methodically searches the inner branches, foliage, and trunks of trees for large, dark, and often cryptic adult moths and prepupal caterpillars that rest on bark by day. Its prey attack rate is the lowest of any of the foliage-dwelling birds at Hubbard Brook, but it captures a much higher proportion of large prey than any other species (Table 5). In contrast, the Red-eyed and Philadelphia Vireos search leaves in the outer parts of trees for smaller green caterpillars. Because of the low densities and variable distributions of these caterpillars, these birds must search a large number of leaves, which explains their frequent flights (Table 2). For example, if 50% of the prey items caught by the Philadelphia Vireo are caterpillars (Table 4) and the density of caterpillars in the canopy is about two per 1000 leaves (J. C. Schultz et al., *personal communication*), then to catch 3 prey items/min (Table 2) a bird must search about 750 leaves/min. Such extremely rapid leaf searching and the variable, often long, distances from which leaves are searched probably means that vireos miss or pass by many small or cryptic prey.

The grosbeak, like the vireos, also searches near and far substrates. In a typical foraging sequence, a grosbeak hops slowly along a branch while carefully peering under leaves. It occasionally gleans insects from leaf surfaces, and then as it approaches the distal end of a branch, it stops and searches foliage up to 1–2 m away. As a result, the grosbeak has a high frequency of both gleans and long hovers (Table 3, Fig. 2). The grosbeak is also highly variable in its foraging behavior, at times searching the leaf litter on the ground, hunting along tree trunks, or moving among the foliage.

Interestingly, there are few counterparts of the Variable-distance Searchers among other studies of bird foraging behavior. Indeed, the most common species that uses this searching mode at Hubbard Brook, the Red-eyed Vireo, uses different searching tactics in the

different parts of its range and at different times. For example, in northeastern Ontario (Rice 1978), Maryland (Williamson 1971), and in southeastern Peru (S. K. Robinson, *personal observation*) it principally hops, searches nearby substrates and gleans prey, all of which are a characteristic of Near-surface Searchers (see below). Similarly, there is some evidence that the Red-eyed Vireo at Hubbard Brook searched more like a Near-surface Searcher during a major caterpillar outbreak from 1970–1972 (R. T. Holmes, *personal observation*). It is thus possible that Variable-distance Searchers only use this searching mode in certain habitats or during periods of relative resource scarcity when a very large number of leaves must be searched in order to catch enough prey.

3. *Flush-chasers*.—This search pattern is intermediate between that of the Variable-distance Searchers and the Near-surface Searchers (see below), but involves rapid movements which flush prey that are actively pursued. The only species that forages in this way at Hubbard Brook is the American Redstart. It catches a very high proportion of homopterans, which often leap from leaves when disturbed (R. T. Holmes, *personal observation*). Root (1967) also found that the tumbling maneuver was associated with the capture of homopterans by Blue-gray Gnatcatchers (*Polioptila caerulea*). This flush-and-chase pattern is therefore used to exploit prey that have active predator-avoidance responses. It is also characteristic of *Myioborus* redstarts in the neotropics (S. K. Robinson, *personal observation*), of some *Monarcha* flycatchers (Monarchidae) in New Guinea and Australia (Pearson 1977), and of the tyrannid genus *Terenotriccus*, which preys almost exclusively on homopterans (T. W. Sherry, *personal communication*).

4. *Near-surface Searchers*.—At Hubbard Brook, this searching pattern is characteristic of the three *Dendroica* warblers. These species make frequent, short movements between perches while searching nearby substrates for prey that are usually close enough to be gleaned or captured with a short hover. The reason we do not call this searching mode "perch-gleaning" (Fitzpatrick 1980) is that the Black-throated Blue Warbler, which is virtually identical in its searching movements to its congeners, hovers more often than it gleans. Rather than reflecting a major difference in searching behavior, this greater use of hovers probably results from the difficulty of gleaning prey from the large, long-petioled leaves of the understory where the Black-throated Blue Warbler does most of its foraging (Holmes et al. 1979a).

Near-surface Searching results in the capture of many small and cryptic prey that might be missed by birds searching from a greater distance. It is a searching pattern characteristic of small insectivorous bird species in a variety of habitats, including warblers in spruce woods (Mac Arthur 1958, Morse 1968) and in

the neotropics (Morton 1980), some flycatchers (Fitzpatrick 1980), vireos in other habitats (Williamson 1971), sparrows (Cody 1968), and neotropical tanagers and antbirds (Snow and Snow 1971, Munn and Terborgh 1979, Gradwohl and Greenberg 1980).

5. Substrate-restricted Searchers.—This is the characteristic foraging pattern of the Black-capped Chickadee. The foraging behavior of chickadees and titmice (family Paridae) have been studied extensively both in the field (e.g., Hartley 1953, Gibb 1954, Morse 1970, 1978, Royama 1970, Hertz et al. 1976) and in aviaries (e.g., Krebs et al. 1973, 1977, Erichsen et al. 1980). Field studies have shown that parids are flexible in their use of substrates and respond rapidly to temporal changes in the spatial distribution of their prey (Hartley 1953, Royama 1970, Edington and Edington 1972, Smith and Sweatman 1974). Observations of the diet of nestling titmice led Tinbergen (1960) to develop his "search image" hypothesis and Royama (1970) to develop his "area-restricted search" hypothesis.

We have found similar patterns in the foraging behavior of the Black-capped Chickadee at Hubbard Brook. Rather than search a generalized substrate such as leaf surfaces for prey, this species seeks specific substrates such as dead, damaged, or curled leaves, twig tips, or tree boles. These birds appear to search for these substrates, fly to them, and then begin to look for prey. For example, in midsummer one individual of a small flock investigated 19 consecutive live curled leaves and ignored all other substrates. Another bird from the same flock searched six consecutive twig tips and then switched to searching dead curled leaves.

This style of foraging, which we call "Substrate-restricted" searching, differs from that of the other foliage-dwelling birds described above. The chickadee's foraging behavior seems to be determined by the distribution and structure of the substrate being searched. For example, when they search dead leaves, the length of search movements depends entirely on the distribution of dead leaves and the rate of movement depends on the length of time it takes to uncurl each leaf. For these reasons the methods we have used to quantify the searching behavior of the other foliage-dwelling birds were inappropriate for chickadees. Since these parids seem to forage differently from other insectivorous birds, attempts to generalize from studies of their search behavior to other kinds of birds must be done with caution.

This Substrate-restricted searching mode is widely used by birds in neotropical forests where, for example, there are many species such as some antbirds (Formicariidae), ovenbirds (Furnariidae), and woodcreepers (Dendrocalaptidae) that specialize on dead leaves, epiphytes, palms, and vines (Munn and Terborgh 1979, Gradwohl and Greenberg 1980, Morton 1980).

Searching modes and bird community structure

Since these searching modes, as we have described them, reflect how these birds search for and capture prey and also the kinds of prey taken, they represent in effect "searching guilds," i.e., groups of species that exploit food resources in similar ways (cf. Root 1967). These same bird species have recently been classified into "microhabitat guilds" by Holmes et al. (1979a), based primarily on where they capture prey (e.g., foraging substrates, heights, position in tree, and tree species). A comparison of the searching modes (Table 6) with the microhabitat guilds (see dendrogram of relationships in Holmes 1981) shows that those species that are most similar in searching behavior generally differ in microhabitat use and vice versa. For example, among the Variable-distance Searchers, the Solitary Vireo searches the inner foliage and branches of trees, while the Red-eyed and Philadelphia Vireos forage among the outer foliage. The latter two species tend to segregate vertically but also exhibit considerable interspecific aggression when they do overlap spatially (Robinson 1981). Among the Near-surface Searchers, the Black-throated Blue Warbler forages exclusively in the understory, while its two congeners actively search leaves in the canopy. These latter two species, Blackburnian and Black-throated Green Warblers, are very similar in both search tactics and microhabitat use, but are present at low densities at Hubbard Brook (Table 1), which is probably marginal habitat for them. Where they occur in spruce woods, their foraging differs in subtle ways (Mac Arthur 1958, Rabenold 1978). Finally, the best example is the Least Flycatcher and American Redstart, which are very similar in their use of microhabitats (Holmes et al. 1979a, Holmes 1981) and bill morphology (Sherry 1979), yet differ markedly in search behavior. The differences in the diets of these two species (Table 4) reflect their different search tactics.

Thus, since diet is determined at least in part by searching mode as well as by microhabitat use, we feel that it is necessary to include information on both of these parameters when characterizing patterns of community resource exploitation. Toft (1980) and Huey and Pianka (1981) have recently come to a similar conclusion for anuran and lizard communities, respectively.

DISCUSSION AND CONCLUSIONS

The results of this study demonstrate a relationship between the search tactics used by birds foraging for insects among forest foliage and the kinds of prey captured. These searching patterns are largely a function of the morphological and perceptual traits of each species, which allow the birds to move through the foliage, locate, detect, and capture prey in specific ways. The fact that closely related species (e.g., con-

genera) use the same basic searching methods (Table 6) indicates the importance of phylogenetic and evolutionary processes in determining these patterns (see also Fitzpatrick 1980). Yet these behaviors are not totally fixed or stereotyped. As mentioned previously, the search tactics and foraging patterns of Red-eyed Vireos vary from place to place and even from one year to another within the same habitat (see Searching modes and diet: Variable-distance Searchers). Furthermore, species with quite different morphologies often utilize the same general searching mode and take similar types of prey (see Table 6), suggesting that morphology does not necessarily predetermine foraging behavior or diet, as has been inferred by some investigators (e.g., Ricklefs and Travis 1980). We therefore agree with Hutto (1981) that morphological analyses alone will never provide a complete characterization of the food exploitation patterns and ecological relations of co-occurring bird species.

What then are the factors that determine the ways in which birds search for and capture prey in a particular habitat? Several investigators have suggested that certain habitat characteristics, particularly the physical structure of the habitat, have been important selective forces in determining the patterns of animal locomotion, foraging behavior, and resource exploitation (e.g., Enders 1975, Moermond 1979a, b). Moermond, in particular, has proposed that the distribution and structural characteristics of perch sites in a habitat affect how *Anolis* lizards search for and capture prey and in turn determine which lizard species will actually be present at that site. He concluded his paper, however, by speculating that birds, because they are able to fly, should be less constrained by their "habitat matrix."

The findings of this study suggest that birds, too, may be constrained by certain habitat characteristics. The 11 passerine species that forage for insects among foliage at Hubbard Brook employ only five major searching modes (Table 6). Furthermore, the searching and prey-attacking behavior of foliage-dwelling birds in a variety of other woodland and forest habitats (e.g., Mac Arthur 1958, Root 1967, Williamson 1971, Eckhardt 1979, Munn and Terborgh 1979, Fitzpatrick 1980, Morton 1980) are basically similar to those we describe here for birds at Hubbard Brook. This apparent convergence on a restricted number of searching modes suggests that there may only be a limited number of ways that birds can search for and capture prey among foliage, and that only those species with the morphological and/or behavioral capabilities for successful searching in a particular habitat will be able to exist there. For forest birds, the habitat features most likely to affect their searching and prey-attacking behavior are the structure of the vegetation and the kinds and characteristics of the available prey.

Vegetation structure is important because it affects

how birds move through the habitat and how they can see and capture prey. The number, arrangement, and positioning of leaves along branches, for example, determine in part how many leaves can be searched from a given perch and how easily prey there can be captured. Furthermore, leaves with short petioles arranged regularly along a branch provide a different searching environment and different prey-attacking conditions compared to leaves on long petioles that are clumped near the ends of branches. Thus, at Hubbard Brook, birds with short prey attack distances (e.g., the Near-surface Searchers such as Blackburnian and Black-throated Green Warblers, Table 6) search for prey more frequently on plant species such as yellow birch that have foliage arrayed continuously along and close to the branches, and tend not to feed in tree species with different foliage configurations (Holmes and Robinson 1981). Also, as indicated earlier in this paper, the foraging behavior of the Black-throated Blue Warbler differs from those of its congeners in ways (more hovering) that reflect the particular foliage structure (larger leaves, longer petioles) of the understory where it forages.

Characteristics of the arthropod prey will also influence bird searching behavior and success. These include their abundances, sizes, distribution patterns, diversities, and antipredator adaptations. We have already suggested that the low abundances and scattered distributions of foliage-dwelling insects in the Hubbard Brook Forest during this study made it necessary for most birds to move rapidly and search a large number of substrates. Moreover, the apparent switch to Near-surface Searching by the Red-eyed Vireo and other species at Hubbard Brook during a caterpillar outbreak (R. T. Holmes, *personal observation*) was probably due to the greater abundance of large prey available at that time. Likewise, we expect forests with a greater number of bark-dwelling prey, for instance, to provide different searching opportunities/constraints for insectivorous birds, compared to Hubbard Brook, where most prey are on foliage or its supporting twigs.

We therefore suggest that vegetation structure and the nature of the food resources at a particular site interact to provide both opportunities and constraints on the ways that birds can successfully search for and capture prey. Since these parameters vary from one place to another, depending on plant species composition, climate, and other factors that affect plant physiognomy and insect availability, the searching options available to birds can also be expected to vary. On an evolutionary time scale, such habitat parameters act as selective forces helping to shape the resident species' foraging styles. In ecological time, they determine which species from the pool of those available are able to occupy and exploit that habitat successfully.

Although this hypothesis may be difficult to eval-

ate, we suggest that further insight can be gained by comparing the search tactics and resource exploitation patterns of bird species in habitats differing in vegetation structure and resource bases. Such studies examining the foraging patterns of individual bird species in different kinds of vegetation, or exploiting different kinds of food resources, will provide critical information on the importance of these habitat variables in affecting bird foraging behavior and habitat selection.

ACKNOWLEDGMENTS

This study was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, under the auspices of the Northeastern Forest Experiment Station, United States Forest Service, Upper Darby, Pennsylvania, and with the continued cooperation of Dr. R. S. Pierce. Funding was provided by a grant from the National Science Foundation to Dartmouth College. We thank J. C. Schultz, T. W. Sherry, H. F. Recher, J. W. Terborgh, B. McP. Beehler, D. C. Wiernasz, D. I. Rubenstein, and R. Greenberg for their very helpful and constructive comments on the manuscript.

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