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FORAGING OF FIVE BIRD SPECIES IN TWO FORESTS WITH DIFFERENT VEGETATION STRUCTURE

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Specific foraging patterns of many bird species have been well studied; however, few studies have dealt with the influence of changes in habitat structure on foraging. This study examines the influence of vegetation structure on the foraging behavior of Acadian Flycatchers (*Empidonax virescens*), Red-eyed Vireos (*Vireo olivaceus*), Black-throated Green Warblers (*Dendroica virens*), American Redstarts (*Setophaga ruticilla*) and Scarlet Tanagers (*Piranga olivacea*). The foraging behavior of each of these species was observed in two habitats that had different vegetation structures. This made it possible to relate differences in foraging by the bird species to changes in habitat structure.

STUDY AREAS AND METHODS

Study areas.—Foraging data were gathered in two stands in the Fernow Experimental Forest (avg. elev. 760 m) located 4.8 km southeast of Parsons, Tucker Co., West Virginia. Major tree species in the Fernow Forest were red oak (*Quercus rubra*), chestnut oak (*Q. prinus*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black cherry (*Prunus serotina*), American beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*) and sweet birch (*Betula lenta*). The relative abundances of these trees, however, varied between stands.

The Fernow Forest is in a region that is warm in summer. Maximum daily temperature was 30°C in 1977 and 29.4°C in 1978. Temperatures at night ranged from near 0°C in May to 16.1°C during July for both years. Weekly precipitation reached a maximum both years of >9 cm in the month of July. Precipitation dropped below 0.25 cm/week only one week during the 1977 season, and never dropped below 1 cm/week in 1978.

The two stands were located on watersheds that have been used for hydrological research by the Forest Service. One stand, the "young forest," (30 ha) was clearcut in 1958 and has since been left to regrow. In 1971 this area was fertilized using 257 kg/ha urea. The stand grows on very steep terrain, with about 75% of the slopes 21.8° or greater (Reinhart et al. 1963). The second stand, the "mature forest," (38.9 ha) was logged early in the 1900's, and has since been left to regrow. None of the slopes in this stand were steeper than 21.8°.

Avifauna.—The bird communities inhabiting the two stands represent an important context within which the species studied should be viewed. The species found in these communities included several species typical of northern coniferous forests, e.g., Blackburnian Warblers (*Dendroica fusca*), as well as species typical of deciduous forest habitats, e.g., Hooded Warblers (*Wilsonia citrina*). The young forest had fewer species of flycatchers, and had several species typical of early stages of forest succession, e.g., Chestnut-sided Warblers (*D. pensylvanica*) and Canada Warblers (*D. canadensis*). Cerulean (*D. cerulea*) and Blackburnian warblers occurred only in mature forest. Further information on the avian communities in these stands is given by McArthur (1980) and Maurer (1980).

Methods.—Both study areas were sampled in July 1978 for vegetation structure and composition. Fifty 0.04-ha circular plots were located randomly in each area. Vertical structural diversity was measured using frequency counts of vegetation in each of eight canopy layers

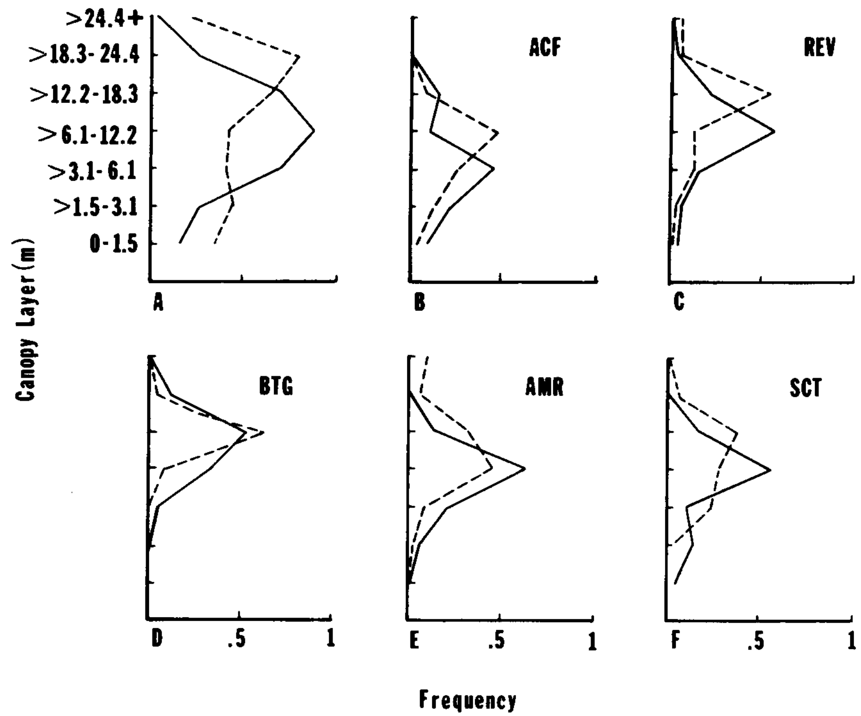

FIG. 1. Foliage height profile (A) and foraging height distribution (B–F) for five canopy-feeding birds in a mature forest (broken lines) and a young forest (solid lines). ACF = Acadian Flycatcher, REV = Red-eyed Vireo, BTG = Black-throated Green Warbler, AMR = American Redstart, SCT = Scarlet Tanager.

(low vegetation; shrubs: 0–1 m, 1.5–3.05; trees: 3.05–6.1, 6.1–12.2, 12.2–18.3, 18.3–24.4, >24.4) at 20 points within each plot and calculating a diversity index, $-\Sigma p_i \ln p_i$ (Pielou 1976), for each plot. Differences in plot diversities between areas were tested using a 2-sided Mann-Whitney test (Conover 1971). A profile of the canopy was obtained for each stand by using the frequency counts of vegetation in each of seven (excluding low vegetation) canopy layers (Fig. 1A). These profiles represent the probability of encountering a given canopy layer at any point in a study area. Probabilities were estimated from the samples taken in each area. Maximum canopy height was determined for each plot, and differences in canopy height between stands were tested using a 2-sided Mann-Whitney test. Relative densities (RD) were calculated for several tree species groups (Table 1) as follows: RD = $\Sigma A_i/\Sigma M_i$, where A_i = number of individuals of species group A in plot i and M_i = total number of trees in plot i.

Foraging behavior of five canopy feeding bird species were recorded from 8 May–27 July 1978 and 7 May–22 June 1979. Observations were classified into categories for each of four foraging variables. The variables (categories are in parentheses) were (1) foraging maneuver (hover, glean, flycatch), (2) foraging substrate (leaf, branch, trunk, air), (3) location in tree (proximal to the trunk, distal to the trunk, air), and (4) tree species used (*Quercus* spp., *Acer* spp., *Betula* spp., *Fagus* spp., other species, shrubs and saplings). Niche metrics (niche

TABLE 1
VERTICAL DIVERSITY, MEAN CANOPY HEIGHT, RELATIVE DENSITIES AND TREE SPECIES DIVERSITY OF TWO STANDS IN THE FERNOW EXPERIMENTAL FOREST BASED ON 50 RANDOM PLOTS LOCATED IN EACH STAND

	Young forest	Mature forest
Mean vertical diversity	1.70	1.89
Mean canopy height (m)	20.31	24.53
Relative density (RD)		
Oaks	0.03	0.15
Maples	0.22	0.39
Beeches	0.06	0.12
Birches	0.07	0.07
Other (total)	0.62	0.26
Hickories	0.02	0.01
Cherries	0.02	0.06
Magnolias	0.16	0.16
Miscellaneous*	0.42	0.03
Tree species diversity	1.08	1.44

* White ash (*Fraxinus americana*), basswood (*Tilia* spp.), eastern hemlock (*Tsuga canadensis*), big-tooth aspen (*Populus grandidentata*), elms (*Ulmus*), service berry (*Amelanchier*), witch hazel (*Hamamelis virginia*), black locust (*Robinia pseudoacacia*).

breadth, niche overlap) were calculated following Colwell and Futuyma (1971) for two niche dimensions: (1) foraging behavior and (2) tree use. The following nine independent foraging states were used to categorize the foraging data and calculate niche metrics related to foraging behavior: (1) hovering at foliage proximal to the trunk of a tree or shrub, (2) hovering at foliage distal to the trunk, (3) hovering at woody structures (branches, bark, etc.) proximal to the trunk, (4) hovering at woody structures distal to the trunk, (5) flycatching, (6) gleaning foliage proximal to the trunk, (7) gleaning foliage distal to the trunk, (8) gleaning woody structures proximal to the trunk, and (9) gleaning woody structures distal to the trunk. Niche metrics of the tree-use dimension were calculated using 13 independent resource states. These states were created using six tree species groups (*Quercus*, *Fagus*, *Acer*, *Betula*, other trees, shrubs) and dividing each of these groups into three groups based on the height of the foraging maneuver (0–3 m, 3–9 m, >9 m). Since the five species did not use some trees at certain heights, 13 instead of 18 resource states were used. Changes in niche widths between areas were tested using Hutcheson's (1970) method of testing for differences in diversity.

Heights of foraging acts were recorded for each species. From these data foraging heights were tested for significant differences between stands using a 1-sided Mann-Whitney test (Conover 1971). Foraging height profiles for each species were constructed for both forests. These profiles are analogous to the foliage height profiles described above and represent the estimated probabilities that any one foraging act by a given species in a given forest will be in a specific canopy layer.

Contingency tables were constructed (forest stand × foraging variable: maneuvers, substrates, locations, tree use) to test for differences in probabilities of each category between the two stands. Since multiple observations were obtained from some of the individuals of each species, the data might not represent a true random sample. This can cause the Chi-square tests to produce liberal significance levels (E. J. Harner, pers. comm.). Thus, for the Chi-square tests, the significance level $P < 0.01$ was used. Tests for preferential use of tree species were performed using a Chi-square goodness of fit test. A hypothetical probability distribution was estimated from the relative densities for each tree species group (Table 1) in each stand. Using a Chi-square goodness of fit test (Conover 1971), the hypothesis that the probability distribution generated from relative densities of the tree species groups was the same as the probability distribution of foraging acts among the tree groups was tested for each bird species in each stand. For a given stand, a significant Chi-square value indicated that a bird species was deviating from a pattern of using tree species based on their abundance by selecting certain tree types over others. If a cell in any contingency table had an expected value <1, categories were lumped together to raise the value, thus reducing the degrees of freedom. When a cell in a contingency table has an expected value of <1, the significance level may be poorly approximated (Conover 1971).

HABITAT STRUCTURE

Canopy structure was more diverse (Mann-Whitney $U = 195$, $P < 0.001$) in the mature forest than the young forest (Table 1). This means that, on the average, a point in the mature forest had more canopy layers than a point in the young forest. The trend of greater complexity in the mature forest was reflected in the vertical profile of that forest (Fig. 1A). The mature forest also had a higher (Mann-Whitney $U = 358$, $P < 0.001$) mean canopy height (Table 1) than the young forest. The frequencies of each canopy layer were significantly different in each stand ($\chi^2 = 867.3$, df = 6, $P < 0.001$). In the mature forest, the most abundant canopy layer was at 18.3–24.4 m (Fig. 1A). Layers below the 18.3–24.4 m layer were well represented in that forest. In the young forest, there was a high incidence of three layers (3.1–6.1 m, 6.1–12.2 m, 12.2–18.3 m), but the rest of the layers were poorly represented.

FORAGING BEHAVIOR

Acadian Flycatcher.—Acadian Flycatchers used essentially the same foraging maneuvers in both forests ($\chi^2 = 0.09$, df = 1, NS). Hovering at various substrates was used most often, while gleaning was rarely used (Table 2). The use of locations (proximity to trunk) ($\chi^2 = 7.28$, df = 2, $P = 0.027$), and the use of substrates ($\chi^2 = 13.20$, df = 3, $P = 0.005$) were different. Woody structures (e.g., branches) were used as foraging sites in the young forest but not in the mature forest.

Acadian Flycatchers also showed significantly different patterns of tree use in both forests ($\chi^2 = 20.90$, df = 5, $P = 0.001$). Shrubs and trees other than maples, beeches, birches and oaks were used more often in the young forest than in the mature forest (Table 3). Acadian Flycatchers did not use tree types based on their abundance in the young forest ($\chi^2 = 36.77$, df = 4, $P < 0.001$) or the mature forest ($\chi^2 = 23.51$, df = 4, $P < 0.001$). In both habitats, beeches were used more often than expected by chance

TABLE 2

RELATIVE FREQUENCIES OF FORAGING VARIABLES FOR FIVE SPECIES OF INSECTIVOROUS BIRDS

Species	No. of observations	Maneuver			Location[a]		Substrate[a]		
		Hover	Glean	Hawk	Prox[b]	Dist	Leaf	Branch	Trunk
E. virescens									
Young forest	72	59.7	1.4	38.9	19.4	40.3	40.3	5.6	15.3
Mature forest	53	58.5	0.0	41.5	3.8	54.7	58.5	0.0	0.0
V. olivaceus									
Young forest	59	52.5	47.5	0.0	8.5	91.5	81.4	15.4	3.4
Mature forest	48	52.1	47.9	0.0	6.3	93.8	91.7	4.2	4.2
D. virens									
Young forest	31	45.2	38.7	16.1	0.0	83.9	61.3	22.5	0.0
Mature forest	30	43.3	30.0	26.7	23.3	50.0	43.3	23.3	6.7
S. ruticilla									
Young forest	71	54.9	7.0	38.0	11.3	50.7	52.1	7.0	4.2
Mature forest	47	34.0	10.6	55.3	6.4	38.3	23.4	19.1	2.1
P. olivacea									
Young forest	35	74.3	25.7	0.0	17.1	82.9	74.3	11.4	14.3
Mature forest	31	67.7	32.3	0.0	12.9	87.1	83.9	16.1	0.0

[a] Air same frequency as hawk (=flycatch).

[b] Prox = proximal to trunk, Dist = distal to trunk.

(cell χ^2 for beeches made up 84% of the χ^2 value for young forest, 64% for mature forest). Smith (1977) found that Acadian Flycatchers tend to use mesic sites, and since beeches are often associated with mesic sites (Fowells 1965, Brockman 1968) the association between beeches and this flycatcher is not unexpected.

Probabilities of using each canopy layer were different ($\chi^2 = 21.26$, df = 4, $P < 0.001$) in each study area (Fig. 1B). In both forests, Acadian Flycatchers concentrated their foraging efforts below the densest part of the canopy (Fig. 1A), as Williamson (1971) also noted. Foraging heights were lowest in the young forest (Table 3).

Acadian Flycatchers had a significantly wider foraging behavior niche in the young forest ($t = 4.77$, df = 124, $P < 0.005$) than in the mature forest. However, tree use was significantly more diverse in the mature forest ($t = 2.35$, df = 125, $P < 0.025$). The wider foraging niche was apparently due to increased use of different substrates (Table 2). In the young forest, Acadian Flycatchers had higher average overlaps with other species in foraging behaviors (Table 4), a pattern observed for other

TABLE 3

RELATIVE FREQUENCIES OF TREE SPECIES USE AND FORAGING HEIGHTS OF FIVE SPECIES OF FOREST BIRDS

	Tree use						Mean foraging height	
Species	Maple	Oak	Birch	Beech	Other	Shrub	(m)	P*
E. virescens								
Young forest	18.1	0.0	2.8	16.7	26.4	36.1	5.18	<0.01
Mature forest	26.4	9.4	11.3	26.4	7.5	18.9	8.09	
V. olivaceus								
Young forest	39.0	11.9	8.5	15.3	16.9	8.5	9.96	0.09
Mature forest	22.9	16.7	12.5	12.5	20.8	14.6	13.31	
D. virens								
Young forest	12.9	12.9	32.3	16.1	22.5	3.2	13.83	<0.01
Mature forest	13.3	20.0	23.3	23.3	20.0	0.0	18.72	
S. ruticilla								
Young forest	40.8	0.0	11.3	22.5	21.1	4.2	9.53	0.10
Mature forest	51.1	19.1	8.5	12.8	4.3	4.3	11.43	
P. olivacea								
Young forest	31.4	34.3	2.9	0.0	17.1	14.3	9.23	>0.10
Mature forest	38.7	6.5	0.0	32.3	12.9	9.7	11.87	

* Significance level from 1-sided Mann-Whitney test (Conover 1971) for differences in foraging heights between the two stands.

species. However, patterns of overlap with individual species varied (Maurer 1980). There was less average overlap between Acadian Flycatchers and other species in tree use in the young forest (Table 4).

Red-eyed Vireo.—Red-eyed Vireos did not show any significant differences in foraging or tree use between the two forests (critical levels for all tests were >0.05). Frequencies of foraging maneuvers, foraging locations and substrates used were very similar, although there was a slightly greater use of branches in the young forest (Table 2). The data indicate that these birds foraged mainly on foliage at the outer perimeter of a tree, hovering and gleaning about equally, as reported previously by James (1976) for southern Ontario and Williamson (1971) for Maryland.

Red-eyed Vireos did not change tree use between areas, but foraged slightly higher in the mature forest (Table 3). Probabilities of foraging in each canopy layer were different between stands ($\chi^2 = 29.33$, df = 6, $P < 0.001$). In the mature forest, the 12.2–18.3 m canopy layer was used most often, whereas the 6.1–12.2 m layer was used most often in the young

TABLE 4
NICHE DIMENSIONS OF FIVE CANOPY-FEEDING BIRDS IN TWO STRUCTURALLY DIFFERENT FORESTS

	Niche width (bits)				Average overlap (%)			
	Foraging		Tree use		Foraging		Tree use	
Species	Y[a]	M	Y	M	Y	M	Y	M
E. virescens	1.33	0.82	1.85	2.13	0.60	0.55	0.38	0.55
V. olivaceus	1.39	1.09	2.07	1.91	0.61	0.47	0.57	0.64
D. virens	1.47	2.01	1.63	1.59	0.64	0.51	0.44	0.53
S. ruticilla	1.30	1.30	1.85	1.66	0.64	0.47	0.50	0.60
P. olivacea	1.26	1.21	1.85	1.74	0.61	0.52	0.43	0.54
$\bar{x}$ =	1.35	1.28	1.85	1.81	0.62	0.50	0.46	0.57
Significance[b]	NS		NS		$P < 0.025$		$P < 0.01$	

[a] Y = young forest, M = mature forest.
[b] Niche widths tested using d-test of Crow et al. (1978); overlaps tested using paired *t*-tests, df = 9.

forest (Fig. 1C). Lower foraging heights in the young forest were related to lower canopy height of that forest (Table 1, Fig. 1A).

Red-eyed Vireos in the young forest had wider niche widths for foraging behaviors (Table 4), although this difference was not statistically significant ($t = 1.89$, df = 3634, NS). The slightly wider niche in the young forest is due to the slight increase in use of branches in that forest (Table 2). Red-eyed Vireos also had a slightly wider tree-use niche in the young forest (Table 4), although again the difference was not statistically significant ($t = 1.50$, df = 102, NS). This suggests relative similarity in tree use between the two forests. In the young forest, tree use was not based on abundance ($\chi^2 = 53.38$, df = 4, $P < 0.001$), but was in the mature forest ($\chi^2 = 5.81$, df = 4, NS). In the young forest, a preference for mature forest types was shown. Niche overlaps of Red-eyed Vireos with other species for foraging were generally higher in the young forest, with the exception of Acadian Flycatchers. For tree use, niche overlaps were generally higher in the mature forest, except for overlap with American Redstarts, where tree-use overlap was higher in the young forest (Maurer 1980).

In summary, Red-eyed Vireos showed little reaction to foliage changes in their foraging behavior, except for foraging higher in the stand with a higher canopy. A slight broadening of their niche may occur in young forest, and relationships (overlaps) with other species change. Changes in relationships with other species were due to foraging shifts by other species rather than foraging changes by Red-eyed Vireos.

Black-throated Green Warbler.—Black-throated Green Warblers showed few changes in foraging between areas, except that they foraged in different locations ($\chi^2 = 7.94$, df = 1, $P = 0.005$). In the mature forest, warblers used the inner parts of branches and trunks, while neither of these locations were used in the young forest (Table 2). Such limited changes in foraging behavior were noticed in other studies conducted in spruce forests (MacArthur 1958; Morse 1968, 1971; Rabenold 1978). Foraging heights were higher in the mature forest than in the young forest (Table 3), although probabilities of foraging in each canopy layer were not different ($\chi^2 = 9.77$, df = 4, $P = 0.046$). In the young forest, Black-throated Green Warblers used a greater variety of foraging heights.

Black-throated Green Warblers had a wider foraging niche in the mature forest than in the young forest (Table 4; $t = 3.78$, df = 58, $P \leqslant 0.001$). Tree-use niches were of similar width in both forests (Table 4, $t = 0.53$, df = 39, $P > 0.1$). As opposed to foraging behaviors, tree use by Black-throated Green Warblers was narrower than other species.

As with other species, foraging overlaps were highest for Black-throated Green Warblers in the young forest, while tree-use dimension overlaps were lowest for all species in that forest (Table 4). Contrary to the pattern, foraging overlaps were higher with American Redstarts in the mature forest (Maurer 1980) because both species did more flycatching in the mature forest (Table 2).

American Redstart.—American Redstarts changed maneuvers ($\chi^2 = 9.47$, df = 2, $P = 0.009$) in the two forests; however, no differences in foraging locations were detected ($\chi^2 = 3.56$, df = 2, $P = 0.24$). The redstart was the only species that changed its foraging maneuvers between forests. Ficken (1962) noted that this species was very versatile in its use of foraging behaviors. The change in maneuvers was probably due to the greater amount of flycatching done in the mature forest, coupled with less hovering. In the young forest, there was a concentration of foraging (mainly hovering) on leaves (Table 2).

Redstarts used different tree species in each forest ($\chi^2 = 16.67$, df = 4, $P = 0.003$). Foraging was concentrated on maples and oaks in the mature forest, while oaks were not used at all in the young forest (Table 3). Use of tree types was independent of their abundance in the young forest ($\chi^2 = 69.74$, df = 4, $P < 0.001$) and the mature forest ($\chi^2 = 11.46$, df = 4, $P = 0.023$). Generally, maples were used more often than expected by chance.

Redstarts foraged significantly higher in the mature forest (Table 3). The distribution of foraging acts (Fig. 1E) among canopy layers was different in each forest ($\chi^2 = 19.11$, df = 5, $P < 0.005$). In the young forest, redstarts foraged heavily in the 6.1–12.2 m canopy layer, the densest layer in that forest. In contrast, redstarts in the mature forest spent more time foraging in higher canopy layers, less time in lower layers and foraging in the 6.1–12.2 m canopy layer was less pronounced.

Widths of foraging niches were not statistically different (t = 0.15, df = 104, NS) between stands (Table 4). Tree-use niches were not significantly different (t = 1.64, df = 103, $P > 0.1$), indicating that the same pattern observed for foraging was present in tree use. That is, redstarts were highly opportunistic in their use of maneuvers and tree species, though this was not reflected in niche breadths. Foraging overlaps were greater in the young forest for redstarts and tree-use overlaps were lower in that forest (Table 4).

Scarlet Tanager.—This species did not show any differences in foraging behavior between stands (critical levels for maneuvers, substrates and locations all >0.01). Hovering at leaves was the foraging technique used most often (Table 2), more so than for any other species. Although no foraging changes occurred, Scarlet Tanagers did show differences in tree use between forests (χ^2 = 26.48, df = 3, $P < 0.001$). Oaks were used more often in the young forest, while beeches were used more often in the mature forest (Table 3).

Scarlet Tanagers foraged at the same heights in both forests (Table 3). No difference in the distribution of foraging acts among canopy layers (Fig. 1F) was detected (χ^2 = 9.47, df = 45, NS).

Niche widths were not different between forests for foraging (t = 0.29, df = 66, NS) and tree use (t = 1.07, df = 45, NS). Scarlet Tanagers showed the same patterns for overlaps that other species did (Table 4). Contrary to the pattern, there was higher tree-use overlap with Black-throated Green Warblers in the young forest (Maurer 1980).

The changes these five bird species demonstrated are summarized in Table 5.

DISCUSSION

Differences in habitat structure between the two stands affected some of the species more than others (Table 5). The amount of foraging changes demonstrated by a species was related to the amount of flycatching that a species did. The two species which did not flycatch, Red-eyed Vireos and Scarlet Tanagers, showed few changes in their foraging patterns between areas. Acadian Flycatchers and American Redstarts, which had the highest frequencies of flycatching, showed the most changes in foraging (Table 5), while Black-throated Green Warblers were intermediate in both amount of flycatching and number of foraging changes. These data suggest that flycatching species tend to be more opportunistic when presented with different foraging opportunities than non-flycatching species.

TABLE 5
CHANGES IN FORAGING STRATEGIES OF FIVE SPECIES OF INSECTIVOROUS BIRDS[a]

	Foraging behavior				
Species	Manuevers	Locations and substrates	Tree use	Foraging heights	Niche width
E. virescens	no changes	decreased use of woody substrates, increase in use of peripheral foliage	increased use of oaks, maples, beeches, decreased use of shrubs	higher	narrower foraging, wider tree use
V. olivaceus	no changes	no changes	no changes	slightly higher	no changes
D. virens	no changes	decreased use of peripheral foliage	no changes	higher	wider foraging, no change in tree use
S. ruticilla	more flycatching	less use of foliage	increased use of maples	slightly higher	no changes
P. olivacea	no changes	no changes	decreased use of oaks, increased use of beeches	no change	no changes

[a] Changes are those that occur in the mature forest relative to the young forest.

The major structural difference between the two forests was an increased amount of open area beneath the main concentration of leaves in the mature forest. Acadian Flycatchers had narrower foraging niches in that forest. Since this species foraged mainly in these open areas beneath the canopy, the increase of open areas in the mature forest suggests more resources were available to the flycatchers. The narrower foraging niche of this species is consistent with the predictions of several optimal resource use models (MacArthur 1972, Pyke et al. 1977). Two other species also appeared to react to the increased open spaces in the mature forest. Black-throated Green Warblers broadened their foraging niche in the mature forest by flycatching more often. Redstarts switched from hovering most often in the young forest to flycatching most often in the mature forest. These last two species reacted opportunistically to an increase in a potential resource by altering their use of foraging techniques to reflect the increase in the resource.

Parallel changes in foraging between forests, such as those discussed in the preceding paragraph, suggest, at least for the species considered, that competition was not a proximate cause of foraging shifts. Similar parallel changes in foraging heights were demonstrated by Red-eyed Vireos, American Redstarts and Scarlet Tanagers. Each of these species concentrated foraging behaviors in the dense 6.1–12.2 m canopy layer in the young forest which again seemed to suggest changes were occurring in response to greater abundance of a potential resource. The results of this study clearly demonstrate that bird species do modify their foraging behavior when presented with altered resource distributions due in part to changes in the structure of the habitat (see Grubb 1979). If species respond opportunistically to changes in resource levels, what role would such opportunism play in determining which species were present in a given habitat? Further, which is more important in determining community structure, the species' own abilities to use resources in a given habitat or the number of competitors using that resource? This study implies that the answer to these questions may be different than the "classical" answers (e.g., Cody 1974). Further research is needed to clarify the relationship between individual species' foraging patterns and patterns of community structure. Holmes et al. (1979) did a community wide study of foraging behavior and concluded that the structure and composition of the plant community played a major role in determining bird community structure within and between habitats. The results of our study are very much in agreement with this idea, and suggest to us that changes in bird communities between habitats are related to altered resource distributions resulting from changes in the structure and species makeup of the plant community.

SUMMARY

The influence of habitat structure on the foraging behavior of five bird species was studied in two stands in the Fernow Experimental Forest. Vegetation structure of the stands was found to be different. One stand had a high, stratified canopy with a well-developed understory and the other had a lower, less stratified, but denser canopy without a well-developed understory. Each bird species showed differences in foraging behaviors that could be related to differences in vegetation structure. One species, American Redstart, changed foraging maneuvers between forests. Changes by other species involved use of different substrates or locations in trees, use of different tree species, or changes in foraging heights. Species that foraged by gleaning and hovering at foliage demonstrated different foraging behaviors less often than species which foraged by flycatching. Some species in this study showed changes in their foraging that coincided with increases in potential resources, e.g., Acadian Flycatchers did more flycatching in the forest with more open subcanopy area. Parallel changes in several instances suggested that competition was not a proximate cause of these changes.

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