

BIRD COMMUNITY STRUCTURE IN ALDER FORESTS IN WASHINGTON

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ABSTRACT.—Bird communities in forests of *Alnus rubra* in Washington were studied by analyzing the number and composition of bird species, and their foraging behaviors, along a successional gradient.

A model for territorial birds acting as central-place foragers was developed, and it was found that birds respond differently to heterogeneous versus homogeneous changes in vegetation structure. Birds responding to homogeneous vertical increases in vegetation during succession had territories which became more spherical. These changes were accompanied by a decreased use of total leaf area. Energy gain from reduced travel by central-place foragers may account for smaller territories. These changes were not found for birds responding to heterogeneous vegetation change.

Additions and subtractions of birds with different methods of foraging are analyzed with respect to specific changes in vegetation structure during succession. It is concluded that such changes alone can account for the addition of bird species and individuals.

Many investigators have shown that bird distributions are related to vegetation succession (Lack 1933, Bond 1957, Brewer 1958, Hagar 1960, Diamond and Terborgh 1967, Karr 1971). MacArthur and his co-workers (MacArthur and MacArthur 1961, MacArthur et al. 1962, MacArthur et al. 1966, Recher 1969, Cody 1970) introduced new insights by demonstrating that bird species diversity (BSD) as measured by the information theory index of diversity ($H = -\sum p_i \log p_i$) could be predicted from a knowledge of the vertical distribution of leaves in the vegetation (foliage height diversity, FHD). Although the physical structure of the habitat apparently either determines the structure of bird communities, or is at least strongly correlated with the real determinant, studies have hitherto provided little information on the actual use of the habitat by the individual species.

Terborgh (1967) and Balda (1969) found little correlation between foliage height diversity and bird species diversity in censuses from Peru and Arizona, respectively. These studies indicated that, on a fine scale, physical complexity of vegetation is not necessarily the most important predictor of complexity of bird communities. Others (James 1971, Anderson and Shugart 1974) have shown relationships between vegetation structure and bird distributions using multivariate techniques.

In simple communities, species segregate horizontally by microhabitat (Cody 1968, Orians and Horn 1969, Wiens 1969) but in more complex vegetation, such as forest,

species also segregate vertically. Terborgh and Weske (1969) and Karr (1971) obtained evidence that tropical species may use a narrower vertical range of their habitats than their temperate counterparts. Data exist on vertical foraging distributions of entire communities of temperate birds (Colquhoun and Morley 1943, Gibb 1954, Martin 1960, Pielowski 1961, Balda 1969, Cody 1974) and for some tropical birds (Pearson 1971, 1975, 1977, Lovejoy 1975). Of these studies only Balda's, Pearson's and Cody's record exact vertical distributions of species, allowing foraging height diversities and overlaps to be calculated for pairs of species, but none examines how changes in vegetation structure affect bird behavior.

Factors that are responsible for changes in the usage patterns of birds within a community can be examined by holding constant many factors, while maximally varying a few. This may be done by examining how changes in the structural complexity of the environment, which accompany plant succession in a simple system, affect avian utilization patterns.

In this study, I examine the species composition and foraging behavior of birds living in four stages of red alder (*Alnus rubra*) succession in western Washington. I explore the role vegetation structure plays in determining foraging patterns and bird community composition.

Structural changes in vegetation may affect birds directly by providing new substrates or eliminating foraging areas. By comparing bird species presence and for-

aging behavior, I will show that qualitative changes in vegetation structure influence modes of foraging. I will also explore the relationship between vegetation structure and foraging behavior for the foliage-gleaning and hovering modes. The foraging pattern which minimizes energy expenditure by birds may change when vegetation structure changes. During the nesting period many species of birds are central-place foragers (Orians and Pearson 1979), food is collected and returned to a central place. Central-place foragers differ from noncentral-place foragers because time and energy expenditure for travel during foraging, with the associated increased risks, are greater than for noncentral-place foragers.

If leaf distribution is homogeneous, and a given leaf area and associated insect biomass are necessary to support a pair of birds and their young during the nesting season, a constant leaf area should be defended as a territory. In this case the optimal shape of a nesting bird's territory is a sphere with the nest located centrally. This minimizes the distance to and from the central place. If the homogeneous resource changes in space, expanding vertically along the short axis of a squashed ovoid territory, it will allow a bird's nesting territory to become more spherical. The total amount of energy needed for travel to and from the central place will decrease because the same leaf area will be included in a smaller volume (Fig. 1). The energy necessary to maintain a territory of constant volume is decreased as the territory approaches spherical shape. The bird has a shorter average travel to and from the nest, and the territory has a smaller surface to patrol, allowing decreased territory volume. If forest height increases because of only one plant species, as in the alder forest, I expect bird territories to become more spherical as long as the horizontal territory diameter is greater than the height of the forest. This will not necessarily be accompanied by an increase in the number of bird species an area will support. If the added height increases the layering and structural heterogeneity of the forest, bird species in younger successional stages will not make their territories spherical. Instead, the number of species should increase.

Habitat characteristics that provide structural configurations and prey-encounter rates that enable a bird to breed successfully need not be related to the structure of the entire habitat, but only to the specific portion which is used by a bird. If different layers in the forest provided different prey-

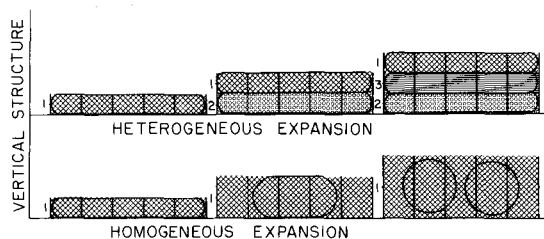


FIGURE 1. Theoretical changes in shape of feeding territory in response to heterogeneous and homogeneous vegetation structural change during succession. Heterogeneous change creates habitats for additional species; homogeneous change creates habitat for additional individuals of the same species.

encounter rates for a species of bird, the best territory shape would be modified by this prey-encounter rate.

These predictions can be tested. In alder forest succession (a) territories should become more spherical, and (b) the total leaf area per territory should decrease.

The degree of overlap or similarity of co-existing species in a community is a measure that is easy to apply but difficult to interpret. Although some studies suggest that niche overlap should decrease with increased number of competing species (Pianka 1974, 1976), others (May and MacArthur 1972, May 1974) demonstrate, at least theoretically, that overlap is relatively insensitive to low or moderate environmental fluctuation. In this paper I examine pairs of species with large niche overlaps in foraging behavior and morphology. I treat the overlap values as indicators that species may be avoiding competition for food by other means.

METHODS

Bird communities were studied on eight sites in Washington, two each of four different successional stages of red alder. Alder is an invading tree which grows in single-species stands to over 90 ft and provides maximal structural change with minimal plant species change during succession. Approximate ages of the successional stages were 4, 10, 35, and 60 years. Each site consisted of a four-hectare area marked every 25 m on a partial grid to provide reference points for plotting observations.

The eight study sites were in two areas. Two, (2A and 2B) were located 1.6 km W of Getchell, Snohomish Co. (122°06'W, 48°05'N). The remaining six (1A, 1B, 3A, 3B, 4A, 4B) were 3 to 5 km N of Clearview, Snohomish Co. (122°07'W, 47°51'N). All sites were between 150 and 210 m elevation.

Selection of the key niche dimensions in an analysis of community structure is critical. Many studies, but particularly those involving nestling starvation (Lack 1954, Crossner 1977), point to the importance of food availability for reproductive success of birds. In this study, I assume that food is of major importance in determining bird foraging behavior and community

TABLE 1. Bird censuses for alder forest plots during the breeding season, 1971.

Bird species	Number of pairs per plot							
	Plot 1A	Plot 1B	Plot 2A	Plot 2B	Plot 3A	Plot 3B	Plot 4A	Plot 4B
Red-tailed Hawk (<i>Buteo jamaicensis</i>)							+	+
Ruffed Grouse (<i>Bonasa umbellus</i>)			0.5		1.0	1.0		
Rufous Hummingbird (<i>Selasphorus rufus</i>)	9.0	4.0	2.0	3.0		0.5	+	+
Common Flicker (<i>Colaptes auratus</i>)	+	0.5						
Pileated Woodpecker (<i>Dryocopus pileatus</i>)			+					
Hairy Woodpecker (<i>Picoides villosus</i>)					0.5			
Downy Woodpecker (<i>P. pubescens</i>)					0.5	1.0	2.0	0.5
Willow Flycatcher (<i>Empidonax traillii</i>)	4.5	3.5	2.5	2.5	0.5	+	2.5	1.5
Western Flycatcher (<i>E. difficilis</i>)					3.0	3.0	3.0	3.0
Western Wood Pewee (<i>Contopus sordidulus</i>)	+	0.5					1.0	
Olive-sided Flycatcher (<i>Nuttallornis borealis</i>)	0.5	0.5						
Steller's Jay (<i>Cyanocitta stelleri</i>)	0.5			+		+	0.5	+
Black-capped Chickadee (<i>Parus atricapillus</i>)	1.5	1.0	2.0	1.0	1.0	+	+	+
Chestnut-backed Chickadee (<i>P. rufescens</i>)		0.5		1.0	2.0	1.5	2.5	1.0
Common Bushtit (<i>Psaltriparus minimus</i>)	0.5							
Red-breasted Nuthatch (<i>Sitta canadensis</i>)								0.5
Brown Creeper (<i>Certhia familiaris</i>)					1.5	0.5	2.0	1.5
Winter Wren (<i>Troglodytes troglodytes</i>)	+				4.0	5.0	3.5	2.0
Bewick's Wren (<i>Thryomanes bewickii</i>)	4.0	6.0	4.5	3.0				+
American Robin (<i>Turdus migratorius</i>)		1.5	3.0	1.0	1.5	2.0	2.0	0.5
Swainson's Thrush (<i>Catharus ustulatus</i>)	8.0	5.0	11.0	11.0	7.0	7.0	8.0	9.0
Cedar Waxwing (<i>Bombicilla cedrorum</i>)	0.5	0.5						
Red-eyed Vireo (<i>Vireo olivaceus</i>)			1.0	1.0	4.0	3.5	4.0	3.0
Warbling Vireo (<i>V. gilvus</i>)					2.0	2.0	5.0	5.0
Orange-crowned Warbler (<i>Vermivora celata</i>)	3.5	3.0	2.0	2.0		0.5		
Yellow Warbler (<i>Dendroica petechia</i>)			+	+				
Black-throated Gray Warbler (<i>D. nigrescens</i>)					0.5	+	0.5	0.5
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	2.0	1.0		0.5				
Wilson's Warbler (<i>Wilsonia pusilla</i>)	0.5		1.5	2.0	1.0	2.0	2.5	4.0
Western Tanager (<i>Piranga ludoviciana</i>)					1.5	1.0	1.5	0.5
Black-headed Grosbeak (<i>Pheucticus melanocephalus</i>)	3.0	4.0	3.0	4.0	1.0	2.0	3.0	1.5
American Goldfinch (<i>Carduelis tristis</i>)	+	0.5	0.5					
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	7.0	4.0	4.0					
Dark-eyed Junco (<i>Junco hyemalis</i>)					5.0	3.0	3.0	3.5
Song Sparrow (<i>Melospiza melodia</i>)	19.0	16.0	3.5	8.0	6.0	3.0	15.0	9.0
Total pairs per plot	64.5	52.0	41.5	40.5	43.5	38.5	62.5	47.0

composition. As two of the significant dimensions of a bird's niche, I picked (a) foraging height, or how far above the ground the food was taken, and (b) foraging technique, a combination of the behavior for obtaining food, the foraging guild or mode (Root 1967), and the substrate on or in which the food was located. Measures of niche breadth along these dimensions were calculated using the information theory index of diversity. Overlap values were calculated using Horn's (1966) formula, $(\text{overlap} = R_o = H_{\max} - H_{\text{obs}}/H_{\max} - H_{\min})$.

Censusing of birds began between 05:00 and 10:00 and lasted from 2 to 4 h depending on bird activity and the weather. I walked the trails and for each bird encountered, I recorded: time, species, age (mature or immature) and sex if positively determinable, the height above ground (estimated to the nearest 5 ft [1.52 m] above 15 ft [4.7 m] and to the nearest 1 ft [0.305 m] below 15 ft), behavior of the bird and the foraging movement if any. I limited the number of foraging observations recorded from any individual to four in an attempt to reduce bias introduced by observing one individual for too long. For each breeding bird species, I mapped the locations and movements of the birds, especially the singing males. From these data the numbers of breeding pairs were estimated (Table 1), and the territories were plotted. Foraging observations were taken during two breeding seasons, May through

August 1970 and March through August 1971, and territories were plotted for 1971. I analyzed the vegetation to provide a quantitative index to serve as an indirect measure of relative food abundance available to the birds. I assumed that availability of insects at any level in the foliage profile was directly proportional to the area of the leaf surface at that level in the foliage column for a given plant species. In sites 2, 3, and 4, over 93% of the leaf surface area above 10 ft was red alder. To test this assumption for alder leaves, I measured insect damage to alder leaves in plots 3 and 4 at 10-ft intervals in the canopy from 10 to 60 ft. Of the 649 leaves examined the mean percent damage for the different height intervals was similar, ranging from 2.64% to 4.57%, but the variances in percent damage were high. The large variances in alder leaf damage prevent making any conclusive statements regarding absolute changes in insect biomass in the canopy. I feel that, judging from the similarity in percent damage at different heights and the lack of demonstrable pattern, it is not unrealistic to use foliage density as an estimator of resource abundance available to alder foliage-gleaning birds. Plant species composition below 10 ft differed markedly during succession as will be discussed below.

Foliage density was measured using a method described by MacArthur and Horn (1969), in which vertical sightings are taken through a 35-mm camera with

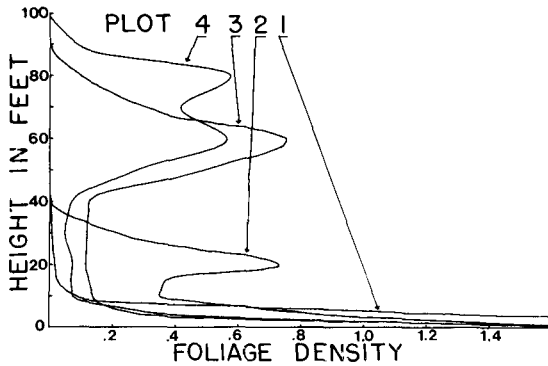


FIGURE 2. Foliage density profiles for the four successional stages in red alder stands in Washington, replicates combined. Foliage density expressed as the average number of leaves above a point in a height interval. Foliage densities for 0–5 ft: plot 1 = 3.85, plot 2 = 1.89, plot 3 = 1.98, plot 4 = 1.98. Metric equivalents: 10 ft = 3.05 m, 20 ft = 6.1 m, 30 ft = 9.1 m, 40 ft = 12.2 m, 50 ft = 15.2 m, 60 ft = 18.3 m, 70 ft = 21.3 m, 80 ft = 24.4 m, 90 ft = 27.4 m, 100 ft = 30.5 m.

a 135-mm lens. The height and identity of the first intersected leaf above each of 16 points, defined by an acetate grid placed on the ground glass of the camera, was recorded. I used MacArthur and Horn's formula, $\ln[P_0(h_1)/P_0(h_2)] = \text{foliage density between } h_1 \text{ and } h_2$, where $P_0(h_1)$ is the proportion of the camera measurements that exceed height h_1 and $P_0(h_2)$ is the proportion of the camera sightings that exceed h_2 . From this formula the leaf area per volume for each level in the forest was calculated. For leaves below 10 ft, a plumb line was dropped from a height of 10 ft and the number of intersected leaves in each one-foot interval was recorded. This gives a direct measure of leaf area per volume below 10 ft.

For each of the plots, the foliage profiles were calculated and plotted. The profiles in the replicates of the four different age groups were so similar that the foliage structure analysis and the bird community analysis for the replicates were combined (three of the four sets of replicates were adjacent), and the final analysis was done on four plots each representing an eight-hectare plot for each successional stage (Fig. 2). The sites were picked to minimize horizontal heterogeneity. Sites 1 and 2, however, did exhibit horizontal patchiness with some more open areas.

RESULTS AND DISCUSSION

VEGETATION AND FOOD AVAILABLE FOR BIRDS

The proximity of my plots, and their similarity in elevation and slope, minimized differences among them in temperature, rainfall, humidity and insolation; the major variable was the distribution of the leaves in the forest. My method of vegetation analysis is most useful in comparing birds that eat insects whose biomass is somehow correlated with the leaf area of different plant species and vertical distribution of leaves.

I selected three variables, all of which are indirect measures of the location and abun-

TABLE 2. Average number of leaves intersected above a random point in alder forests.

Plot number	Replicate A	Replicate B	Mean
Plot 1	5.45	4.69	5.07
Plot 2	4.03	4.56	4.29
Plot 3	4.39	5.50	4.94
Plot 4	4.40	4.76	4.57

dance of the food on which the birds depend. First, the total foliage area should be positively correlated with insect abundance in similar habitats. Second, a change in plant species composition may influence the insect resource because of the different chemical and physical defenses that plants employ to repel insects (Whittaker 1970). Different species of plants may support different insect biomasses. Third, the structure of the vegetation or the arrangement of the leaves in the forest may be important to the birds, as optimal foraging in different types of vegetation requires specific morphological adaptations.

Although distribution of leaves in the forest changed markedly with succession, the total leaf area in the four stages showed no discernible trend (Table 2). This is important in the analysis of the bird community structure, because the food supply for birds that consume leaf-eating insects may not change significantly in biomass as succession proceeds, if the biomass of insects per unit leaf area does not change. There is, however, a major change in the arrangement of leaves in the forest, which should affect avian foraging behavior (Fig. 2). The insect fauna may change as the leaf area of different plant species changes. Two factors are important here, the first being the change in the plant species composition with increasing age of plot. Cates and Orians (1975) found that early successional plants are more palatable to generalized herbivores than later successional plants. Early successional plants may yield more insects for birds. My data on leaf damage to four of the most abundant plants indicate that alder supports twice the insect biomass per unit leaf area as the other three species (Table 3). As the proportion of alder leaves increases during succession, the potential increase in insect biomass may be countered in part by the decrease in many of the palatable early-successional species. The elimination of these early-successional species, accompanied by the increase of the palatable alder, may not greatly affect total insect biomass in any one plot but could

TABLE 3. Percent of leaves consumed by insects of four common alder forest plants, abundance of these plants expressed as a percent of the total leaf area on the plots.

Plant species	Percent consumed	Number of leaves examined	Plant abundance (%)			
			Plot 1	Plot 2	Plot 3	Plot 4
<i>Alnus rubra</i>	3.84	649	6.5	40.7	54.4	51.2
<i>Rubus spectabilis</i>	1.63	89	36.8	10.3	5.5	8.6
<i>Rubus ursinus</i>	1.45	191	8.8	10.6	8.5	12.0
<i>Acer circinatum</i>	1.32	238	5.8	0	5.0	4.3
Percent of total leaf area of four species			57.9	61.6	73.4	76.1

cause a marked vertical shift in the availability of insects.

A plot of the percentage of the total leaf area under 10 ft against the percentage of foraging observations under 10 ft will yield points on a 45° line if the insect abundance is directly proportional to the leaf area (Fig. 3). Almost all non-alder foliage was found below 10 ft (Figs. 2 and 4). If palatability changes as indicated by the leaf damage data, I expect a curve which starts at the 45° line when all the vegetation is under 10 ft and remains on or dips below the 45° line as the alder trees start to grow, the palatable early-successional plants remain in the understory. The curve would then rise above the 45° line as the early-successional herbs were replaced by the less-palatable, later-succession plants, shifting the insects and hence the birds higher into the canopy. This trend may be present (Fig. 3) but confirmation would require a more detailed analysis of the leaf damage to all species of plants.

My data suggest that the insect damage per unit leaf area to alder leaves does not vary greatly with height above the ground. Alder foliage, and hence food for the birds, changes as succession proceeds, primarily because of changes in the arrangement of the leaves of the alder trees (Fig. 4). The profile of the alder foliage moves up and broadens vertically, providing more, fairly homogeneous vegetation for the alder foliage-foraging birds.

BIRD COMMUNITY STRUCTURE

Feeding territory sizes were recorded for all breeding species. For the three species recorded both by Schoener (1968) and this study, the territory sizes were similar. For analysis of the changes in the bird community structure, I considered only those species common enough to have at least one complete territory on the combined plots for each successional stage. The results are

similar when all breeding species are considered, but I know less about the foraging habits of the rarer species.

Niches could have broadened for several reasons, including increased intraspecific competition, relaxed interspecific competition, increase in available structural components in the habitat, a decrease in the resource predictability or combinations of these. Other factors, such as time of day, specific nature of the food, or the effect of predation on the bird community were not considered in this study.

Foraging techniques should be conservative, especially the foraging mode. An analysis of changes in foraging behavior diversity of individual species shows no demonstrable trend in the diversity of techniques used with increasing foliage height diversity (Table 4). A bird can alter the vertical distribution of its foraging activity more easily. For the majority of species, especially those which forage in the canopy (Red-eyed Vireo, Warbling Vireo, Western Tanager and Western Flycatcher), the foraging height diversity increases with increasing canopy height (Table 4). However, foraging height diversity for the primary understory bird, the Song Sparrow, does not increase. Succession may add habitat unsuitable for the Song Sparrow, making vertical expansion of foraging impractical. Also two understory foragers that were found only in the first and second successional stage, the Bewick's Wren and the Orange-crowned Warbler, may be unable to use the lower layers of the forest due to successional changes.

Changes in the bird community structure may be examined by looking at the different types of foragers. The distribution of foraging types may tell which factors are responsible for addition or subtraction of species (Table 5).

The scratching mode, represented by the Rufous-sided Towhee, ceases after the second successional stage; at least the towhee

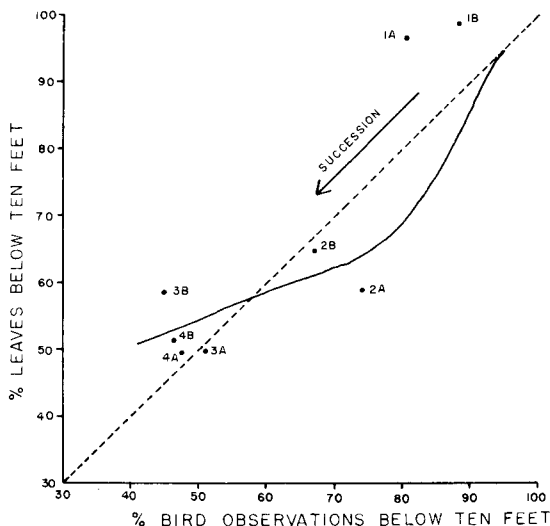


FIGURE 3. Distribution of birds and leaves in alder forest plots. Dashed line = theoretical curve if a unit area of leaf for all plant species supports the same biomass of insects. Solid line = theoretical curve if plant palatability changes with succession (see text). Points = alder forest plots.

is absent in the later stages. Ground cover in sites 3 and 4 did not differ significantly from that in site 2 (Fig. 2).

The nectar-feeding mode was represented by both male and female Rufous Hummingbirds on the younger two sites, 1 and 2, and very sparingly by females on the older sites, 3 and 4. Male hummingbirds held mating and feeding territories in areas of abundant food supply furnished by the flowers of *Rubus spectabilis*, *Lonicera involucrata*, and various ericaceous shrubs. Sites 1 and 2 contained open areas where the aerial display of the males could be seen readily by the females. The older sites had fewer flowers, few open spaces for aerial displays, and the males did not hold territories. Females, on the other hand, occasionally moved into the older stands to nest. During the nesting period female hummingbirds need protein for making eggs and feeding young, and my few observations for this period report insect food.

The pecking mode is absent from sites 1 and 2 because proper substrate is lacking. In the older stands of alder, ample dead branches and trunks provided resources for woodpeckers. The youngest plot contained some dead standing trees, as well as many fallen trees that had not yet decayed, which supplied a partial territory for a Common Flicker. In site 2, vegetation consisted almost entirely of young, vigorous growth and

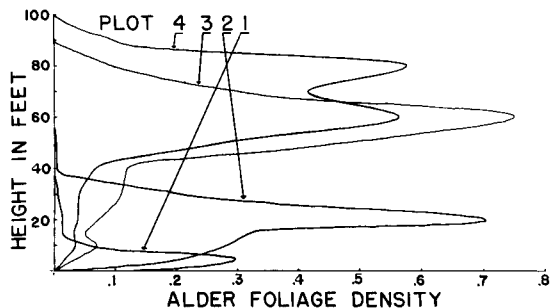


FIGURE 4. Density of alder foliage in the four successional stages in Washington.

most of the older dead wood had decayed substantially and was no longer attractive to pecking birds.

The closing of the forest mid-story in the second and third successional stages occluded the space for sallying. In site 1, the Olive-sided Flycatcher, and the Western Wood Pewee sallied. In the oldest alder site the forest mid-story had opened enough to provide space for sallying below the canopy and the Western Wood Pewee reappeared. The remaining members of the bird community, snatchers and gleaners, responded primarily to the changes in the distribution of leaves. Two species were added between sites 1 and 2, four species between sites 2 and 3, and no species between sites 3 and 4. These additions were correlated with the changes in foliage complexity as measured by foliage height diversity.

FOLIAGE USE BY GLEANERS AND SNATCHERS

In alder forest succession, the canopy increases not only in height but also in breadth (Fig. 4). To test for the predicted change toward spherical territory shape and associated decrease in total leaf area per territory, I used a measure of the leaf area used by each pair of birds on the different plots, the Foliage Utilization Index (FUI). I multiplied territory size by the density of leaves at each forest level, modified by the percentage of time each bird species spent foraging in each foliage layer. (Foliage Utilization Index = $T \left(\sum_{i=1}^{20} D_i \cdot P_i \right)$, where T = the territory area of a given plot, D_i = the density of leaves at the i^{th} level in the forest and P_i the proportion of the foraging observations of a bird species in any given plot in the i^{th} layer in the forest. The sum is taken over five-foot layers in the forest.) This index could be modified to include percentages of time spent at varying dis-

TABLE 4. Niche breadths for foraging height and foraging technique.

Bird species	Foraging height H _{max} = 2.99				Foraging technique H _{max} = 2.86			
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 1	Plot 2	Plot 3	Plot 4
<i>Picoides pubescens</i>			2.06	2.35			1.20	1.23
<i>Empidonax traillii</i>	1.83	1.79		2.07	0.35	0.18		0.67
<i>E. difficilis</i>			2.36	2.47			0.61	0.62
<i>Contopus sordidulus</i>				1.32				0.00
<i>Nuttallornis borealis</i>	1.99				0.97			
<i>Parus atricapillus</i>	0.62	1.33	2.50		1.46	1.49	1.39	
<i>P. rufescens</i>		1.39	2.44	2.70		0.82	1.81	1.83
<i>Certhia familiaris</i>			2.20	1.94			0.00	0.84
<i>Troglodytes troglodytes</i>			1.42	1.66			1.37	0.75
<i>Thryomanes bewickii</i>	1.35	1.21			1.12	1.41		
<i>Turdus migratorius</i>	2.14	1.99	2.32	2.09	0.00	0.88	1.46	1.39
<i>Catharus ustulatus</i>	1.73	1.53	2.04	2.22	0.84	0.52	1.49	1.11
<i>Vireo olivaceus</i>		1.43	2.18	2.19		0.86	1.01	0.88
<i>V. gilvus</i>			1.92	2.32			1.14	1.16
<i>Vermivora celata</i>	1.93	1.70			0.19	0.51		
<i>Dendroica nigrescens</i>				1.70				0.69
<i>Oporornis tolmiei</i>	1.09				0.27			
<i>Wilsonia pusilla</i>		1.23	2.18	2.24		0.46	1.24	0.75
<i>Piranga ludoviciana</i>			1.92	2.16			0.91	0.95
<i>Pheucticus melanocephalus</i>	2.14	2.03	2.42	2.50	0.95	0.53	0.53	0.88
<i>Pipilo erythrophthalmus</i>	1.71	1.48			1.35	1.25		
<i>Junco hyemalis</i>			2.19	2.28			1.48	1.53
<i>Melospiza melodia</i>	1.46	1.21	1.11	1.45	1.37	1.24	1.13	1.12

tances from the central place, but in most cases the nest site was not known, and since alder forests were less heterogeneous horizontally than vertically, not much resolution is lost.

The total area of territories of each species on each site was divided by the number of pairs holding territories on a site. Estimates of the number of territories per site were made to the nearest half territory and only gleaners and snatchers with at least two territories in any successional stage were included in this portion of the analysis. In all cases, the average territory area for each species on each site was greater than the canopy height. Therefore, any increase in use of the vertical axis in the forest indicates an approach toward a spherical shape, providing the territory does not expand proportionally. An index of spherical shape is given by the vertical foraging usage divided by the territory diameter. For the measure of vertical foraging usage I used foraging height diversity which

weights each foliage layer according to the intensity of its use. Thus, I have a measure of approach toward spherical shape: Foraging Height Diversity/Territory Diameter; and a measure of the foliage use: the Foliage Utilization Index.

I first examined changes in the FUI with succession. If birds are using the same area of leaf surface in different successional stages, I expect no change in the index. I plotted the FUI and the foraging height diversity against the successional stage for two gleaners (Black-headed Grosbeak and Wilson's Warbler) that span the last three stages of the alder succession. As succession proceeds foraging height diversity increases, indicating use of more forest layers, and FUI decreases, indicating a reduction in the total leaf area used by the average pair of birds of these species (Fig. 5). The same trend is present among three snatchers that are present in the last two successional stages (Fig. 6). In addition, FUI plotted against the index of approach toward

TABLE 5. Numbers of species of birds using various modes of foraging.

Plot number	Numbers of species in foraging guild						Total species	Foliage height diversity
	Gleaning	Snatching	Pecking	Sallying	Scratching	Nectar		
1	7	2	0	1	1	1	12	0.361
2	8	3	0	0	1	1	13	0.722
3	10	5	1	0	0	+	16	1.072
4	9	6	1	1	0	+	17	1.069

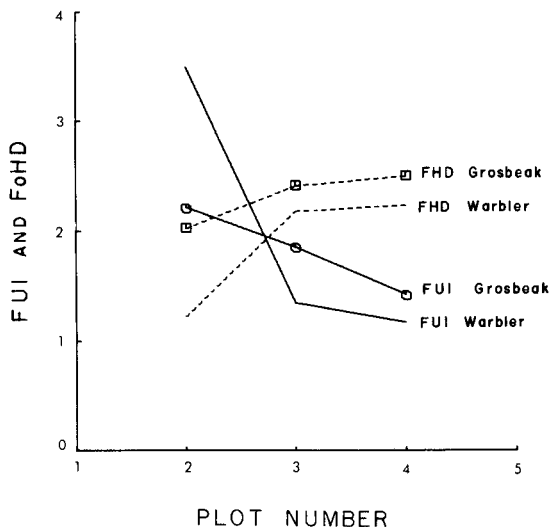


FIGURE 5. Foliage Utilization Index and Foraging Height Diversity for Black-headed Grosbeak and Wilson's Warbler for plots 2, 3, and 4.

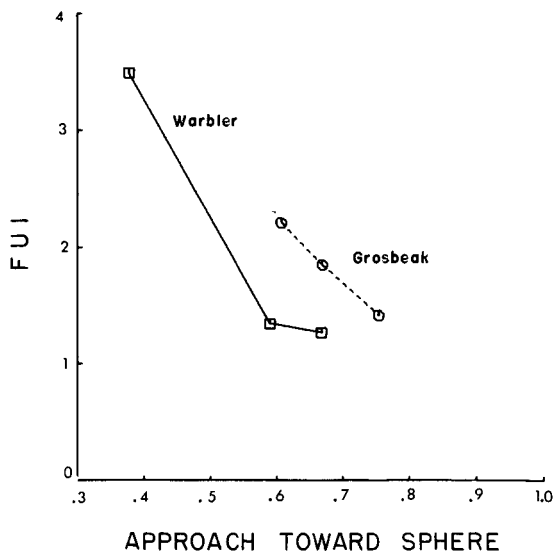


FIGURE 7. Foliage Utilization Index plotted against Approach Toward Spherical Shape for Black-headed Grosbeak and Wilson's Warbler for plots 2, 3, and 4. For both curves, plot 2 is the left point and plot 4 is the right point.

spherical territory shape has a negative slope (Figs. 7 and 8). As alder succession proceeds, these species establish more spherical territories, possibly because of shorter traveling to and from the central place. The Red-eyed Vireo, a snatcher, showed the same trend across three plots, but the Swainson's Thrush, which spends over 75% of its time in the vegetation below 25 ft and does not respond to the expansion of alder foliage, followed a different pattern (Figs. 9 and 10). Similarly, I found no demonstrable trend for the Song Sparrow

(Figs. 11 and 12) which is common in all four successional stages but does not occupy the alder foliage and may respond to changes in plant species composition and abundances in the understory. Gleaners and snatchers which forage primarily in the forest canopy show the predicted change toward spherical territory shape and associated decrease in total leaf area per territory, but species which do not forage in the canopy do not.

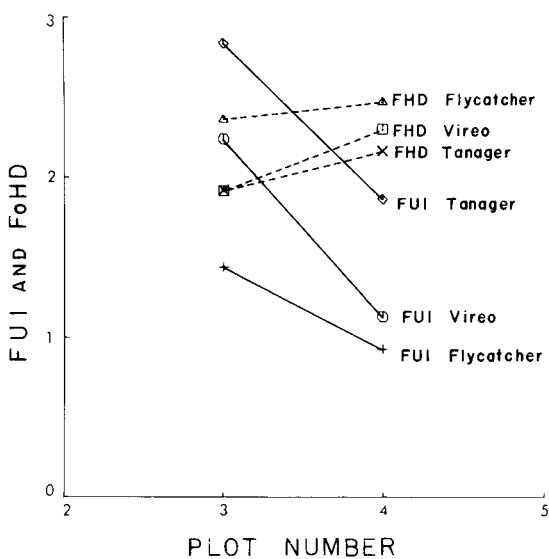


FIGURE 6. Foliage Utilization Index and Foraging Height Diversity for Western Tanager, Western Flycatcher and Warbling Vireo for plots 3 and 4.

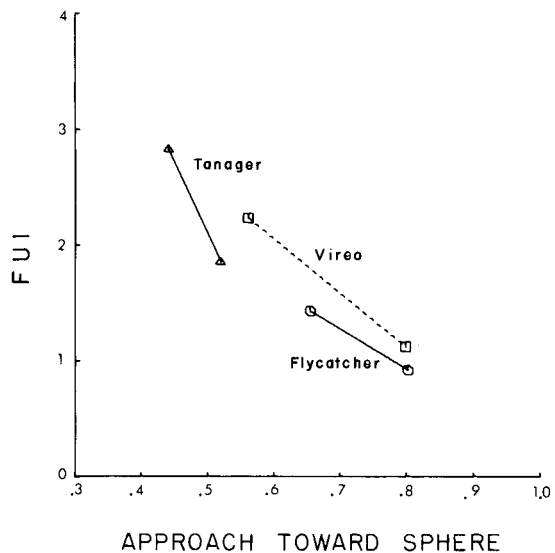


FIGURE 8. Foliage Utilization Index plotted against Approach Toward Spherical Shape for Western Tanager, Western Flycatcher, and Warbling Vireo on plots 3 and 4. For all three curves, plot 3 is the left point.

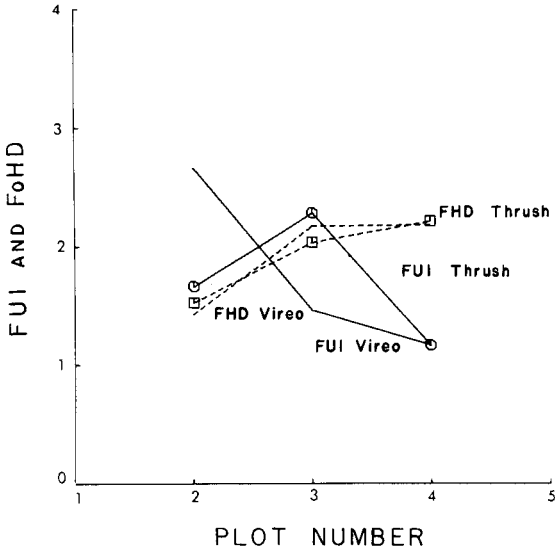


FIGURE 9. Foliage Utilization Index and Foraging Height Diversity for Swainson's Thrush and Red-eyed Vireo for plots 2, 3 and 4.

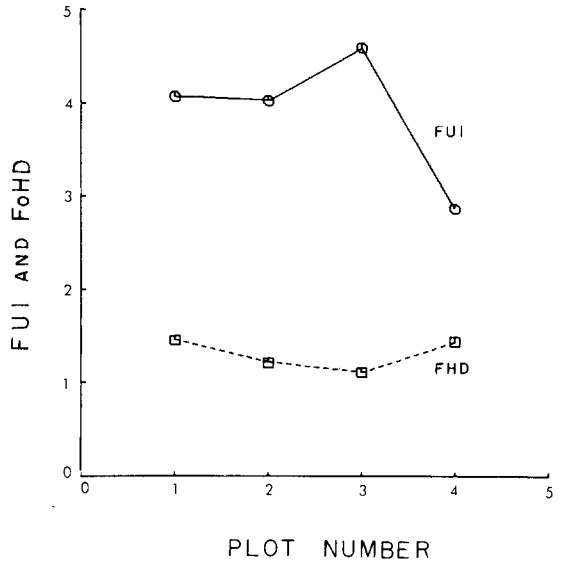


FIGURE 11. Foliage Utilization Index and Foraging Height Diversity for the Song Sparrow on all plots.

OVERLAP

I measured overlap for the two major food-associated dimensions and computed measures of morphological similarity using a measure of Pythagorean distance combining three morphological parameters: bill length, bill width and wing chord (data on overlap values are available from the author). Bill measures have been shown to be related to prey size for some species (Selander 1966), as has body size (Hespenheide 1971), which is correlated with wing chord among related species. In comparing overlap and degree of similarity between and within species along the successional gradient, several points are of interest. First, in almost all cases where birds coexist in the same successional stage, at least one of the three measures, and usually more, falls below an overlap or similarity of 0.8. This figure was picked arbitrarily. Cases of potential interest are those in which all three

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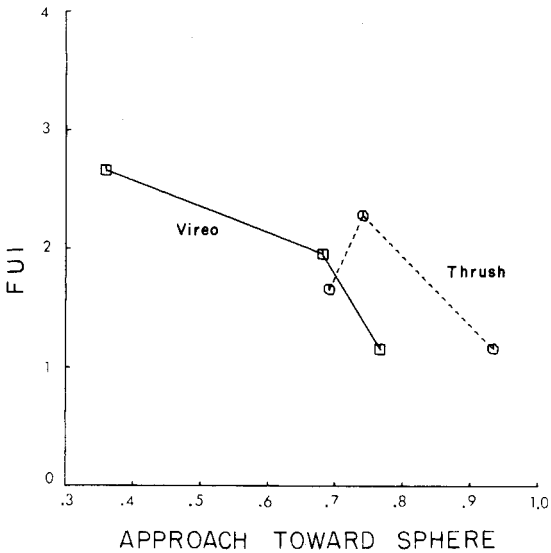


FIGURE 10. Foliage Utilization Index plotted against Approach Toward Spherical Shape for Swainson's Thrush and Red-eyed Vireo on plots 2, 3 and 4. For both curves plot 2 is the left point and plot 4 is the right point.

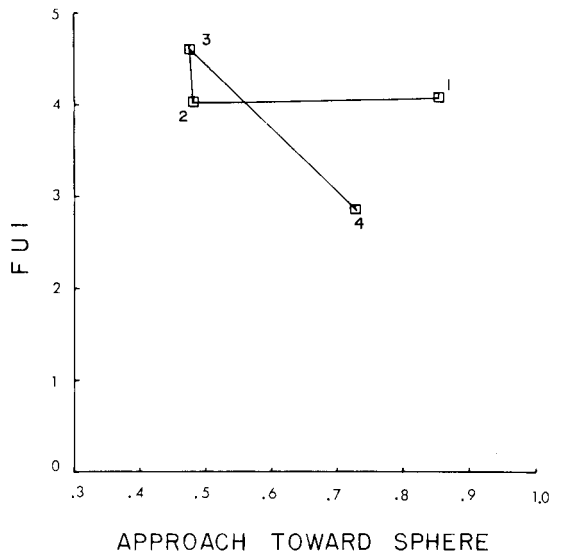


FIGURE 12. Foliage Utilization Index plotted against Approach Toward Spherical Shape for the Song Sparrow on all plots. Plot numbers indicated next to points.

TABLE 6. Territory overlap for two pairs of species.

Plot number	Species	Percent of 4-hectare plot occupied A	Percent overlap with the other species B	Percent of possible non-overlap within a plot* = actual/potential
3A	Red-eyed Vireo	72.5	34.5	72.8
	Warbling Vireo	45.0	55.5	
3B	Red-eyed Vireo	68.75	29.1	72.0
	Warbling Vireo	42.5	47.1	
4A	Red-eyed Vireo	66.25	67.9	55.5
	Warbling Vireo	72.5	62.1	
4B	Red-eyed Vireo	41.25	69.6	71.7
	Warbling Vireo	82.5	34.8	
2A	Orange-crowned Warbler	28.75	17.4	82.6
	Wilson's Warbler	37.5	13.3	
2B	Orange-crowned Warbler	42.5	23.5	66.6
	Wilson's Warbler	30.0	33.3	

* Example: $WaV = \text{Warbling Vireo}$; $ReV = \text{Red-eyed Vireo}$, percent of possible non-overlap with a plot = $WaV"A" - (ReV"A" \times ReV"B") / 100 - ReV"A"$.

measures (foraging height, foraging technique overlap and morphological similarity) have values of over 0.8. This occurs in only five pairwise comparisons. The Black-capped Chickadee and Chestnut-backed Chickadee have values exceeding 0.8 in all forests in which they coexist. Sturman (1968) demonstrated that although these species separate primarily by habitat—the Chestnut-backed Chickadee preferring conifers—they do coexist in broad-leaf forests. My results agree with his findings that Chestnut-backed Chickadees feed higher in the foliage column and tend to use the outer twigs more than Black-capped Chickadees. This difference is also reflected by the number of breeding pairs on the different plots, Black-capped Chickadees predominating in plots 1 and 2 and Chestnut-backed Chickadees in plots 3 and 4 (Table 1). The Orange-crowned Warbler and MacGillivray's Warbler in plot 1, and the Swainson's Thrush and Willow Flycatcher in plot 2, all show values above 0.8. In both cases, there are micro-habitat preferences which are not reflected in the overlap indices. The MacGillivray's Warbler prefers closed tangles, while the Orange-crowned Warbler forages more in the open. Similarly, the Swainson's Thrush prefers closed areas, while the Willow Flycatcher forages more in open areas. A difference here in body size is masked by the similarities of the bill measurements in the similarity index. The Red-eyed Vireo and Warbling Vireo overlap the most of any of the species pairs, but in all four plots where they co-occurred their territories overlapped only slightly (Table 6). The only other case in which all values exceed 0.8 involves the Wilson's and Orange-crowned

warblers. My study areas appear to be on the lower edge of the successional stages suitable for the Wilson's Warbler and the upper edge of those suitable for the Orange-crowned Warbler. The heterogeneity of plot 2, some areas being slightly earlier in the successional sequence than others, may be enough to account for coexistence, as their territories do not overlap greatly (Table 6). Orange-crowned Warblers forage more along edges and in open areas while Wilson's Warblers stay in thicker and higher vegetation.

Only one replacement of species occurred; the Bewick's Wren in plot 1 and 2 was replaced by the Winter Wren in plots 3 and 4. These species forage in similar places and in similar ways. However, the Winter Wren feeds more on the ground and under tangles of vegetation as well as on fallen logs and branches. The Bewick's Wren feeds on twigs and small branches off the ground. The reduction of the number of lower branches and the increase in fallen debris as succession proceeds may account for the replacement.

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