

## FOLIAGE STRUCTURE INFLUENCES FORAGING OF INSECTIVOROUS FOREST BIRDS: AN EXPERIMENTAL STUDY

CHRISTOPHER J. WHELAN<sup>1</sup>

Illinois Natural History Survey, Midewin National Tallgrass Prairie, 30071 S. Rt. 53, Wilmington, Illinois 60481 USA

**Abstract.** Preferences for foraging in particular tree species have been well documented in a variety of bird species, but underlying reasons remain little investigated. Understanding the causal bases for such patterns of habitat use can help to elucidate mechanisms of habitat selection and, therefore, community organization and structure. I experimentally tested the hypothesis that fine-scale foliage structure of two deciduous tree species influences the foraging behavior of three small, insectivorous bird species. On sugar maple (*Acer saccharum*), with its orbicular leaves elevated above the branch, Black-throated Blue Warblers (*Dendroica caerulescens*) and American Redstarts (*Setophaga ruticilla*) captured prey predominantly from lower leaf surfaces, whereas Black-throated Green Warblers (*Dendroica virens*) captured prey predominantly from upper leaf surfaces. In contrast, on yellow birch (*Betula alleghaniensis*), with its oblong-ovate leaves held within the plane of the supporting branch, all three bird species captured prey disproportionately from upper leaf surfaces. Overall, aerial maneuvers were used more frequently to capture prey from upper than from lower leaf surfaces on sugar maple, but the opposite occurred on yellow birch, where non-aerial maneuvers were used more frequently to capture prey from upper than from lower leaf surfaces. Those results indicate that the leaf surface from which prey are more easily captured (with less energetically costly non-aerial maneuvers) differs between those tree species. Experimental manipulation of leaf dispersion and distance to prey demonstrated that leaf dispersion is the chief determinant of prey capture location (upper vs. lower leaf surfaces), and that distance to prey is the chief determinant of prey capture maneuver (aerial vs. non-aerial). When foraging on artificial branches in which vertical distance between branches was systematically increased experimentally, Black-throated Green Warblers captured a significantly smaller proportion of prey from lower surfaces of leaves on the upper branch than did Black-throated Blue Warblers. Taken together, these results indicate that different tree species, as well as different locations within tree species, present insectivorous birds with distinct foraging environments and, therefore, constitute distinct foraging microhabitats. Furthermore, even closely related bird species that are generally similar morphologically respond in behaviorally unique ways to differences in foliage structure. For those reasons, forest management practices that enhance tree species diversity could concomitantly enhance foraging opportunities (niche diversity) for forest insectivores and may thus help to promote high bird species diversity and maintain abundant populations.

**Key words:** aviary experiment; bird community structure; deciduous foliage; foliage structure; foraging behavior; insectivorous birds; New Hampshire; northern hardwoods; Parulidae; vegetation structure; warblers.

### INTRODUCTION

Ecologists have long recognized that vegetation physiognomy influences habitat selection (MacArthur and MacArthur 1961, Hildén 1965, Willson 1974, Gorman and Karr 1978, Klopfer and Ganzhorn 1985, Pribil and Picman 1997), foraging ecology and resource use (Morse 1976, Moermond 1979a, b, 1986, Holmes and Robinson 1981, Huey and Pianka 1981, Paszkowski 1984, Diehl 1993, Parrish 1995a, b, Gunnarsson 1996), and refuge from predation (Crowder and Cooper 1979, 1982, Brönmark 1985, Kotler and Brown 1988, Hacker and Madin 1991) in a wide variety of taxa. Although most studies have focused on vegetation structure at

the level of the habitat (e.g., MacArthur and MacArthur 1961, MacArthur et al. 1966, Willson 1974, Roth 1976, Gorman and Karr 1978, Moermond 1979a, b, Crowder and Cooper 1982, Brown 1989a, b, Brown et al. 1994), microvegetation structure has also been suggested (Kendeigh 1945, Holmes and Robinson 1981, Brönmark 1985), or demonstrated, to affect foraging behavior (Partridge 1974 1976a, b, Moermond 1979a, b, Moermond and Denslow 1983), microhabitat (foraging site) selection (Klopfer 1963, Diehl 1993, Parrish 1995a, b), or predator avoidance (Hacker and Madin 1991). Understanding how vegetation structure at both the macro- and microscales influences habitat selection and resource exploitation can help to elucidate mechanistic bases of community organization and structure (Moermond 1986, 1990).

Insectivorous birds foraging within the complex

Manuscript received 15 January 1999; revised 3 January 2000; accepted 3 January 2000.

<sup>1</sup> E-mail: virens@attglobal.net

structure of forest trees are a particularly appropriate system in which to examine the relationship between vegetation structure and foraging behavior (Partridge 1974, 1976, Holmes et al. 1979, Holmes and Robinson 1981, Robinson and Holmes 1982, 1984, Klopfer and Ganzhorn 1985, Holmes and Schultz 1988, Parrish 1995a,b). Nonetheless, in recent years, most research on the relationship between bird species and their habitats has focused on fragmentation and associated ramifications for nest predation and brood parasitism. Although those effects are important, other relationships between birds and their habitats should not be ignored. For example, forest fragmentation and other habitat disturbances are often accompanied by changes in environmental conditions that may affect plant species composition (e.g., Wilcove et al. 1986, Hobbs and Huenneke 1992, Archibald et al. 1997, Luken et al. 1997). Because plant species that differ in foliage structure may also differentially affect foraging behavior of birds (Kendeigh 1945, Balda 1969, Partridge 1976a, b, Franzreb 1978, Holmes and Robinson 1981, Parrish 1995a, b), these changes may, in turn, influence resource exploitation, habitat suitability, and bird community organization.

As described by Holmes and Robinson (1981), foliage structure of broad-leaved, deciduous tree species can differ in several ways that may lead to contrasting sets of foraging opportunities and constraints for insectivorous forest birds. Those features include leaf characteristics (e.g., shape, size, and dispersion around the supporting branch), petiole length, branch characteristics (e.g., diameter, length, and angle), and branching patterns (e.g., distance between forks within a branch, vertical distance between branches). From foraging theory, foliage structure is most likely to affect bird foraging behavior by influencing encounter rates with prey, prey accessibility, and energetic costs of attacking and capturing those prey (Greenberg and Gradwohl 1980, Robinson and Holmes 1982, Schmidt 1998). Similar relationships have been documented for *Anolis* lizards (Moermond 1979a, b) and tropical frugivorous birds (Moermond and Denslow 1983, 1985, Moermond et al. 1987).

The overall goal of this study was to experimentally test the hypothesis that such finescale differences in broad-leaved foliage structure influence the foraging behavior of insectivorous forest birds. First, I quantified differences in fine-scale foliage structure between two deciduous hardwood tree species, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*), common in forests of temperate latitudes of North America (Curtis 1959, Bormann and Likens 1979). That information was used to guide a series of aviary experiments using natural and artificial foliage.

Second, I examined general behavioral capabilities of three small, closely related, insectivorous bird species, Black-throated Green Warbler (*Dendroica virens*), Black-throated Blue Warbler (*D. caerulescens*), and

American Redstart (*Setophaga ruticilla*), when foraging from artificial perches of two different diameters, and when distance to prey was systematically manipulated. Third, I tested the hypothesis that foliage structure of sugar maple (raised leaves on long petioles) facilitates prey capture on lower leaf surfaces, whereas that of yellow birch (leaves held in plane of branch on short petioles) facilitates prey capture on upper leaf surfaces. In that experiment, birds foraged on natural substrates (potted saplings) on which I experimentally controlled prey type, abundance, and distribution. Fourth, I tested the hypothesis that leaf dispersion (relative to the branch) was the major determinant of prey capture location, but that distance to prey was the major determinant of prey capture maneuver. In that experiment, birds foraged on artificial foliage whose structure I experimentally manipulated. Finally, I tested the hypothesis that as distance between branches increases, birds will tend to capture prey from upper leaf surfaces of leaves of the lower branch. In that experiment, birds foraged among artificial foliage on two branches; I experimentally varied the vertical distance between these branches while controlling prey type, abundance, and distribution. Taken together, results indicate that insectivorous bird species respond uniquely to differences in tree foliage structure, strongly suggesting microhabitat specialization, a key mechanism of coexistence.

## METHODS

*Choice of tree species and bird species.*—This study was conducted during the summers of 1984–1986. Sugar maple and yellow birch, two canopy dominants of hardwood forests in northeastern North America, were selected because they appear to present birds with contrasting foraging environments, based on differences in foliage structure (Holmes and Robinson 1981). For instance, sugar maple has orbicular leaves with large leaf surfaces that tend to be elevated above the branch by large petioles, whereas yellow birch has ovate or oblong-ovate leaves that are typically held in the horizontal plane of the branch by short petioles. The three bird species investigated, Black-throated Green Warbler, Black-throated Blue Warbler, and American Redstart, are closely related and fairly similar in overall size and morphology. Previous observational studies (Holmes et al. 1978, 1979, Holmes and Robinson 1981, Robinson and Holmes 1982, 1984, Holmes and Schultz 1988) found differences in both foraging behavior and use of tree, sapling, and shrub substrates among the three bird species. All individual birds used in experiments were adult males, captured in mist nets near Hanover, New Hampshire, United States, and held singly in indoor aviaries (1.5 × 2.5 × 2.0 m) at Dartmouth College for up to two weeks under permits of the U.S. Fish and Wildlife Service, during which experiments were conducted. All individual birds gained or main-

tained their body mass during captivity, and all were subsequently released at the site of capture.

*Foliage structure parameters.*—Conspicuous differences in deciduous foliage structure that could presumably affect bird foraging behavior (Holmes and Robinson 1981) include petiole length, leaf size or area, and leaf dispersion around supporting branches. Petiole lengths and leaf areas were obtained from R. T. Holmes and J. C. Schultz (*unpublished data*). Leaf dispersion around branches was quantified in two different ways. In 1985, the position of a leaf relative to its branch was measured for each leaf attached along a 1 m length of branch (measured from the branch tip), on each of 10 sugar maple and 10 yellow birch trees. Branches were chosen haphazardly, with the constraint that they had to be at  $\geq 1$  m in length and within reach from the ground (i.e.,  $\leq 2$  m high). For each leaf, both leaf blade–petiole junction and leaf tip were classified as positioned above, even with, or below the plane horizontal to the branch.

In 1986, dispersion of leaves around a haphazardly chosen “target” branch (including leaves attached to the target branch, as well as leaves attached to other branches in the vicinity of the target branch) was measured on 10 branches from each of five sugar maple and five yellow birch trees (10–20 cm dbh). Branch heights ranged from 2 to 10 m. To reach branches above 2 m, each tree was cut and lowered gently to the ground with ropes. The tree was then cut into smaller segments that could be held upright on the ground, with the trunk at a similar angle to that of the intact tree. For each branch, distance to nearest leaf was measured in each of eight 45° sectors in a vertical plane orthogonal to the direction of the branch at each of three locations along the branch: branch tip, 0.5 m from tip (referred to hereafter as midbranch), and 1 m from tip (referred to hereafter as inner branch). Because bird species used in this study search for prey within a 1 m radius (Robinson and Holmes 1982), only leaves falling within that distance were included. Because all nearest leaves within 1 m of the target branch were thus included, differences in leaf dispersion due to different branching patterns are accounted for by this method. Data were pooled for all sectors above and all sectors below the branch, and significant differences in leaf dispersion were determined with goodness-of-fit tests. Branch diameter was measured with vernier calipers at branch tip, midbranch, and inner branch on a subsample of 30 branches.

*Effect of distance to prey and perch diameter.*—To examine general behavioral responses of subject species to variation in perch diameter (e.g., Pierce and Grubb 1981) and distance to prey (e.g., Moermond and Denslow 1983, 1985, Levey et al. 1984), I quantified the foraging maneuver used by individual birds of each species on artificial perches. Specifically, eight Black-throated Green Warblers (five in 1984 and three in 1985), eight Black-throated Blue Warblers (five in 1984

and three in 1985), and five American Redstarts (all in 1984) served as subjects. In a given foraging trial, each bird was presented with a single perch (wooden doweling) along which were arrayed five prey items (three-segment pieces of mealworm, *Tenebrio molitor*), each of which was impaled on 24-gauge stainless steel wire hooks connected to the perch. Distance between perch and prey (hereafter, prey distance) varied from 70 to 110 mm in 10-mm increments. Each steel hook was separated by 100 mm along the perch. Two perches were used, one of 7 mm and one of 13 mm diameter. Each bird was tested twice on each perch at each prey distance, with a minimum of 2 h (and often  $>24$  h) separating tests. For each prey distance, I recorded whether the bird took prey (1) while remaining perched and without extending or fluttering its wings (glean); (2) while remaining perched but fully extending or fluttering its wings, presumably to maintain balance while extending its reach (glean with wings); (3) after leaving the perch in flight (hover flight).

Data were analyzed with a partially hierarchical multivariate analysis of variance (MANOVA) using SYSTAT 7.0 (Systat 1997). The prey capture maneuver was analyzed by using the mean proportion (following arcsine-square root transformation) of prey taken at each prey distance for all foraging trials for each individual bird for each perch diameter (Morrison et al. 1992). The full model examined the main effects of bird species, individual nested within bird species, perch diameter, prey distance, and interactions of bird species  $\times$  perch diameter and bird species  $\times$  distance to prey.

*Effects of foliage structure.*—Eight Black-throated Green Warblers (three in 1984 and five in 1985), five Black-throated Blue Warblers (two in 1984 and three in 1985), and five American Redstarts (all in 1984) served as subjects. In a single foraging trial, each bird foraged among the foliage of either a transplanted sugar maple or a yellow birch sapling on which six three-segment mealworm pieces were attached (with vegetable shortening) to leaves, half on upper and half on lower leaf surfaces. Each sapling had  $\sim 400$  leaves distributed among its canopy of several branches. Prey were placed on leaf surfaces systematically so that prey were located more or less evenly throughout the canopy of each tree. To determine whether distance to prey from the supporting branch (hereafter, prey distance) affects prey capture location (upper vs. lower leaf surface) and prey capture maneuver (aerial vs. non-aerial), prey in half of the foraging trials were located close to the leaf petiole (small prey distance;  $22.9 \pm 0.85$  mm on yellow birch and  $72.5 \pm 4.98$  mm on sugar maple, all values mean  $\pm 1$  SE), and they were located close to the leaf tip in the other half (large prey distance;  $77.5 \pm 2.45$  mm on yellow birch and  $128 \pm 5.96$  mm on sugar maple). Records were taken on prey capture location (upper vs. lower leaf surface) and foraging maneuver used (aerial vs. non-aerial), until half of the prey were taken. Each individual bird was used

in at least eight foraging trials on each tree species, thus capturing a minimum of 24 prey items per tree species (at least eight foraging trials  $\times$  three prey captures per trial).

I tossed a coin to determine whether a bird foraged first on sugar maple or on yellow birch, and whether distance to prey was first small or large. Subsequently, tree species and prey location, as well as other ongoing experiments, were alternated arbitrarily to prevent each individual subject from forming expectations about its foraging environment. All birds foraged among the foliage of each tree species one to three times before actual testing, to ensure that they would behave naturally (compared to my field observations) in the experimental environment.

Data were analyzed with a partially hierarchical analysis of variance (ANOVA). First, prey capture location was analyzed by taking the mean proportion (following arcsine-square root transformation) of prey taken from each leaf surface for all foraging trials in a given tree species and by distance to prey for each individual bird. The full model examined main effects of bird species (tested with the individual nested within bird species as the error term), tree species, prey distance, and a priori hypothesized interactions. For instance, following Holmes and Robinson (1981), I expected the more typically aerial foragers, American Redstarts and Black-throated Blue Warblers, to show more flexible behavior in response to differences in foliage structure and prey distance than the less aerial Black-throated Green Warbler. This, in turn, led to the expectation of a bird species  $\times$  tree species interaction and a bird species  $\times$  prey distance interaction for both dependent responses, prey capture location and prey capture maneuver. Next, prey capture maneuver was analyzed by taking the mean proportion (following arcsine-square root transformation) of aerial (vs. non-aerial) maneuvers used when capturing prey for all foraging trials in a given tree species and by leaf surface and prey distance, for each individual bird. The full model examined main effects of bird species (tested with the individual nested within bird species as the error term), tree species, leaf surface, prey distance, and a priori hypothesized interactions.

*Manipulations of artificial foliage structure.*—Results from the preceding experiment suggested that raised leaves of sugar maple enhanced access to prey residing on lower leaf surfaces, whereas the planar arrangement of leaves on yellow birch enhanced access to prey residing on upper leaf surfaces. That finding led to the hypothesis that leaf dispersion relative to the branch is the major determinant of prey capture location (upper vs. lower leaf surface). Furthermore, distance to prey tended to be greater on sugar maple than on yellow birch, irrespective of prey placement (close to petiole, close to leaf tip) on the leaf (Whelan 1987). The greater use of aerial maneuvers on sugar maple suggested that distance to prey is the major determinant

of prey capture maneuver. To test those hypotheses, I constructed artificial foliage, based on the measurements of natural foliage of sugar maple and yellow birch (both in the field and for potted plants), which allowed independent experimental manipulation of prey distance and leaf dispersion.

Three adult male Black-throated Green Warblers and three adult male Black-throated Blue Warblers (all in 1985) served as subjects. Artificial foliage was constructed from green construction paper for leaf blades, thin-gauge, stainless steel wire for petioles, and doweling for branches. To eliminate variation in leaf shape as a confounding effect, a single yellow birch leaf served as the template for all artificial leaves. Two petiole lengths were used, corresponding to the mean petiole lengths of yellow birch and sugar maple (see *Results*). Three foliage structures were constructed, referred to hereafter as regular yellow birch, long-petioled yellow birch, and maple-oriented yellow birch. Regular yellow birch had petioles of yellow birch length with leaves held in the plane horizontal with the branch. Long-petioled yellow birch had petioles of sugar maple length, but leaves were held even with the branch. Maple-oriented yellow birch had petioles of sugar maple length, but petioles were oriented 45° above the branch, with leaves held parallel to the plane horizontal to the branch. On each branch, seven pairs of leaves were arranged along the branch. In a given trial, two prey items (three-segment mealworm pieces) were placed on the upper and lower leaf surface in identical locations on six different leaves, half to the right and half to the left of the long axis of the perch. I recorded the leaf surface from which prey were taken and the maneuvers used (aerial, non-aerial) until the bird took half of the available prey. Each bird was allowed to forage from each branch for familiarity, and then was tested twice. Mean capture location and mean capture maneuver were analyzed with partially hierarchical ANOVA as described earlier.

*Effect of distance between branches.*—The previously described experiments examined responses of birds to changes in leaf dispersion and distance relative to the supporting branch. However, birds sometimes attack insects residing on foliage attached to branches other than that on which the bird is perched. If trees differ in branch spacing (either because of inherent growth characteristics or because of varying site conditions, e.g., amount of sunlight or crowding), such differences could also affect bird foraging behavior. To test that possibility, I conducted the following experiment. Two artificial branches simulating yellow birch foliage were arrayed with one branch directly above the second branch. A three-segment mealworm piece was attached to the lower surface of each of six leaves of the upper branch, half to the right of the branch and half to the left of the branch. Six three-segment mealworm pieces were also attached to the upper surface of each of six leaves of the lower branch, each directly

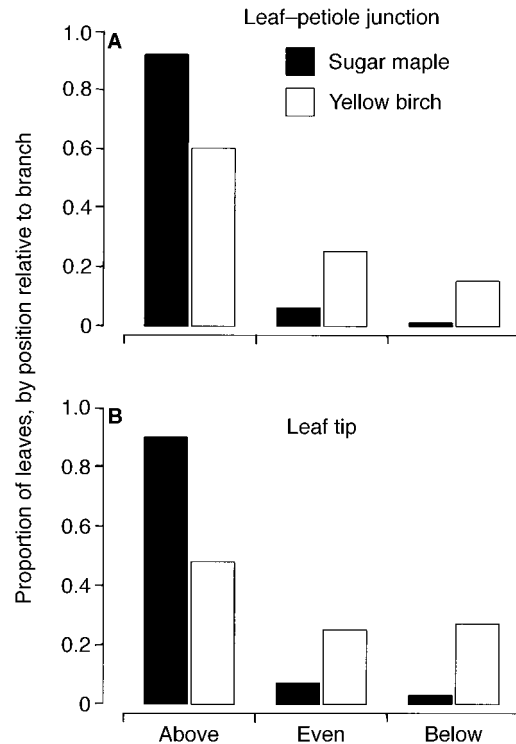


FIG. 1. Position of leaves relative to the supporting branch on sugar maple (*Acer saccharum*;  $n = 10$ ) and yellow birch (*Betula alleghaniensis*;  $n = 10$ ). The histograms show the proportion of sugar maple and yellow birch leaves for which (A) the junction of the leaf blade and petiole and (B) the leaf tip were oriented above, even with, and below the plane horizontal to their supporting branch.

under a corresponding mealworm on leaves attached to the branch above. Distance between branches was varied from 10 to 50 cm in 10-cm increments. Each subject (four Black-throated Green Warblers and five Black-throated Blue Warblers, all in 1986) was tested once at each distance. I recorded the leaf surface from which prey were taken and the maneuvers used (aerial, non-aerial) until the bird took half of the available prey. Results (prey capture location) were analyzed with partially hierarchical ANOVA as previously described.

## RESULTS

**Foliage structure parameters.**—Sugar maple leaves had larger surface areas in both canopy (all values reported as mean  $\pm$  1 SE: sugar maple,  $53.3 \pm 19.0$  mm<sup>2</sup>,  $n = 188$ ; yellow birch,  $26.2 \pm 12.0$  mm<sup>2</sup>,  $n = 382$ ) and subcanopy (sugar maple,  $53.5 \pm 17.7$  mm<sup>2</sup>,  $n = 183$ ; yellow birch,  $35.0 \pm 14.2$  mm<sup>2</sup>,  $n = 284$ ). Sugar maple leaves had longer petioles ( $42.7 \pm 15.0$  mm,  $n = 40$ ) than those of yellow birch ( $12.7 \pm 2.5$  mm,  $n = 40$ ). Although the absolute difference in branch diameter was not great, sugar maple had branches of significantly larger diameter than yellow birch at branch tip (sugar maple,  $2.43 \pm 0.12$  mm,  $n = 30$ ; yellow birch,  $1.55 \pm 0.08$  mm,  $n = 30$ ), mid-branch (sugar maple,  $5.15 \pm 0.16$  mm,  $n = 30$ ; yellow birch,  $3.59 \pm 0.09$  mm,  $n = 30$ ), and inner branch (sugar maple,  $8.35 \pm 0.21$  mm,  $n = 30$ ; yellow birch,  $6.13 \pm 0.22$  mm,  $n = 30$ ).

Both leaf blade–petiole junction ( $\chi^2 = 79.7$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 1A) and leaf tip ( $\chi^2 = 130.9$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 1B) were positioned above the branch

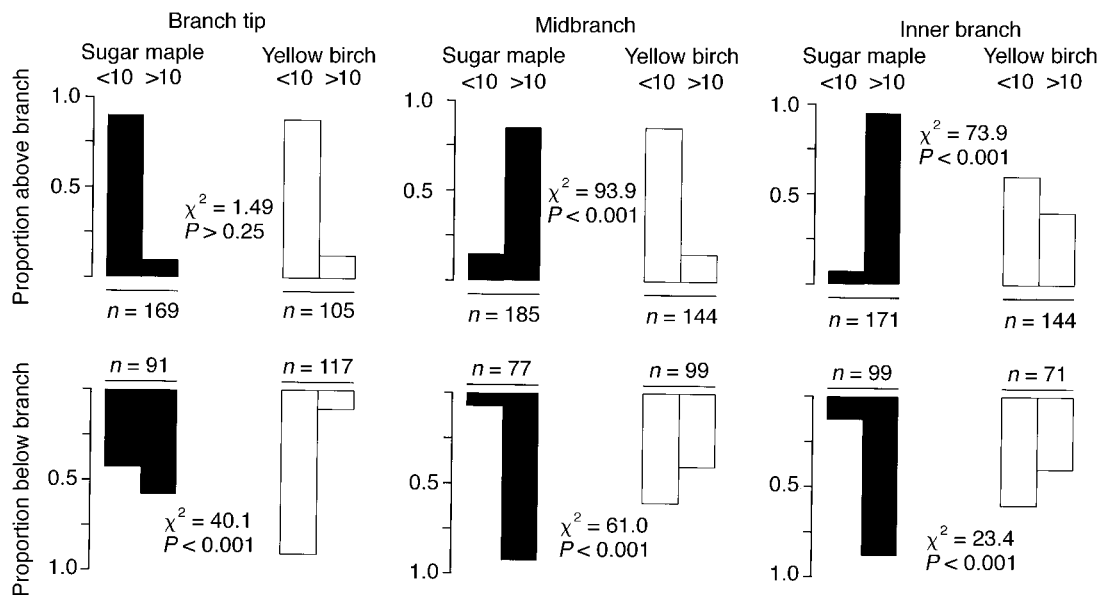


FIG. 2. Dispersion of leaves within 1 m of the branch ( $n = 10$  branches) for sugar maple ( $n = 5$  trees) and yellow birch ( $n = 5$  trees). The figure shows the proportion of sugar maple and yellow birch leaves falling within 10 cm (<10) and between 10 cm and 1 m (>10), both above and below branches at branch tip, midbranch, and inner branch. In contrast to Fig. 1, leaves are not limited to those attached to the target branch. Sample size,  $n$ , is the number of leaves.



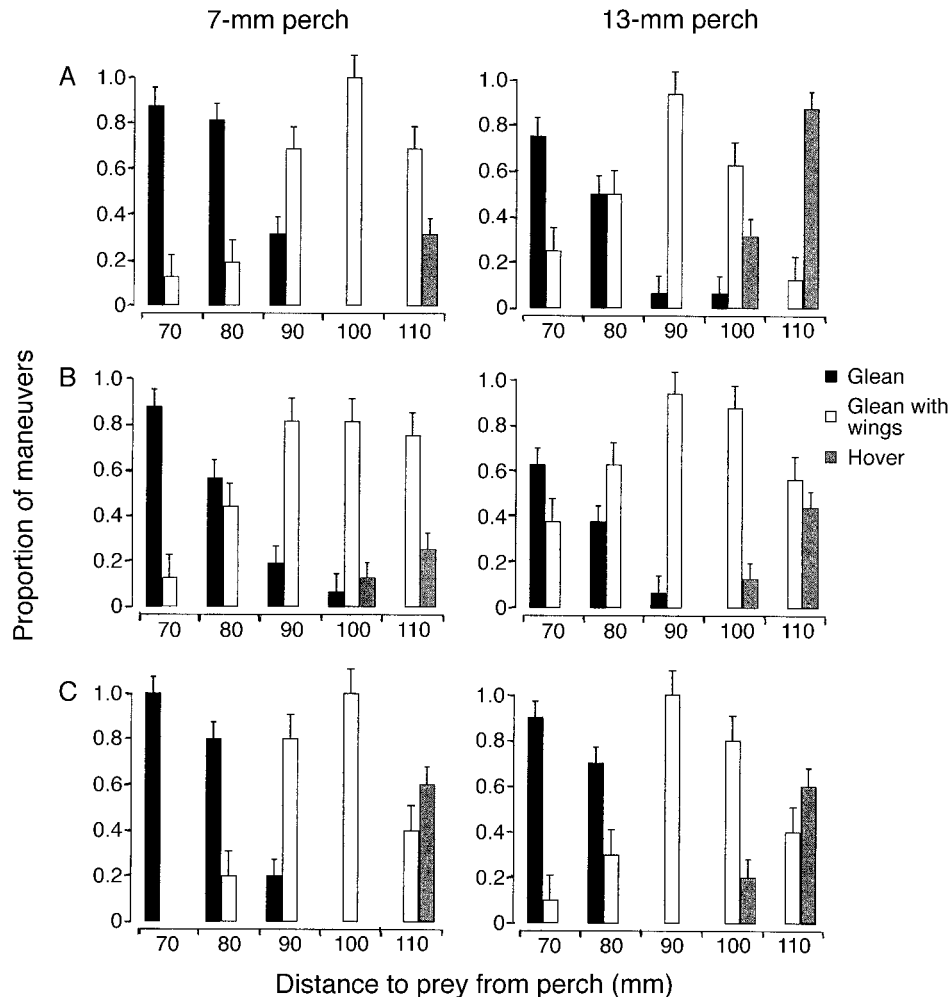


FIG. 3. Effects of perch diameter and distance to prey on capture maneuvers of birds. The histograms show the mean proportion ( $\pm 1$  SE) of maneuvers (glean, glean with use of wings, hover) used by three bird species to capture prey, as a function of distance to prey and perch diameter. Data are based on two prey captures for each individual of each bird species at each distance on each perch diameter: (A) Black-throated Green Warblers ( $n = 8$ ), (B) Black-throated Blue Warblers ( $n = 8$ ), and (C) American Redstarts ( $n = 5$ ).

more often on sugar maple than on yellow birch, whereas they were positioned even with and below the branch more often on yellow birch than on sugar maple. On yellow birch, most leaves both above and below the plane horizontal to the branch fell within 10 cm of the branch (Fig. 2), regardless of trunk proximity. On sugar maple, in contrast, only at the branch tip did most leaves above the plane horizontal with the branch fall within 10 cm of the branch. At all other branch locations, for leaves both above and below the plane horizontal to the branch, most leaves fell beyond 10 cm of the branch. Comparisons of leaf dispersion showed no difference between the two tree species at the branch tip for leaves above the branch, but all other comparisons revealed significant differences, with sugar maple having a greater proportion of leaves farther from the supporting branch than did yellow birch (Fig. 2).

*Effect of prey distance and perch diameter.*—Using

MANOVA, I found no significant differences among bird species (Wilks'  $\lambda = 0.957$ ,  $F_{6,344} = 1.27$ ,  $P = 0.271$ ), nor were there significant interactions between bird species  $\times$  perch diameter (Wilks'  $\lambda = 0.958$ ,  $F_{6,344} = 1.24$ ,  $P = 0.285$ ) and bird species  $\times$  distance to prey (Wilks'  $\lambda = 0.835$ ,  $F_{24,499} = 1.338$ ,  $P = 0.132$ ). There was, however, a significant effect of individual nested within bird species (Wilks'  $\lambda = 0.392$ ,  $F_{54,513} = 3.514$ ,  $P < 0.001$ ), perch diameter (Wilks'  $\lambda = 0.862$ ,  $F_{3,172} = 9.19$ ,  $P < 0.001$ ), and distance to prey (Wilks'  $\lambda = 0.142$ ,  $F_{12,455} = 41.49$ ,  $P < 0.001$ ). The main effects of both increased perch diameter and increased distance to prey were to increase both use of wings and hover flights to capture prey, and they affected all bird species similarly (Fig. 3).

*Effects of foliage structure.*—Although there was significant variation in prey capture location among individuals within each of the three bird species (Table

TABLE 1. Results of partially hierarchical ANOVA examining (A) prey capture location or (B) prey capture maneuver among three bird species (Black-throated Blue Warblers, Black-throated Green Warblers, and American Redstarts).

Source	ANOVA statistics			
	df	MS	F	P
A) Prey capture location†				
Bird species	2	75.85	0.77	0.48
Tree species	1	923.77	38.94	<0.01
Distance	1	80.08	3.37	0.07
Bird × Tree	2	298.10	12.57	<0.01
Bird × Distance	2	0.09	>0.01	0.99
Tree × Distance	1	253.38	10.68	<0.01
Bird × Tree × Distance	2	41.10	1.73	0.19
Individual (Bird)	15	97.95	4.13	<0.01
Error	45	23.72		
B) Prey capture maneuver‡				
Bird species	2	269.42	0.37	0.70
Tree species	1	216.69	0.72	0.39
Distance	1	6891.28	22.78	<0.01
Surface	1	1423.65	4.71	0.03
Bird × Tree	2	517.16	1.71	0.19
Bird × Distance	2	24.77	0.08	0.92
Bird × Surface	2	454.27	1.50	0.23
Tree × Distance	1	674.70	2.23	0.14
Tree × Surface	1	4089.49	13.52	<0.01
Bird × Tree × Distance	2	5.54	0.02	0.98
Bird × Tree × Surface	2	99.46	0.33	0.72
Individual (Bird)	15	738.21	2.44	<0.01
Error	111	302.48		

Notes: Birds were observed foraging for a single prey type among the natural foliage of saplings of two tree species (sugar maple and yellow birch) saplings. Individual nested with bird species served as the error term to test the significance of the main effect of bird species. The main effect of distance refers to the distance between the branch and the relative position of the prey item on leaf blade (resulting in either a small or a large distance).

† Proportion of prey captured from upper leaf surfaces.

‡ Proportion of prey captured with aerial foraging maneuvers.

1), they did not differ in overall capture location (i.e., the main effect of bird species was not significant; Table 1A). They did, however, differ in prey capture location contingent upon tree species: Black-throated Green Warblers took prey disproportionately from upper leaf surfaces on both tree species, whereas both Black-throated Blue Warblers and American Redstarts took prey disproportionately from lower leaf surfaces on sugar maple, but upper leaf surfaces on yellow birch (Table 1A, Fig. 4A). Overall, prey captures occurred significantly more often from lower leaf surfaces of sugar maple, but from upper leaf surfaces of yellow birch (Table 1A, Fig. 4B). Finally, there was a significant tree species × prey distance interaction (Table 1A), which reflected that, on sugar maple, the proportion of prey captured from upper leaf surfaces increased for the large prey distance when compared to that for the small prey distance, but on yellow birch, the proportion of prey captured from upper leaf surfaces decreased for the large prey distance when compared to that for the small prey distance (Fig. 4C).

Individuals within each of the three bird species also differed significantly in prey capture maneuvers (Table 1B), but overall, the bird species did not (Table 1B). Across all three species, aerial maneuvers were used disproportionately more often when prey were captured

at large prey distances (Table 1B, Fig. 5A) and from lower leaf surfaces (Table 1B, Fig. 5B). Finally, there was a significant tree species × leaf surface interaction (Table 1B), which reflected that, on sugar maple, aerial maneuvers were used more frequently when prey were captured from upper than from lower leaf surfaces, but on yellow birch, aerial maneuvers were used more frequently when prey were captured from lower than from upper leaf surfaces (Fig. 5C).

*Manipulations of artificial foliage structure.*—Individual Black-throated Green and Black-throated Blue warblers differed significantly in prey capture location on the artificial foliage structures ( $F_{1,4} = 9.27$ ,  $P = 0.04$ ), but there was no significant overall difference between bird species ( $F_{1,7} = 0.55$ ,  $P = 0.5$ ). Prey were captured more frequently from upper leaf surfaces on regular and long-petioled yellow birch, but they were captured more frequently from lower leaf surfaces on maple-oriented yellow birch ( $F_{2,8} = 74.58$ ,  $P < 0.01$ ; Fig. 6A). A significant interaction between bird species and structure type ( $F_{2,8} = 8.74$ ,  $P = 0.01$ ) indicates that Black-throated Green Warblers captured prey from upper leaf surfaces more frequently on long-petioled yellow birch than on regular yellow birch, whereas Black-throated Blue Warblers captured prey more frequently from upper leaf surfaces on regular yellow

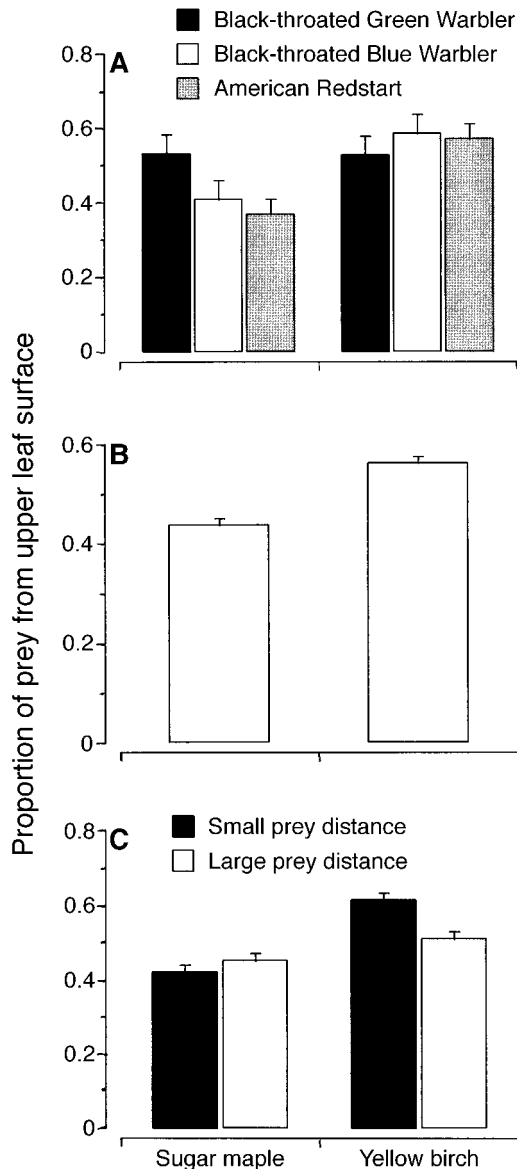


FIG. 4. Effect of natural foliage of sugar maple and yellow birch on prey capture location. (A) Mean proportion ( $\pm 1$  SE) of prey captured from upper leaf surfaces by Black-throated Green Warblers ( $n = 16$  foraging bouts, each of three prey captures), Black-throated Blue Warblers ( $n = 10$  foraging bouts), and American Redstarts ( $n = 10$  foraging bouts). (B) Mean proportion ( $\pm 1$  SE) of prey captured from upper leaf surfaces ( $n = 36$  foraging bouts on each tree species), combining results for Black-throated Green Warblers, Black-throated Blue Warblers, and American Redstarts. (C) Mean proportion ( $\pm 1$  SE) of prey captured from upper leaf surfaces at small and large prey distances ( $n = 36$  foraging bouts on each tree species), combining results for Black-throated Green Warblers, Black-throated Blue Warblers, and American Redstarts.

birch than on long-petioled yellow birch (Fig. 6B). Both species captured prey most frequently from lower leaf surfaces on maple-oriented yellow birch (Fig. 6B).

There was no significant variation in the use of prey

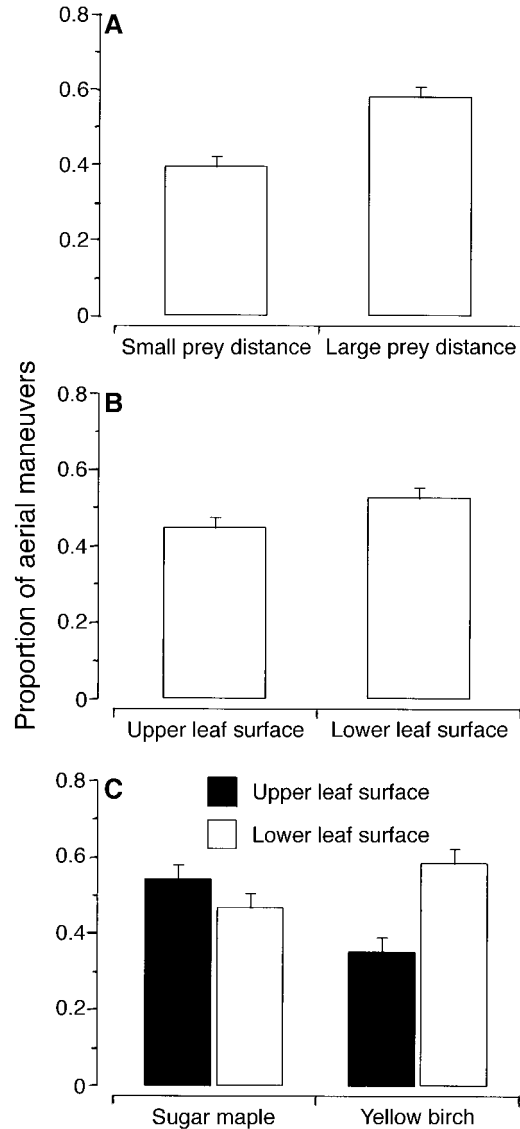


FIG. 5. Use of aerial prey capture maneuvers as a function of distance to prey and natural foliage structure of sugar maple and yellow birch. (A) Mean proportion ( $\pm 1$  SE) of prey captured using aerial maneuvers at small ( $n = 72$  foraging bouts) and large ( $n = 72$  foraging bouts) prey distances, combining results for Black-throated Green Warblers, Black-throated Blue Warblers, and American Redstarts foraging on both tree species. (B) Mean proportion ( $\pm 1$  SE) of prey captured using aerial maneuvers from upper ( $n = 72$  foraging bouts) and lower ( $n = 72$  foraging bouts) leaf surfaces, combining results for Black-throated Green Warblers, Black-throated Blue Warblers, and American Redstarts foraging on both tree species. (C) Mean proportion ( $\pm 1$  SE) of prey captured using aerial maneuvers from upper and lower leaf surfaces ( $n = 36$  foraging bouts for each leaf surface  $\times$  tree species combination), combining results for Black-throated Green Warblers, Black-throated Blue Warblers, and American Redstarts.

capture maneuvers on the artificial foliage structures, either among individuals within bird species or among bird species. There were, however, large differences in the proportional use of maneuvers, depending upon ar-



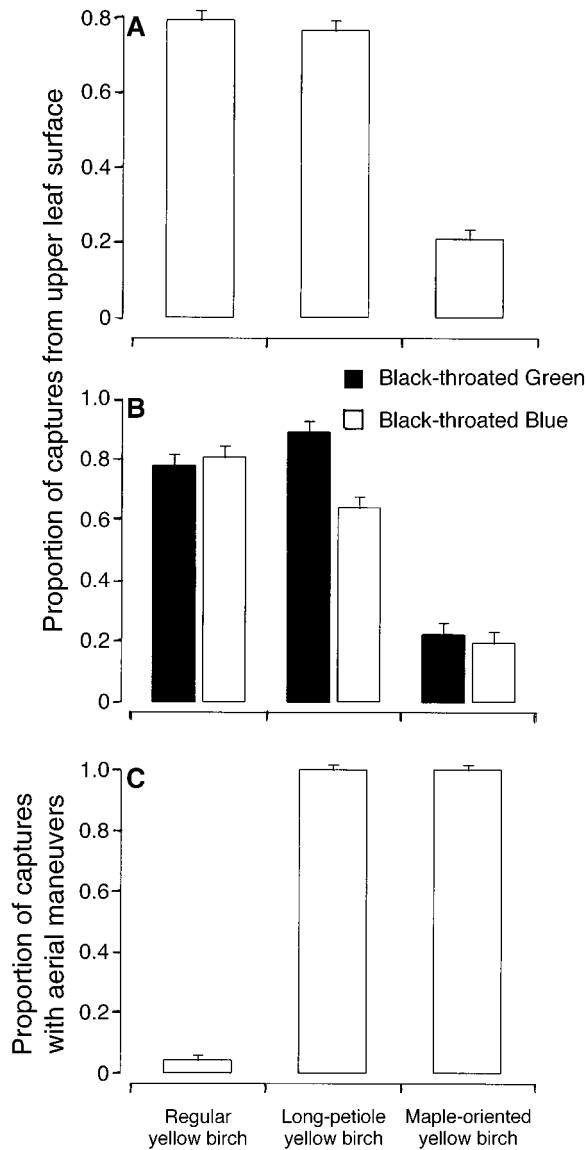


FIG. 6. Effects of leaf dispersion and distance to prey on prey capture location and prey capture maneuver, based on structural manipulation of artificial foliage. (A) Mean proportion (+ 1 SE) of prey captured from upper leaf surfaces on artificial foliage structures, combining results for Black-throated Green and Black-throated Blue warblers ( $n = 6$  foraging bouts on each foliage structure type). (B) Mean proportion (+ 1 SE) of prey captures from upper leaf surfaces by Black-throated Green and Black-throated Blue warblers, contingent upon foliage structure type ( $n = 3$  foraging bouts for each bird species  $\times$  foliage structure combination). (C) Mean proportion (+ 1 SE) of prey captured using aerial maneuvers, combining results for Black-throated Green and Black-throated Blue warblers ( $n = 6$  prey captures on each foliage structure type).

tificial foliage structure ( $F_{2,8} = 288.98$ ,  $P < 0.01$ ). On regular yellow birch, almost no prey were captured with aerial maneuvers, whereas on long-petioled yellow birch and maple-oriented yellow birch, all prey were captured with aerial maneuvers (Fig. 6C).

*Effect of distance between branches.*—Black-throated Green Warblers captured a significantly smaller proportion of prey from the undersides of leaves on the upper branch than did Black-throated Blue Warblers ( $F_{1,7} = 5.64$ ,  $P = 0.05$ ; Fig. 7A). Also, there were significant differences in the proportion of prey taken from the undersides of leaves from the upper branch, depending upon distance between branches ( $F_{4,28} = 4.54$ ,  $P = 0.06$ ; Fig. 7B). As branch distance increased, greater proportions of prey were captured from the upper leaf surfaces of the lower branch.

There was no interaction of bird species with branch distance, indicating that both Black-throated Green and Black-throated Blue warblers, despite overall differences in capture location, responded to increasing distance between branches in generally similar ways. Specifically, they decreased the proportion of prey captured from the lower surfaces of leaves on the upper branch.

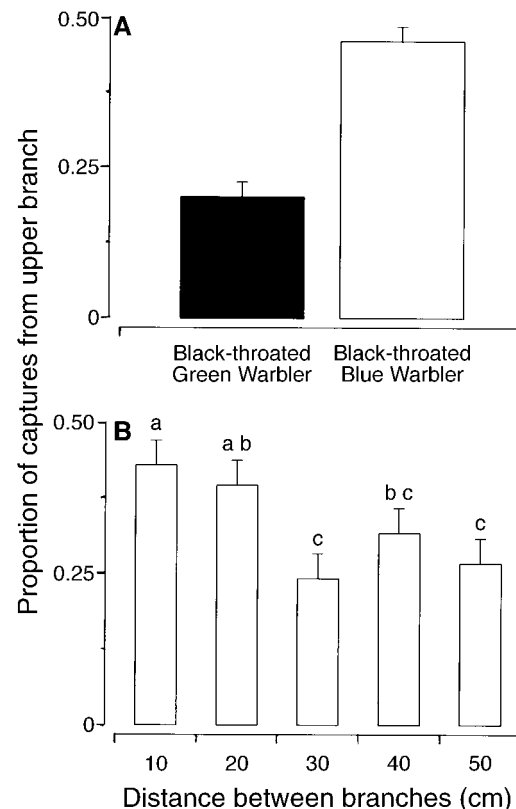


FIG. 7. Effect of vertical distance between branches on prey capture location. (A) Mean proportion (+ 1 SE) of prey captures on lower surfaces of leaves on the upper branch by Black-throated Green Warblers ( $n = 20$  foraging bouts: four individuals  $\times$  five branch distances) and Black-throated Blue Warblers ( $n = 25$  foraging bouts). (B) Mean proportion (+ 1 SE) of prey captures from lower surfaces of leaves on the upper branch, depending upon distance between branches, combining results for Black-throated Green and Black-throated Blue warblers ( $n = 9$  foraging bouts at each branch distance). Different lowercase letters above bars indicate significant differences (based on Fisher's LSD pairwise comparison).

## DISCUSSION

When foraging among natural foliage of sugar maple and yellow birch, Black-throated Blue Warblers and American Redstarts both captured prey predominantly from the lower surfaces of the raised leaves of sugar maple, but from the upper leaf surfaces of the planar leaves of yellow birch. In contrast, Black-throated Green Warblers took prey predominantly from the upper leaf surfaces of both tree species. Because all species exhibited similar physical capabilities in the perch experiments, difference in the leaf surface attacked may represent species-specific behavioral predilections. Overall, prey were captured more from lower leaf surfaces of sugar maple, but from upper leaf surfaces of yellow birch. In addition, increasing distance to prey increased the proportion of prey captured from upper leaf surfaces on sugar maple, but decreased the proportion of prey captured from upper leaf surfaces on yellow birch.

Prey capture maneuvers also differed depending upon tree species. On yellow birch, non-aerial maneuvers were used predominantly by each bird species when capturing prey from upper leaf surfaces, whereas aerial maneuvers were used predominantly by each bird species when capturing prey from lower leaf surfaces. The opposite was true for sugar maple. Overall, aerial maneuvers were used to a greater extent when prey were captured from lower leaf surfaces than from upper leaf surfaces. Not surprisingly, capture maneuver was also affected by prey distance, with frequency of aerial maneuvers increasing with increasing prey distance. In contrast to prey capture location, there were no differences among bird species in capture maneuver contingent upon tree species. Those results demonstrate that differences in foliage structure between tree species require different attack maneuvers, or perhaps constrain the maneuvers used most efficiently when attacking insect prey. For instance, on sugar maple, the large distance between branch and leaves, together with their elevated arrangement, necessitate use of aerial maneuvers, particularly to attack prey residing on upper leaf surfaces. In contrast, on yellow birch, the planar leaf arrangement necessitates use of aerial maneuvers to attack prey residing on lower leaf surfaces, but the smaller distance between branch and leaves allows birds to glean prey from upper leaf surfaces.

Together, my results suggest that leaf dispersion primarily determines prey capture location, whereas prey distance primarily determines prey capture maneuver, as is clearly demonstrated by experimental manipulations of artificial foliage. Prey were captured predominantly from upper leaf surfaces on regular and long-petioled yellow birch, despite large differences in prey distance. In contrast, prey were captured predominantly from lower leaf surfaces on maple-oriented yellow birch, even though prey distance on that foliage structure was similar to that of long-petioled yellow birch.

Moreover, capture maneuvers were identical when birds foraged on long-petioled yellow birch and maple-oriented yellow birch (only aerial maneuvers were used), despite different leaf dispersions, but differed drastically from those used on regular yellow birch (non-aerial maneuvers were more frequent).

Although not directly examined here, these results suggest that birds may generally choose to forage in ways that minimize (or at least decrease) the need for more energetically costly aerial maneuvers in contrast to non-aerial maneuvers (see also Whelan 1989b). For example, with the exception of Black-throated Green Warblers, proportionally more prey were captured from upper leaf surfaces of yellow birch, but lower leaf surfaces of sugar maple, both of which can be accomplished with fewer aerial maneuvers. This, in turn, suggests that foraging site selection in the wild, at least for some bird species, may often favor tree species (or parts of trees) that minimize the need for aerial foraging maneuvers. This could be one possible mechanism by which preferences for foraging in particular tree species arise (Holmes and Robinson 1981). As noted by Marquis and Whelan (1994, 1996), bird consumption of leaf-damaging insects affects host tree fitness; hence, such foraging-site preferences could potentially contribute to forest tree composition and the evolution of tree architecture.

Results of these experiments support suggestions of Holmes and Robinson (1981) that leaf morphology and arrangement affect the foraging behavior of birds that glean their prey from nearby substrates, and that the ability (or propensity) to use aerial foraging maneuvers, such as hovering or sallying (Remsen and Robinson 1990), reduces constraints imposed by foliage structure. In subsequent studies, Robinson and Holmes (1984) found that Red-eyed Vireos (*Vireo olivaceus*) and American Redstarts often changed behavior among vegetative strata, but not among tree species. Philadelphia Vireos (*V. philadelphicus*) had variable attack rates among different tree species, and Black-throated Blue Warblers showed few changes in behavior, regardless of strata or tree species. In field studies by Robinson and Holmes (1984), prey abundance, distribution, and type could not be controlled. Hence, birds observed by Robinson and Holmes (1984) were probably detecting and attacking a wide array of insect taxa (Robinson and Holmes 1982, Holmes and Schultz 1988), each of which may have had distinct crypsis patterns or escape behaviors, and each of which may require specific pre-consumption handling to be successfully subdued (which may have affected the likelihood of attack). In contrast, in my experiments, birds were detecting and capturing pieces of mealworm, which obviously are not cryptic, have no evasive behaviors, and are easily handled. The strong effect of foliage structure revealed in the present study was clearly evident when prey effects were controlled. Foraging behavior of birds in natural habitats will also be influenced by other factors, such as prey type, abundance,

distribution, and antipredator behaviors (Holmes and Schultz 1988); separating out relative effects of each in the field is often difficult. Consequently, it may be hard to detect unambiguous effects of foliage structure in purely observational studies, because other factors cannot be controlled.

Parrish (1995a) demonstrated that fine-scale differences in needle architecture between red and white spruce affected microhabitat and foraging-site selection in Black-throated Green Warblers. He suggested that the strong effect of foliage structure detected in his experiments, in contrast to the lack of strong effects found by Robinson and Holmes (1984), probably reflected differences in the extent to which conifer and deciduous foliage constrain bird foraging. However, Parrish (1995a) also used mealworm pieces for prey in his experiments, which suggests again that differences between aviary and field studies may be influenced by differences in prey, as well as by differences in foliage.

Greenberg and Gradwohl (1980) suggested that greater agility is required to capture prey residing on lower leaf surfaces than on upper leaf surfaces. My results indicate that this may depend upon the architecture of particular tree species. On tree species in which leaves are held horizontal to the plane of the branch, aerial maneuvers are required to attack prey on lower leaf surfaces. On tree species with elevated foliage, however, foliage architecture facilitates access to lower leaf surfaces. Relative leaf surface access will also be influenced by other tree characteristics, such as mean distance between branches. Some bird species may gain access to prey on lower leaf surfaces from branches beneath that supporting the leaves (S. K. Robinson, *personal communication*; C. J. Whelan, *unpublished data*). Frequency with which the undersides of leaves will be attacked from lower, surrounding branches may decrease as the distance between branches increases, and apparently depends upon physical and perceptual abilities of each bird species (Fig. 7).

Moreover, Black-throated Green Warblers, unlike Black-throated Blue Warblers and American Redstarts, captured prey predominantly from upper leaf surfaces of both tree species. That behavior is consistent with both their use of those substrates, as documented in earlier field studies (Holmes and Schultz 1988), and with the suggestion that their foraging behavior is more stereotypical than that of other warbler species (Morse 1971, Whelan 1989b, Parrish 1995a, b). This species is more typically associated with conifer foliage throughout its breeding range (e.g., Collins 1983, Sherry and Holmes 1985, but see Parrish 1995b) than are the other two bird species (Sherry and Holmes 1985), and Holmes and Robinson (1981) suggested that conifer foliage may facilitate the use of non-aerial foraging maneuvers. Morse (1976) noted that red spruce, the preferred foraging substrate of Black-throated Green Warblers in coastal Maine, has vertically narrow foliage, which may make prey easily available to a

perched bird, regardless of branch (foliage) surface. Conifer branches also often form relatively large planar mats (*personal observation*) that may facilitate both radial and tangential movements across them. Although Parrish (1995b) showed geographic variation in intrinsic preferences for coniferous vs. deciduous foliage in Black-throated Green Warblers, their widespread association with conifers (e.g., Collins 1983) may help predispose them to prefer foraging for arthropods residing primarily on upper leaf surfaces. Consequently, that may lead Black-throated Green Warblers to select habitat composed of deciduous tree species on which these leaf surfaces are more readily accessible (Holmes and Robinson 1981, Whelan 1989b).

If the effect of tree architecture on bird foraging commonly influences habitat selection in this way, then that relationship may be an important determinant of bird community composition. This recalls the classic case of MacArthur's (1958) warblers, in which differential use of spruce trees for foraging was suggested to be a predominant mechanism of coexistence among five parulid warbler species (including the Black-throated Green Warbler). As shown here in highly controlled experiments, even closely related bird species respond uniquely to natural and artificial foliage (see also Whelan 1989a, b), resulting in unique patterns of resource exploitation or microhabitat specialization (MacArthur 1958), one of four mechanisms of coexistence discussed by Brown (1989a) for desert rodent communities.

Finally, my findings have implications for forest management practices. For instance, Temple et al. (1979) and Holmes and Robinson (1981) suggested that maintenance of tree species diversity, at least in the northern hardwoods biome, promotes high bird species diversity because high tree species diversity enhances foraging opportunities for bird species. My study demonstrates that differences in foliage architecture influence where and how birds capture prey (Parrish 1995a, Gunnarsson 1996), indicating that forests with high tree species diversity present birds with diverse macro- and microenvironments for foraging. Coupled with a dynamic arthropod resource base (e.g., Holmes et al. 1986), profitability of different tree species for foraging may also fluctuate over time (Whelan 1989b, Parrish 1995b). Thus, a forest with high tree species diversity may, at any given time, provide birds with diverse combinations of foliage structure and prey availability, as well as other requisite resources, such as diverse nesting opportunities (Martin 1992, Steele 1993).

#### ACKNOWLEDGMENTS

This work was conducted while I was at Dartmouth College, in partial fulfillment of the Ph.D. degree. I am most grateful to Richard T. Holmes for his advice and enthusiastic encouragement, for fostering the stimulating intellectual environment present throughout all phases of this study, and for his continuing support and advice during work on the present revision. I received much useful and critical advice

from many individuals, especially Timothy Moermond, Ian Baldwin, Joel Brown, Carol Folt, Megan Haney, Richard Hutto, Robert Marquis, Thomas Martin, Brenda Molano-Flores, Kevin Omland, David Peart, Leonard Reitsma, Scott Robinson, Nicholas Rodenhouse, Jack Schultz, Thomas Sherry, Benjamin Steele, Dan Wenny, and two anonymous reviewers. The study was funded, in part, by grants from the Frank Chapman Memorial Fund of the American Museum of Natural History and the Sigma Xi Scientific Society, and a Cramer Fellowship from Dartmouth College.

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