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FEEDING ECOLOGY OF THE RED-EYED VIREO (*VIREO OLIVACEUS*) AND ASSOCIATED FOLIAGE-GLEANING BIRDS¹

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ABSTRACT

The sexes of the Red-eyed Vireo, an abundant insectivorous bird in eastern deciduous woodlands, differed in their foraging heights, with an overlap of only about 35%. The males foraged higher than the females, and non-random sequences of movements were employed to maintain this separation. The foraging level and the nest height of female Red-eyes was similar, whereas the males foraged closer to their singing perches. Thus the foraging efficiency of both sexes was likely greater in accordance with their differing behavioral roles. The "small" territory (1.3–1.7 acres) of this species actually consists of a cylinder extending from the forest canopy to the low understory.

The associated White-eyed Vireo (*Vireo griseus*) was generally separated from the Red-eyed Vireo by habitat, and the Yellow-throated Vireo (*Vireo flavifrons*) overlaps in habitat but possesses structural and behavioral differences which indicate different prey preferences. Foraging behavior of migrating Red-eyed Vireos differs markedly from that of breeding birds. Differences were also noted between summer and winter foraging behavior patterns in the White-eyed Vireo.

All three vireo species exhibit species-specific patterns of foraging movements. Two other foliage-gleaning insectivorous birds occupying the same forests, the American Redstart (*Setophaga ruticilla*) and the Acadian Flycatcher (*Empidonax virens*), also possess species-specific foraging behaviors (niche-exploitation patterns).

INTRODUCTION

The objectives of this study were to determine the manner in which five small insectivorous birds utilize a common space for foraging, the deciduous woodland of Maryland, and to clarify further the concept of the ecological niche. Hutchinson (1957) defined

the niche as a multidimensional space with each parameter corresponding to a different requirement of a species. This study is a critical examination of several such parameters, particularly those related to foraging patterns.

Interspecific competition has long been considered extremely significant in evolution. Darwin (1859) recognized that since congeneric species are, by definition, similar in structure and usually in habits, the likelihood of competition is greater between them than between distantly related species. Thus, it follows that intraspecific competition is likely to be even

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more intense due to an almost total overlap of requirements, structures, and behaviors (Darwin 1859). The latter consideration led to MacArthur's (1958) suggestion that the specialization of the five congeneric species of wood warblers (Parulidae) resulted in each population limiting its own numbers; all could therefore exist in sympatry. The possible mechanisms evolved in response to intraspecific competition, such as sexual dimorphism, have only recently been examined.

Kilham (1965) showed that in the Hairy Woodpecker (*Dendrocopos villosus*) significant sexual differences in feeding behavior were correlated with differences in bill size. Further, Selander (1966) pointed out that such sexual dimorphism in woodpeckers (*Centurus*) and other avian species could be related to differential niche utilization and concomitant reduction of intraspecific competition. Dimorphic structures, which were usually related to foraging (e.g., bill size and shape), were most evident in insular and polygamous species. Johnson (1966) found sexual dimorphism in bill size and wing shape in the Dusky Flycatcher (*Empidonax oberholseii*) and the Grey Flycatcher (*Empidonax wrightii*) and attributed it to intraspecific competition between members of territorial pairs. Sexual dimorphism in size correlated with different foraging preferences has also been shown by Storer (1966) in three species of acciptrine hawks, by Keast (1966) in several species of fresh-water fishes, and by Schoener (1967, 1968) in island-inhabiting species of *Anolis*.

In 1966 Selander suggested that polymorphism may operate on a behavioral level without obvious morphological correlates. Recently Morse (1968) showed that structural differences were not necessary prerequisites for behavioral divergence between sexes. In four congeneric species of wood warblers, he found that males foraged higher than their females, a difference that correlated with singing perch height for males and nest height for females. The foraging rates of females were significantly greater than those of their males during incubation.

The present study presents evidence for strong divergence of male and female behavior with little structural difference between the sexes of the Red-eyed Vireo (*Vireo olivaceus*). Data were insufficient to evaluate this phenomenon in the other species studied. White-eyed Vireos (*Vireo griseus*) and Yellow-throated Vireos (*Vireo flavifrons*) were observed to determine if they have elements in common with the similarly structured Red-eyed Vireo. It was hypothesized that the three vireos (as well as two other sympatric insectivorous passerines, the American Redstart and the Acadian Flycatcher) would possess species-specific patterns of foraging.

THE STUDY AREAS

Patuxent Research Center

The principal study area, the Patuxent Research Center, is located in Prince Georges and Anne Arundel Counties, Maryland. The research center is divided into hectares with permanent benchmarks at each intersection. Cleared narrow lanes between the benchmarks greatly facilitated observation. Supplementary markers were added which permitted precise mapping of movements of color-banded birds.

A 14-ha plot (35 acres) was chosen to include both flood-plain and terrace forests. Beech (*Fagus grandifolia*) and white oak (*Quercus alba*) are dominant. The Patuxent River, bordering the northeast edge, and an artificial pond in the southeast provided riparian habitat. Here most of the observations of foraging behavior of Red-eyed and Yellow-throated Vireos and their associates (American Redstart, *Setophaga ruticilla*, and Acadian Flycatcher, *Empidonax virescens*) were made during the 1967 and 1968 breeding seasons. In 1967 foraging White-eyed Vireos were observed in many hedgerows and wood margins around the center.

A complete vegetation analysis of the center by Hotchkiss and Stewart (1947) is an accurate guide for the study area. The beech-white oak terrace forest exists on well-drained soils. The two dominant trees are 60–85 ft high and form the upper canopy beneath which other oaks (*Quercus falcata*, *Quercus borealis*, et al.), young beech, red maple (*Acer rubrum*), pignut and mockernut hickory (*Carya glabra* and *C. tomentosa*), and sweet gum (*Liquidambar styraciflua*) form a second layer intermediate in height, approximately 25–40 ft, between that of the larger trees and the lower shrubs and saplings (2–25 ft). In contrast, the flood-plain forest (seepage swamp) is poorly drained. Blackgum (*Nyssa sylvatica*) and red maple are common. The understory is often dense and is composed primarily of sweet pepperbush (*Clethra alnifolia*), green brier (*Smilax rotundifolia*), and *Viburnum* spp.

The woodland margins vary in plant composition. Bordering the terrace and flood plain river birch (*Betula nigra*), sassafras (*Sassafras albidum*), and black cherry (*Prunus serotina*) are predominant; in the drier uplands birch is lacking. The hedgerows are composed primarily of sassafras, cherry, and many young sweet gums. The shrubs and vines are often dense tangles with green brier (*Smilax* spp.), blackberry (*Rubus* spp.), honeysuckle (*Lonicera japonica*), and shining sumac (*Rhus copallina*) in profusion.

Chesapeake Bay Center for Environmental Studies

A subsidiary study area was located at the Chesapeake Bay Center for Environmental Studies

(CBCES), Anne Arundel County, Maryland. The deciduous woodland of beech and maple, described by Higman (1968) and similar to the upland terrace forest at Patuxent (Fig. 1), provided an area for additional observations of the Red-eyed Vireo and Acadian Flycatcher during the breeding season of 1968. At that time White-eyed Vireos were observed in the abundant edge vegetation bordering or actually comprising the many old fields at the bay center (Fig. 2). The tulip tree (*Liriodendron tulipifera*), black cherry, sassafras, and sweet gum are characteristic species (25–35 ft high) above a dense, often impenetrable understory of Japanese honeysuckle, poison ivy (*Rhus radicans*), and staghorn sumac (*Rhus typhina*).

Gainesville, Florida

White-eyed Vireos were observed in the winter of 1968 near Gainesville, Florida, in several habitats (Fig. 2). These included mesic and xeric hammocks, characterized by laurel oak (*Quercus laurifolia*), live oak (*Q. virginiana*), and slash pine (*Pinus caribaea*); and a riparian vegetation comprised of speck-



FIG. 1. The breeding habitat of the Red-eyed and Yellow-throated Vireos. Above: The flood-plain forest at the Patuxent Research Center. Note the configuration of the trees comprising the canopy layer and the lower plants which form the understory in late spring. Below: The deciduous upland terrace forest in summer at the Chesapeake Bay Center for Environmental Studies. Note the density of the foliage.

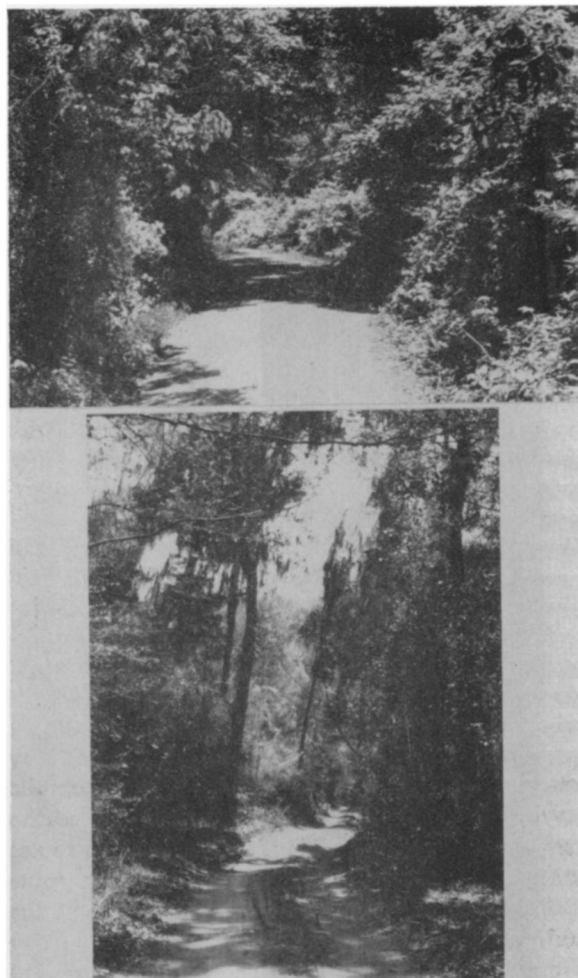


FIG. 2. Above: The dense tangle of vines, shrubs, and trees that comprises the breeding territory of a White-eyed Vireo—Chesapeake Bay Center for Environmental Studies. Below: Xeric hammock in the upper peninsula of Florida that is typical of the winter range of the White-eyed Vireo.

led alder (*Alnus serrulata*), wax myrtle (*Myrica cerifera*), and birches (*Betula* spp.).

FIELD OBSERVATIONS

From April 21 to August 23, 1967, and April 29 to August 29, 1968, vireos and their foraging associates were observed on their breeding territories at the research center and the bay center (1968 only). In addition, the foraging behavior of migrating vireos was studied at the bay center from September 11 to September 29, 1968. Data on the winter foraging behavior of White-eyed Vireos were collected from January 26 to March 1, 1968, at Gainesville, Florida.

The birds were observed with 7-by-35 binoculars; a portable tape recorder permitted the continual recording of moment-by-moment observations of feeding behavior. Descriptions were so worded that

specific events could be timed with a stopwatch during transcription. A forester's measuring instrument (altimeter) was used for determining both the heights of trees and of the birds within them.

Birds at Patuxent were color-banded to permit individual recognition. In 1967, 62 Red-eyed Vireos and five Yellow-throated Vireos were banded; and in 1968, 27 Red-eyed Vireos and five Yellow-throated Vireos. Nineteen of the 1967 Red-eyes were recaptured in 1968. When banded, 36 Red-eyes (18 males, 18 females) were weighed, aged, sexed, and the following measurements were made: length, width, and depth of the bill; length of leg, tarsus, hallux, and middle toe; and the length and area of the wings. When possible, these measurements were made with needle-nosed calipers. The wing area was determined on millimeter graph paper. Since birds were color-banded in the peak of the breeding season, adult females were recognizable by their brood patch and the adult males by their cloacal protuberance. Immature birds lack the above features; juvenile Red-eyes have brown irides. Except for singing males, or color-banded birds, sex and age differentiations were not possible in the field.

Initially, considerable time was spent in becoming familiar with the repertoire of behaviors and activity patterns of the three vireos. Base-line data on the activity of each species during the breeding season were obtained by walking predetermined routes through the entire study area. Varying the route taken between days ensured that all portions of the study area were traversed at all times of the day (from 5:30 AM to 6 PM) during each 2-week period of observation. An average of 6 hr/day was spent in the field (approximately 1,700 hr total).

The following data were recorded at each sighting of Red-eyed or Yellow-throated Vireos: color-marked individuals, location, and time. Size of the perch (trunk, limb, branch, or twig) and position (inner, middle, or outer portion of the tree) were also recorded for foraging birds. The height and species of tree and the height of the bird from the ground were noted. When a feeding bird moved more than 5 ft, the same information was recorded. The observation period was limited to 10 min. At least 60 different Red-eyed Vireos and eight different Yellow-throated Vireos were observed the first season (1967).

"Foraging behavior" is defined as any movements which are terminated by or punctuated with food-getting motions. Other information included: the maneuver(s) used to obtain food; the location of the food item; and, when possible, the identification of food items. The behavior of non-foraging birds was recorded, particularly territorial singing and defense,

courtship behavior, nest-building, and inter- and intraspecific encounters.

Making observations along the open paths reduced the difficulty of observing birds foraging high in the trees. Neither the bird's height nor position in the tree required a continual full view; a brief look often sufficed. I also moved as needed to keep the bird in view. An observation was terminated if a bird disappeared from view for more than 30 sec. The same procedures were followed for White-eyed Vireos at six specific edge situations.

Four pairs of color-banded Red-eyes were observed in detail, and data were collected on an additional 26 males and 30 females (color-banded) at the Patuxent Center to determine how individual foraging behavior compared to total species' patterns. The four pairs were observed for periods of up to 6 hr at or near the nest. Red-eyed Vireos are relatively fast-moving birds that forage as high as 75 ft in thick foliage; they are extremely difficult to keep in view for very long. Hence, the long periods of observation were necessary for collecting small bits of information. Shorter periods of time were spent collecting similar data from birds either color-marked or otherwise of known sex.

Additional methods were devised for assessing small differences in the use of foraging space by Red-eyes and their associates. For each move in a foraging sequence the following were listed: (1) estimated distance (inches or feet); (2) direction (up, down, or horizontal); (3) whether the move was followed by actual feeding; and (4) what tactic was used to procure food (hover, etc.). Interruptions by other activities, e.g., singing or preening, and the simultaneous singing and foraging of the males were also noted.

Such precise data required an unobstructed view of any bird at a distance of 50 ft or less. Long observation periods of known birds resulted in their definite habituation to the observer in a week or two. Scolding, alarm notes, and close inspection of the observer ceased, and the foraging behavior became similar to that of birds seen at great distances. Estimations of distances moved could often be verified with actual measurements and were found to be accurate within 2 inches.

Comparable data were collected for Yellow-throated and White-eyed Vireos, Redstarts, Acadian Flycatchers, fall migrants, and White-eyed Vireos in winter. Data on the latter were collected in 10 different places in central Florida. Data presented in the tables and figures were collected in Maryland unless otherwise indicated. The statistical methods used in analysis of the data are described in the appendix.

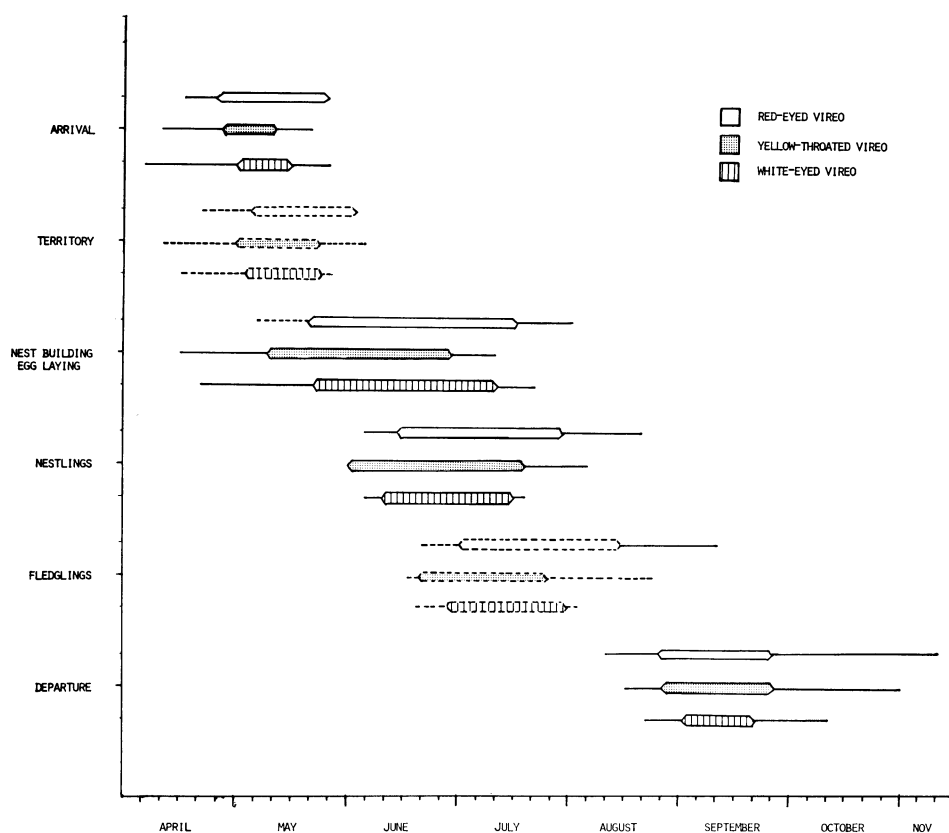


FIG. 3. Major features in the annual breeding cycles of the Red-eyed, Yellow-throated, and White-eyed Vireos in Maryland (data from Stewart and Robbins 1958 and this study). Dashed lines indicate a lack of concise data; thin lines indicate known ranges; thickened portions indicate the periods of maximum activity.

TABLE 1. Heights of nests of White-eyed, Red-eyed, and Yellow-throated Vireos^a

Item	White-eyed Vireo	Red-eyed Vireo	Yellow-throated Vireo
Mean height above ground (ft)	3.2	10.5	28.6
Number of nests	34	176	36
Range (ft)	1-10	2-70	10-60
Standard deviation	1.3	9.2	5.1
Standard error of mean	0.2	0.7	0.8

^aData from Laboratory of Ornithology, Cornell University; Division of Birds, Smithsonian Institution; this study.

THE RED-EYED VIREO

Territory size and breeding cycle

The Red-eyed Vireo weighs approximately 17 g and is primarily insectivorous. About 85% of its food is animal matter (Chapin 1925, McAtee 1926) and is characteristically gleaned from foliage in broad-leaved woods.

In Maryland, Red-eyed Vireos arrive in spring from late April to early May. Within a week follow-

ing arrival their persistent song is one of the most characteristic features of the woods. Censuses of singing males have established the territory size at the Patuxent Center to be approximately 1.3 acres per pair (Robbins, *unpublished data*), close to the size measured by others (e.g., Lawrence 1953, Southern 1958). However, Stewart and Robbins (1958) found that the number of territorial males per 100 acres can vary from 10 to 100 depending on the nature of the habitat.

The breeding cycle of the Red-eyed Vireo in Maryland is shown in Fig. 3. The clutch size is usually four, but three, or rarely five, eggs may be laid. Females are solely responsible for incubation of eggs; both sexes share in the brooding and feeding of young (females do a major portion of the former). The nest is usually built about 10 ft above the ground in the fork of a small tree, although sites as high as 70 ft have been found (Table 1). Individual records did not indicate geographic variation in the heights of nests, but considerable variation is manifest in forest structure for at least the Red-eyed and Yellow-throated Vireos.

Exploitation of the food resource

Foraging activity and tactics.—In spring and summer the Red-eyed Vireo is a common bird of Maryland's deciduous woodlands. It characteristically gleans the foliage of insects in areas where canopy is abundant and understory is moderate to dense. In such foliage Red-eyes forage at all levels. The manner of searching for food is slower paced and more deliberate than that of the wood warblers (Parulidae), and bouts of movement are punctuated with periods of searching the vicinity of leaves and

twigs. Usually food items are promptly swallowed, although on occasion larger prey, such as caterpillars, are held by a foot and eaten piecemeal.

It is customary for males to sing at all times during the day and throughout the season, even in the heat of summer. Song was frequently accompanied by foraging, although at times males simply sang from one or two perches for as long as 3 hr. Males may also forage for long periods (up to 4 hr) in complete silence, which stresses the necessity of marking for positive sex identification. Otherwise, both sexes fed

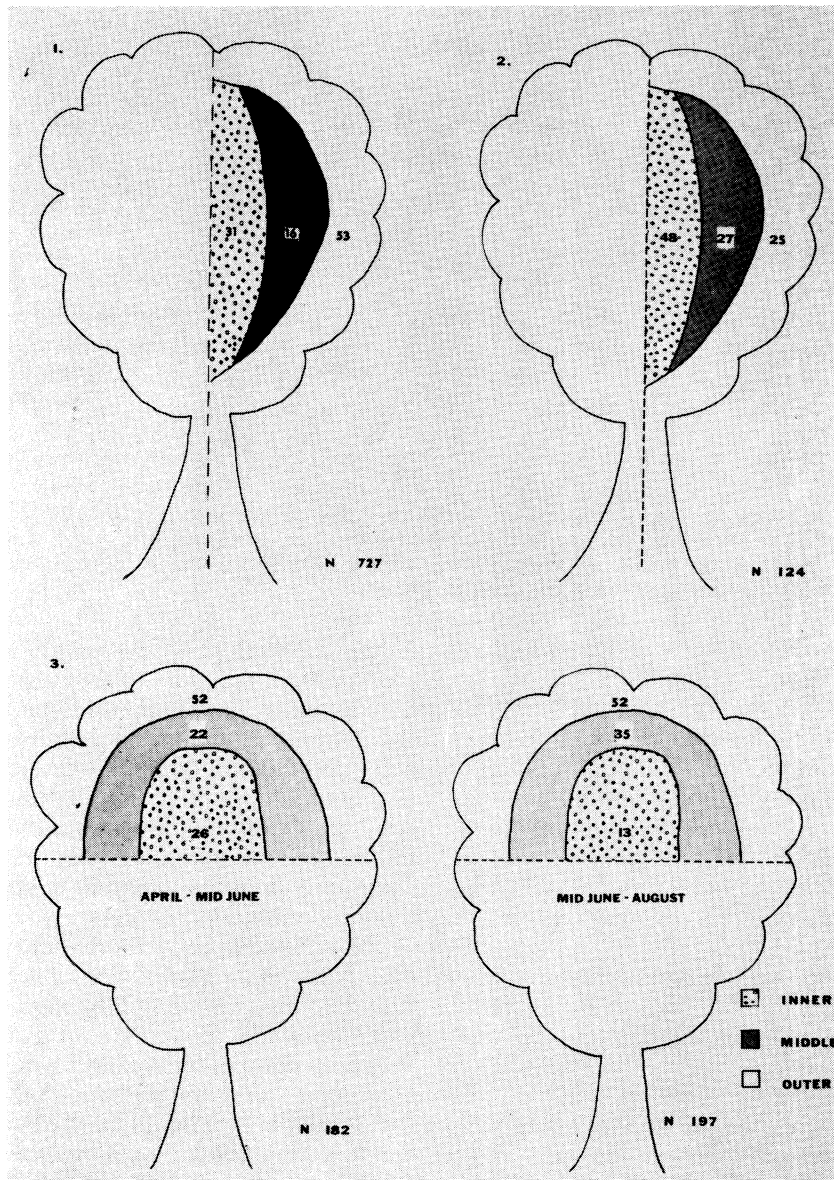


FIG. 4. A diagrammatic representation of the foraging areas of the Red-eyed Vireo (1), White-eyed Vireo (2), and Yellow-throated Vireo (3) in deciduous trees. *N* indicates the total number of timed observations of foraging birds, and the frequency distributions (percentage of observations) are indicated in the appropriate parts of the trees.

TABLE 2. The percentage of use of various foraging sites throughout the season by the Red-eyed, Yellow-throated, and White-eyed Vireos

Category	Red-eyed Vireo		Yellow-throated Vireo		White-eyed Vireo	
	April-mid-June	Mid-June-August	April-mid-June	Mid-June-August	April-mid-June	Mid-June-August
Trunk	1.0	0.0	3.0	0.0	0.0	1.0
Limb (3 inches in diameter)	1.0	0.6	1.0	2.0	1.0	0.0
Branch (1/2-3 inches in diameter)	33.0	40.0	38.0	62.0	65.0	63.0
Twig (1/2 inch in diameter)	56.0	40.0	42.0	26.0	31.0	32.0
Hovering	9.0	19.4	12.0	9.0	3.0	4.0
Number of observations	392	425	214	212	118	89

TABLE 3. The percentage of use of various foraging tactics by the Red-eyed, Yellow-throated, and White-eyed Vireos, Redstart, and Acadian Flycatcher

Tactic	Red-eyed Vireo (Males)		Red-eyed Vireo (Females)		Yellow-throated Vireo	White-eyed Vireo	Redstart	Acadian Flycatcher
	April-mid-June	Mid-June-August	April-mid-June	Mid-June-August				
Gleaning	72	41	50	41	50	69	41	34
Hovering	22	33	41	40	17	23	19	19
Hawking	2	10	0	5	17	0	24	41
Pecking	4	16	9	14	17	8	16	6
Number of tactics observed	109	112	97	128	48	60	70	133

throughout the day with equal intensity. Foraging activity was low in the early morning hours.

Different portions of the tree (with respect to the trunk) were preferentially used by the Red-eyed Vireo for foraging (Fig. 4). One-half of the time was spent feeding in the outer portions, one-third in the inner core, and the remainder in the middle portion. (Records of varying duration were weighted to determine average periods spent foraging at different locations). As the season progressed, foraging sites (trunk, limbs, branches, twigs) were utilized with changing frequency (Table 2).

Foraging tactics, i.e., any movement resulting in the procurement of food, include gleaning (picking an arthropod from a leaf surface), hovering under or next to a leaf, pecking from branches or twigs, and hawking (aerial sallies to capture flying insects). The frequency of use of each tactic was subject to seasonal change (Table 3), most likely reflecting changes in arthropod abundance, diversity, and distribution and changing energy demands during the feeding of young. Gleaning was the predominant tactic, but hovering, and to some extent hawking and pecking, were more frequent later in the season. These conclusions are based on timed observations of approximately 60 different color-marked males and females. Differences between the sexes are presented below and in Table 3.

Sexual divergence in foraging behavior.—In 1967 more females than males were captured in mist nets that were approximately 12 ft high. Of the 215 Red-eyed Vireos captured in 1967, 130 of the 191 birds of known sex were females. Since it is presumed that the sex ratio for passerine birds is close to 1:1, or

slightly higher for males (Kolman 1960, MacArthur 1961), this observation led to the hypothesis that female Red-eyed Vireos forage more frequently at lower levels than males. Banding records from this plot for 8 previous years revealed the same tendency. In each year the ratio of females to males banded at low levels was approximately 1.6 to 1.0 (range, 2.1 to 1.0–1.5 to 1.0). In 1967 the assembled data on the height of foraging activity of banded and un-

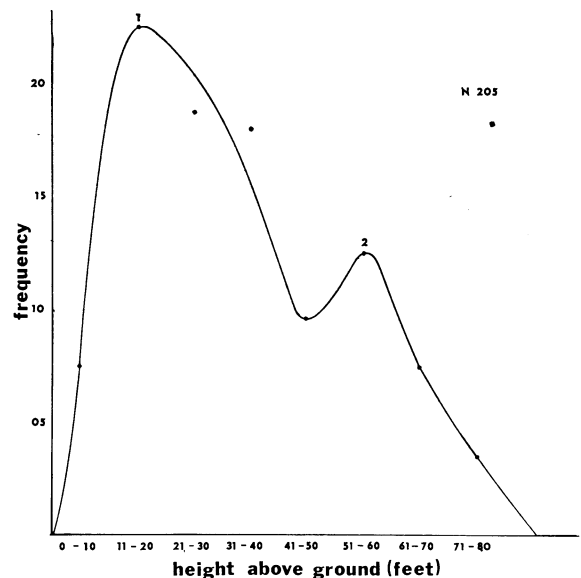


FIG. 5. Foraging activity of Red-eyed Vireos at various heights above the ground—Patuxent Research Center, 1967 breeding season. The curve includes data from birds of unknown sex as well as singing and foraging males. The bimodal curve (peaks 1 and 2) corresponds with the sexual separation in feeding-activity patterns.

banded Red-eyed Vireos revealed a bimodal distribution (Fig. 5), adding further strength to the above hypothesis. Lawrence (1953) noted that males often foraged in the crowns of trees, and females near or on the ground, and Sutton (1949) found that Red-eyes spent much time in the lower half of the forest and often fed at little more than eye level.

Data from color-marked Red-eyed Vireos of known sex that were observed in the 1968 breeding season present conclusive evidence of a sex-related difference in heights of foraging activity. Four pairs of Red-eyed Vireos were watched throughout the season, and about 30 males and 30 females were observed at least once. The curves (Fig. 6) represent percentages of the total observations. The observations on marked birds permitted the elimination of two alternative explanations for these curves: (1) that all birds of one sex feed at the same level at a given time of day, and (2) that different individuals feed at one height and each curve reflects a frequency of differing behavioral phenotypes. (There was a tendency for males to be active higher in the trees in early morning hours (Table 4), but at that time the primary activity was singing; little time was devoted to foraging.) A third, more plausible, explanation was that all birds of the same sex feed similarly, and the probability of seeing a bird at a given height is a function of the bird's movement. The assembled data on marked birds provided the necessary proof for this alternative. Male and female Red-eyes spent 64.2% of their time foraging at different levels and 35.8% of their time foraging at the same heights (see shaded area of Fig. 6).

Patterns and timing of movements.—Detailed measurements of consecutive foraging movements were collected to determine quantitatively how the Red-eyed Vireo uses space. The preliminary hypothesis

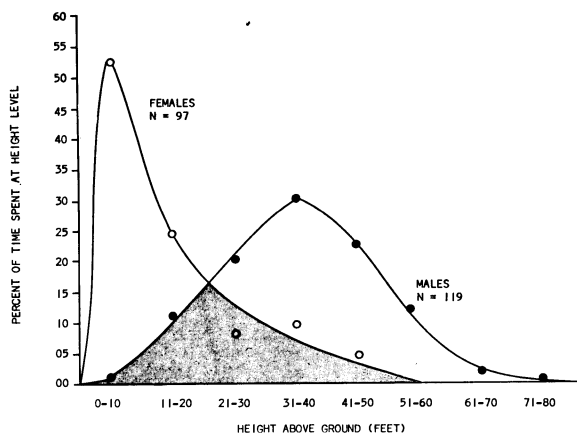


FIG. 6. Separation by height of foraging male and female Red-eyed Vireos. (Mean height for males, 37.1 ft; S.D., 12; S.E. 1.0; range 9-75. Mean height for females, 14.2 ft; S.D., 10.8; S.E. 1.1; range 2-50.)

TABLE 4. The daily sequence of height distribution of singing and foraging male Red-eyed Vireos

Hour of day	Mean height (ft)	Range (ft)	Number of observations	SD	SE
5AM-8AM	50	25-77	30	17	3.1
8AM-11AM	34	7-72	115	16	1.5
11AM-2PM	38	6-70	92	12	1.2
2PM-6PM	36	11-70	46	16	2.2

was that species-specific, non-random patterns of searching behavior are exhibited by this and other species, and that the patterns are responsive to environmental pressures.

The estimation of the distance of each foraging movement showed two non-overlapping size classes: moves from 0 inches (in place) through 6 inches ("hops"); and those from 1 ft through 10 ft ("flights"). Figure 7 shows their frequency distribution. Fifty-seven per cent of the foraging moves of Red-eyed Vireos were hops. This value did not vary significantly either with sex or with season. The pattern of hops and flights was random for both males and females early in the breeding season (April-mid-June). That is, whether a hop or flight had just been performed had no bearing on whether the next movement was a hop or a flight. This was determined by plotting the curve generated from the 0.57 frequency of hopping (Fig. 7), and which predicts the number of hops expected to appear together, assuming movement occurs in a random manner (i.e., one hop in a row, two hops in a row, etc., or the number of hops uninterrupted by a flight). The data are a good fit to this curve (Fig. 8 A and B). (See the Appendix.)

From mid-June to August the pattern of hops and flights became non-random for females. Longer sequences of hops (series of consecutive hops) occurred than were predicted from the probability

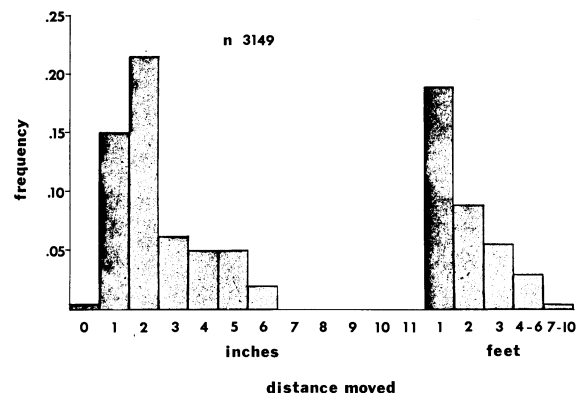


FIG. 7. Frequency distribution of distances moved during the foraging of the Red-eyed Vireo. Hops are expressed in inches and flights in feet. The frequency of hopping is 0.57. Total number of foraging movements recorded was 3,149.

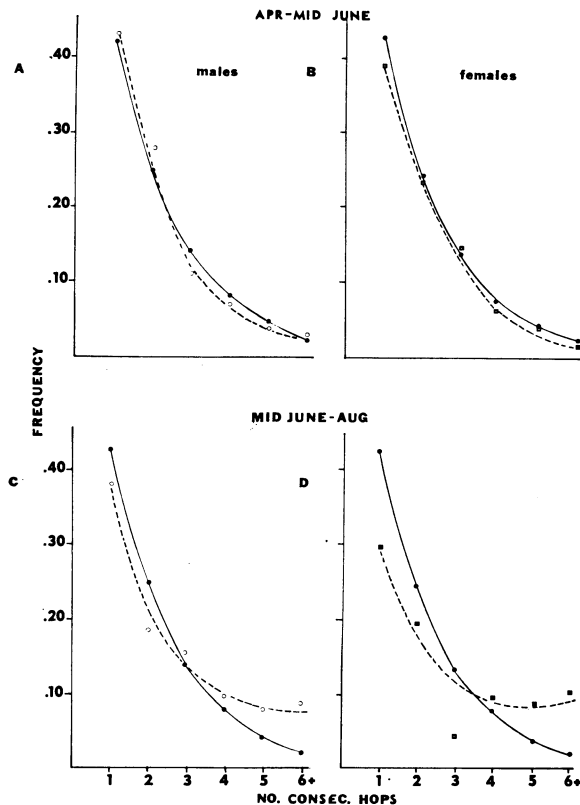


FIG. 8. Seasonal changes in the number of consecutive hops during the foraging of the Red-eyed Vireo. The solid lines represent the expected frequencies of consecutive moves (based on the 0.57 frequency of hopping); the dotted lines represent the frequencies actually observed. Early in the breeding season (A and B) the number of consecutive hops was random and followed the expected geometric distribution for both males and females (χ^2 used for determination). Later in the season (C and D) the number of consecutive hops observed departed from the expected geometric distribution (χ^2 : males, $P < .10$; females, $P < .01$).

curve (Fig. 8); likewise fewer solitary hops occurred than were predicted. A chi square showed that this was significant at the 1% level; the same trend occurred for males, but only at the 10% level of significance (Fig. 8 C and D).

The directional components of foraging moves of Red-eyed Vireos (vertical vs. horizontal) occurred in a non-random manner. This species had an 0.46 frequency of vertical movements. A curve generated from this frequency of vertical moves allowed the prediction of the probability of occurrence of runs consisting of different numbers of consecutive vertical movements. Females showed a significant departure from this curve ($P < .001$), and their vertical movements once started tended to continue (Fig. 9). When foraging was the sole activity, males showed the same tendency of vertical sequences ($P < .01$) (Fig. 9). However, those vertical sequences for males

both singing and foraging did not differ significantly from the expected. When the same analysis was performed for horizontal sequences based on the 0.54 frequency of horizontal movements, the foraging males (Fig. 10) showed a significant departure from the expected curve ($P < .001$); singing and foraging males and foraging females did not. Thus there emerged a consistent pattern of both vertical and horizontal moves of foraging males, once either direction of movement was initiated.

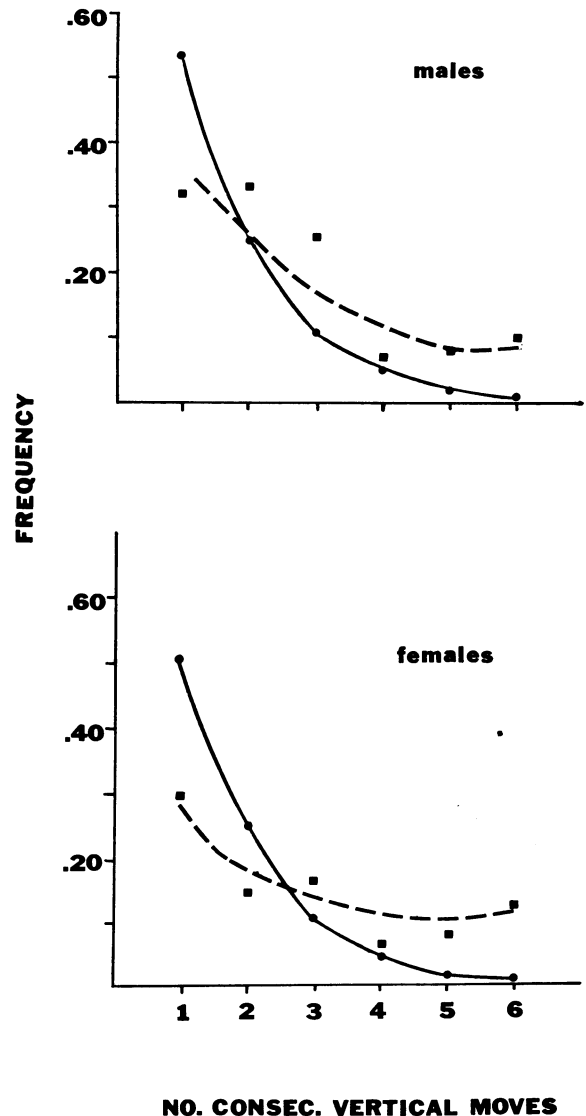
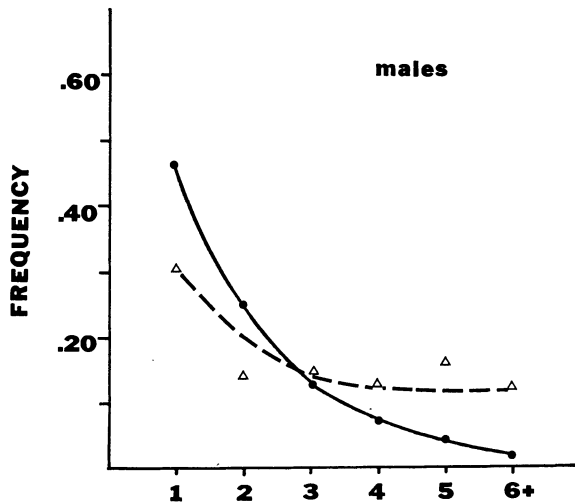


FIG. 9. The frequency of numbers of consecutive vertical moves for foraging Red-eyed Vireos. The solid lines represent the expected frequencies of consecutive vertical moves (based on the 0.46 frequency of vertical movement); the dashed lines represent the numbers actually observed. For both sexes the numbers of consecutive vertical moves observed differed significantly from the expected geometric distribution (χ^2 : males, $P < .01$; females, $P < .001$).



NO. CONSEC. HORIZONTAL MOVES

FIG. 10. The frequency of numbers of consecutive horizontal moves for foraging male Red-eyed Vireos. The solid line represents the expected frequencies of consecutive horizontal moves (based on the 0.54 frequency of horizontal movement); the dashed line represents the frequencies actually observed. For the males the numbers of consecutive horizontal moves actually observed differed significantly from the expected geometric distribution (χ^2 : males, $P < .001$).

To test the possible relationship between distance and direction of movements, the vertical and horizontal shifts in position were grouped into categories of "hop" or "flight." During the period April–mid-June, the hops of both males and females were associated with horizontal and upward movements and their flights were linked with downward movements (males, $P < .05$ and females, $P < .02$). From mid-June through August this association was more marked (males and females, $P < .001$).

Examination of many individual foraging sequences has revealed a major difference in strategy between males and females. Males make many moves at one stratum, and their vertical moves often appear to shift the bird to a new level rather than to involve major searching tactics. The profile of female sequences, on the other hand, shows many more peaks and troughs and in general more vertical activity (Fig. 11 A and B).

The preceding data demonstrated that males forage significantly higher than females. This separation should be a consequence of differences in the foraging patterns of each sex. Thus, for males the time intervals following a substantial upward move (≥ 2 ft) should be significantly greater than those following the subsequent downward move (≥ 2 ft). A move of 2 ft was arbitrarily chosen as a lower

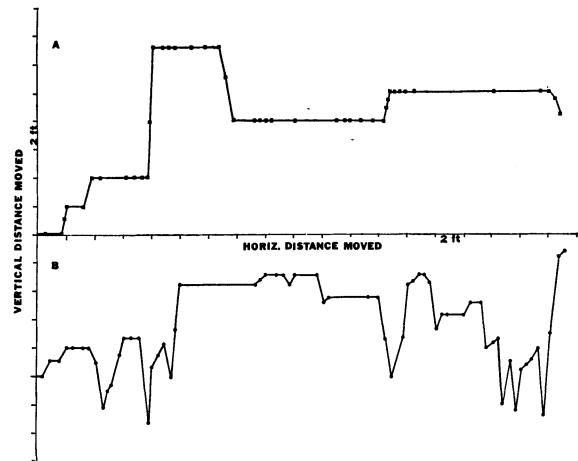


FIG. 11. The foraging patterns of male (A) and female (B) Red-eyed Vireos based on observations of single individuals. Sequences of movements of other individuals follow these typical patterns.

TABLE 5. The time intervals (seconds) between long vertical moves of foraging Red-eyed Vireos (number of observed sequences in parentheses)

Item	Male	Female
Mean time between moving up 2 or > 2 ft and moving down 2 or > 2 ft	70 (103)	21 (132)
Mean time between moving down 2 or > 2 ft and moving up 2 or > 2 ft	24 (105)	40 (125)
Ratio of upper to lower time	2.9 to 1	1 to 1.9

limit because it is slightly above the mean flight distance of 1.5 ft. If a height difference is to be maintained, then the reverse must be true for the female. Data support this hypothesis (Table 5). Moves of greater than 10 ft were not considered foraging moves and thus were not counted as parts of feeding sequences. They did, obviously, contribute to shifting positions to new zones.

Behavioral divergence and capture of prey.—The rate of foraging (number of moves per minute) was used as one parameter of feeding behavior. Females foraged faster than males, particularly during spring and late summer (Table 6). Females captured a mean of 2.1 items per minute (number of observations = 127, range = 1.0–6.3, $SD = 1.2$), whereas the mean number of items taken per minute by males was 1.3 (number of observations = 97, range = 0.2–4.0, $SD = 1.0$). These figures are based on sightings of arthropods actually taken as well as those of presumed captures after food-getting motions (pecking at leaves or twigs, hawking, hovering). Together they serve as valid approximations. These figures did not

TABLE 6. Seasonal foraging rates of Red-eyed Vireos

Sex	Age	Number of observations	Activity	Moves per minute		
				April-May	June	July-August
Female.....	Adult	150	Foraging	19.4±4.0 ^a	18.2±2.0	23.1±2.0
Male.....	Adult	131	Foraging	15.0±1.8	15.0±1.8	15.0±1.8
Male.....	Adult	206	Singing and foraging	10.4±2.5	14.2±2.5	13.4±2.6

^aRate ± twice the standard error of the mean.

differ significantly with season. Furthermore, there were no differences between females with and without broods. In her study of Red-eyed Vireos in Ontario, Lawrence (1953) also found that there was no significant increase in the rate of feeding of young by parents, but that the size of meals was enlarged. The above data indicate that the ratio of female to male rate of foraging was 1.3/1; ratio of rate of prey capture was 1.6/1. Males and females moved approximately 21 ft/min.

Analysis of moves that lead to the capture of prey (200 attacks by males and 200 attacks by females) revealed that in females this was upward (55%) and horizontal (33%). In males, the move prior to capture of prey was horizontal (52%) and upward (31%). The same analysis was carried out for the move following feeding; the predominant direction of movement for females was downward (63%), whereas that for males was horizontal (53%).

To determine whether the capture of prey had an effect on the subsequent sequence of foraging, the three moves preceding and following feeding were examined. In both sexes the moves before feeding were nearly always hops, and those following were generally flights. Of course, when the young are being fed, one might suspect that a flight would follow the capture of prey. Nonetheless, this pattern was present throughout the breeding season and was significant for both males ($P < .05$) and females ($P < .02$).

The major foraging tactics have been described (Table 3). Females hovered more than males. Males gleaned more than females. Gleaning dominated the feeding behavior of both sexes during early and mid-summer. Later in the summer pecking insects from twigs and branches increased in both sexes, as did hawking activity; in males, hovering increased slightly.

Foods eaten during the breeding season.—In his detailed analysis of over 560 stomachs, Chapin (1925) found that the Red-eyed Vireo feeds primarily on insects and some spiders for most of the breeding season. Late in the summer and in fall berries and fruits are eaten more frequently. During the period April–October, 85% of the food was an-

imal matter, and 15% was plant material. For example, Chapin's July sample was as follows:

	Approximate percentage (by individual prey)
Coccinellidae	2.7
Other Coleoptera	15.3
Caterpillars	44.4
Other Lepidoptera	2.7
Pentatomidae	4.1
Other Hemiptera	7.0
Hymenoptera	7.0
Diptera	4.1
Other insects	3.5
Spiders	5.6
Plant matter	3.5

Differences in size or kinds of foods taken by males and females were not considered. Since the sexes differ in their exploitation patterns and foraging positions in the woodland, corresponding differences in the diet (size class of item, species differences, frequency of occurrence, etc.) are a distinct likelihood.

Foraging behavior of autumn migrants

From September 11 to 29, 1968, foraging flocks of migrating Red-eyed Vireos of mixed sex and age were observed. Their behavior differed markedly in three major respects from that of birds during the breeding season:

1) The birds fed in mixed flocks comprised of as many as 30 Red-eyed Vireos, several White-eyed Vireos, wood warblers, Carolina Wrens, and other species. The total flock size ranged from 15 to approximately 60.

2) The primary habitat types utilized were edge situations of low (20–30 ft) vegetation rather than mature deciduous woodland.

3) Berries comprised over 40% of the diet and replaced a diet containing 85–90% arthropods. These marked differences were accompanied by alterations in the foraging pattern.

The foraging movements were a combination of sluggish motions alternating with rapid darting

flights from tree to tree, not necessarily combined with feeding. The Red-eyed Vireos within a mixed flock moved together slowly down the roadside vegetation and wood margins, and individual birds were often within a few inches of each other. The rather slow overall rate of movement, 13.3 moves/min, reflected the pace mentioned above. All portions of the tree were used equally (i.e., inner, middle, or outer), as were twigs and branches (169 observations). Gleaning of insects or fruits was the most prominent foraging maneuver, with some interspersed hovering, particularly under clumps of berries (70% and 21%, respectively; $n = 72$). Pecking and hawking were negligible (6% and 3%, respectively). Although a few Red-eyed Vireos were seen foraging in stands of large deciduous trees, the majority foraged in the edge situations. The range of feeding heights was great (3–55 ft), but the mean was low, 14.4 ft (SD = 11.1, SE = 2.3, $n = 35$).

The same 0.57 frequency of hopping (and 0.43 frequency of flying) observed earlier during breeding was continued at this time. Similarly, the frequency distribution of hops and flights present during the breeding season did not change (Fig. 7). The pattern of hops and flights was non-random ($P < .001$), with many more sequential hops than would be expected from the earlier described 0.57 frequency.

Again, Red-eyed Vireos moved vertically 46% of the time and horizontally the remainder. The probability curves generated from these frequencies (refer to Fig. 9 and 10) show that the pattern of horizontal movements was non-random, and that these tended to continue once started ($P < .02$). The number of consecutive vertical moves, on the other hand, did not differ significantly from the expected, nor was the relation of the distance moved (hop or flight) to its direction (vertical or horizontal) significant. Moves preceding feeding ($n = 72$) were predominantly horizontal and upwards (44% and 35%, respectively); post-feeding moves ($n = 72$) were predominantly horizontal and downwards (53% and 31%, respectively). The same trends were present in the breeding season. The three particular moves preceding and following a specific capture were examined. Hops were nearly always associated with both pre-feeding and post-feeding actions ($n = 216$ and 216, respectively), in contrast to the nearly constant flight which followed feeding during the breeding season.

During fall migration Red-eyes were seen taking the fruits of wild cherry, sassafras, mulberry (*Morus rubra*), wild grape (*Vitis vulpina*), and poison ivy. Other plants present were tulip, Japanese honeysuckle, trumpet vine (*Campsis radicans*), and pokeberry (*Phytolacca americana*). Birds were observed

taking food on 72 occasions; on 30 of these, berries were taken, and on the remainder presumably arthropods were captured.

Seventeen Red-eyed Vireos were collected from several flocks to determine sex and age ratios of the migrating birds. The ratio of immatures to adults and of males to females was nearly 2:1 in both cases. Two males and four females were adults. From this small sample it can be estimated that the flocks were composed largely of immature birds and that the sex ratio was markedly disproportionate.

Analysis of measurements

Measurements of structures possibly related to foraging (bill, feet, wings, legs) were made in the field and from skeletons. The following measurements were taken with needle-nose calipers: bill length (exposed culmen); bill width (tomial width at the anterior margin of the nares); bill depth (the culmen to the lower edge of the ramus over the anterior margin of the nares); the length of the femur, tibio-tarsus, and tarso-metatarsus. Additional measurements made with a millimeter ruler were: wing length (the relaxed wing from the wrist to the tip of the longest primary); and the middle toe and hallux (each fully extended from the tip to the center of the foot). Wing area was obtained by tracing an outline on millimeter graph paper such that the outermost primary made a right angle with the body, allowing the other primaries and secondaries to fall naturally from that point (after Baldwin, Oberholser, and Worley 1931). The weights were taken on a triple beam balance.

Males and females showed no significant differences in size of any structure except wing length and area (Tables 7 and 8). The females had shorter, broader wings.

THE YELLOW-THROATED AND WHITE-EYED VIREOS

Territory size and breeding cycle

In the eastern United States during the breeding season, the Yellow-throated and the White-eyed Vireos are sympatric with the Red-eyed Vireo. Yellow-throated Vireos, weighing about 16 g, are slightly smaller than Red-eyed Vireos. Their primary food is insects gleaned from leaves; only 1.7% of the diet is plant material (Chapin 1925). This species usually breeds in forests with a partially opened canopy (Stewart and Robbins 1958) and occurs regularly in such habitat with the Red-eyed Vireo. At the northern periphery of its range, however, populations of the two species exhibit "lateral separation" in woodlands of varying character (Hamilton 1962, James 1967).

The Yellow-throated Vireo is usually uncommon,

TABLE 7. Measurements of breeding Red-eyed Vireos, Patuxent Research Center (all values are means, $n = 18$; ranges in parentheses)

Sex	Wing area (cm ² \pm 2SE)	Wing length (mm \pm 2SE)	Bill			Foot		Weight (g)
			Length (mm)	Width (mm)	Depth (mm)	Mid toe (mm)	Hallux (mm)	
Male	46.3 \pm 1.6 (40.9–55.4)	80.4 \pm 1.0 (77–83)	9.6 (9.1–10.5)	4.4 (4.0–4.8)	4.3 (4.0–4.5)	10.8 (10–12)	10.5 (9–12)	16.8 (15.2–21)
Female	40.9 \pm 1.6 (35.3–46.9)	75.8 \pm 1.0 (74–78)	9.3 (9.0–10.5)	4.3 (4.0–4.7)	4.4 (3.9–5.5)	10.8 (9–13)	10.7 (10–12)	17.0 (15.0–21.5)

TABLE 8. Skeletal measurements of Red-eyed Vireos collected in Florida (values are means, $n = 10$; ranges in parentheses)

Sex	Femur length (mm)	Tibio-tarsus length (mm)	Tarso-metatarsus length (mm)
Male	15.3 (14.8–15.8)	25.0 (24.2–25.7)	17.9 (17.5–18.3)
Female	15.3 (14.4–15.9)	25.1 (23.0–25.9)	17.9 (16.7–18.6)

although Sutton (1949) found it more abundant than the Red-eyed Vireo on his study area in Michigan. During the breeding season its activities are confined largely to the uppermost stratum of vegetation where males defend large territories. Data from censuses of singing males at the Patuxent Center indicate a territory size of approximately 10 acres (Robbins, *unpublished data*). Elsewhere in Maryland (seven locations), the mean number of males per 100 acres was 10, range 3–19 (Stewart and Robbins 1958).

Events comprising the breeding behavior of the Yellow-throated and Red-eyed Vireos are almost completely overlapping (Fig. 3); however, there seems to be more synchrony among local (Maryland) populations of Yellow-throated Vireos than is shown for Red-eyed Vireos. The normal clutch for the Yellow-throated Vireo is also four (range, 3–5), and similarly, the nest is suspended from the joint of a forked twig. However, it is usually more than 25 ft above the ground (Table 1).

The White-eyed Vireo is the smallest of the three vireos and weighs about 12 g. Its diet of over 88% animal food, mostly insects (Chapin 1925), and its characteristic behavior mark this vireo as a typical insectivorous foliage gleaner. While breeding, this species is commonly found in edges and thickets and thus, in areas of sympatry, it is usually separated from the forest-dwelling Red-eyed and Yellow-throated Vireos. Hoiberg's suggestion (1954) that Red-eyed and White-eyed Vireos are separated only by strata is not borne out by my data. Only rarely have the two species been found in the same habitat (wood margins, or advanced stages of old-field

succession). Both species have a broad vertical foraging range that overlaps in situations where they occur together.

In Maryland, White-eyed Vireos arrive in spring from mid to late April, often preceding Red-eyed Vireos by a few days. Territory size at the Patuxent Center has been established as just under 2 acres per pair (Robbins, *unpublished data*). In three other locations (in Maryland), Stewart and Robbins (1958) found that the number of territorial males per 100 acres ranged from 28 to 40, or approximately 2.5–3.5 acres per male. Brewer (1955) indicated that White-eye territories could be as small as 0.33 acres per male.

Nests of the White-eyed Vireo are most often near the ground in shrubs or small saplings (Mengel 1965). The mean height is slightly over 3 ft (Table 1). As with the other sympatric vireo species, the clutch size is normally four (3–5 range). The breeding schedule for the White-eyed Vireo in Maryland almost totally overlaps those of the Red-eyed and Yellow-throated Vireos (Fig. 3).

Exploitation of the food resource by the Yellow-throated Vireo

Foraging activity and tactics.—The Yellow-throated Vireo forages more slowly than the Red-eyed Vireo; however, frequent long flights interrupt the brief bouts of feeding or singing (males). The song is penetrating and can be heard at distances of over 100 m. Although not as persistent a singer as either White-eyed or Red-eyed Vireos, Yellow-throated Vireos sing intermittently throughout the day and late into the summer. The restriction to a relatively narrow, high level in the forest canopy, combined with the size of the territory and the extensive movements of the birds, mitigates against continued observations of this species.

Yellow-throated Vireos foraged preferentially in the outer portions of trees, increasing their use of the middle parts as the season progressed (Fig. 4). The choice of specific foraging site also underwent a seasonal change, and the latter half of the breeding period was characterized by a shift from the use of

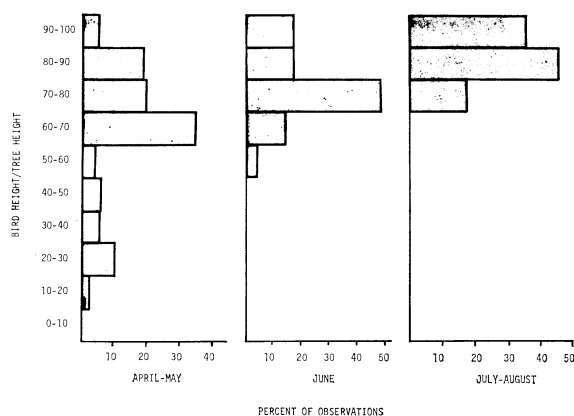


FIG. 12. Seasonal change in the height distribution of foraging activity of the Yellow-throated Vireo. (Number of observations for April-May, June, and July-August were 70, 65, and 15, respectively. Mean heights in feet \pm S.D. = 39.2 ± 6.6 , 53.1 ± 7.0 , and 63.9 ± 8.2 .)

twigs to branches (Table 2). The amount of time spent feeding at or near the tops of trees also increased as the season progressed (Fig. 12).

Gleaning was the predominant foraging tactic (Table 3), and hovering, hawking, and pecking were secondary. No seasonal change in the frequency of use of these tactics was observed. The data are based on 2-min observation periods of at least eight different birds.

Patterns and timing of movements.—Estimates of the distance of each movement in a foraging sequence revealed that the moves of the Yellow-throated Vireo fell into two non-overlapping size classes similar to the Red-eyed Vireo (hops 0–6 inches, flights 1–10 ft) and with a like frequency distribution (Fig. 7). The percentage of hops was somewhat lower (48 vs. 57) and remained stable throughout the season.

The pattern of hops and flights was random throughout the breeding season (see the Appendix for method of determination); however, there was a marked directional emphasis in the foraging moves. A curve generated from the 0.30 frequency of vertical moves predicted the number of such moves expected to appear in sequence. Yellow-throated Vireos showed a significant departure from the expected ($P < .02$); longer sequences of vertical moves occurred than were predicted by use of this "random" curve (Fig. 13, top). Similar methods revealed that horizontal sequences were random for this species (Fig. 13, bottom). The grouping of vertical and horizontal moves into categories of "hop" or "flight" showed that flights were associated with vertical shifts, and hops with horizontal moves ($P < .01$). This correlation was present throughout the season.

Individual foraging sequences were plotted and revealed a pattern markedly similar to that found for

male Red-eyed Vireos (Fig. 11 A). However, the pattern for the Yellow-throated Vireo is characterized by longer uninterrupted sequences of moves in a single plane. This would be expected from the observed 0.70 frequency of horizontal movements.

The capture of prey.—As stated earlier, the rate of foraging of Yellow-throated Vireos was slower than that of Red-eyed Vireos (13.5 moves/min; $n = 115$; $SE = 1.2$), and the intervals between captures of prey greater (mean number of food items taken per minute = 1.0; $n = 125$; $SE = 1.0$). The analysis of moves preceding capture of prey ($n = 48$) revealed a predominant horizontal direction (55%). Movements after feeding also tended to be horizontal (63%). The three moves preceding and following feeding were examined (48 sets for each) to measure the effect a capture had on the subsequent foraging sequence. As in the Red-eyed Vireo, a significant number of the pre-feeding moves were hops, whereas those after feeding were flights ($P < .03$).

Analysis of measurements.—Structures possibly related to foraging were measured in the field and from skeletons. The methods used were the same as those for the Red-eyed Vireo. Although the samples were too small for critical analysis, interesting indications emerged (Table 9). Whereas the Yellow-throated Vireo is smaller than the Red-eyed Vireo in most dimensions, the bill is deeper, and the tibiotarsus, tarso-metatarsus, and parts of the foot are longer. James (1968) made measurements of Red-eyed and Yellow-throated Vireo bill parts with similar results. If the bill of the Yellow-throated Vireo is significantly stouter than that of the Red-eyed Vireo, and the feet and legs significantly longer, it may be that Yellow-throated Vireos feed on larger food items than Red-eyed Vireos. Root (1967) found poor correlation between bill size and food size. The assumption of such a correlation is made by many, but there are few data to support it.

Exploitation of the food resource by the White-eyed Vireo

Foraging activity and tactics.—Like the Red-eyed Vireo, White-eyed Vireos forage by alternating deliberate periods of searching with intervals of movement. They often forage in one area for 10–20 min and then fly 100–200 ft to an adjacent area and continue. Early in the breeding season, males sing persistently throughout the day, and foraging is interspersed with territorial defense. However, singing is rare by mid-June, the females are attending nests, and the preferred habitat of impenetrable vegetation has grown so lush as to make continued observations difficult.

Unlike the Red-eyed and Yellow-throated Vireos, this species foraged primarily in the inner portions

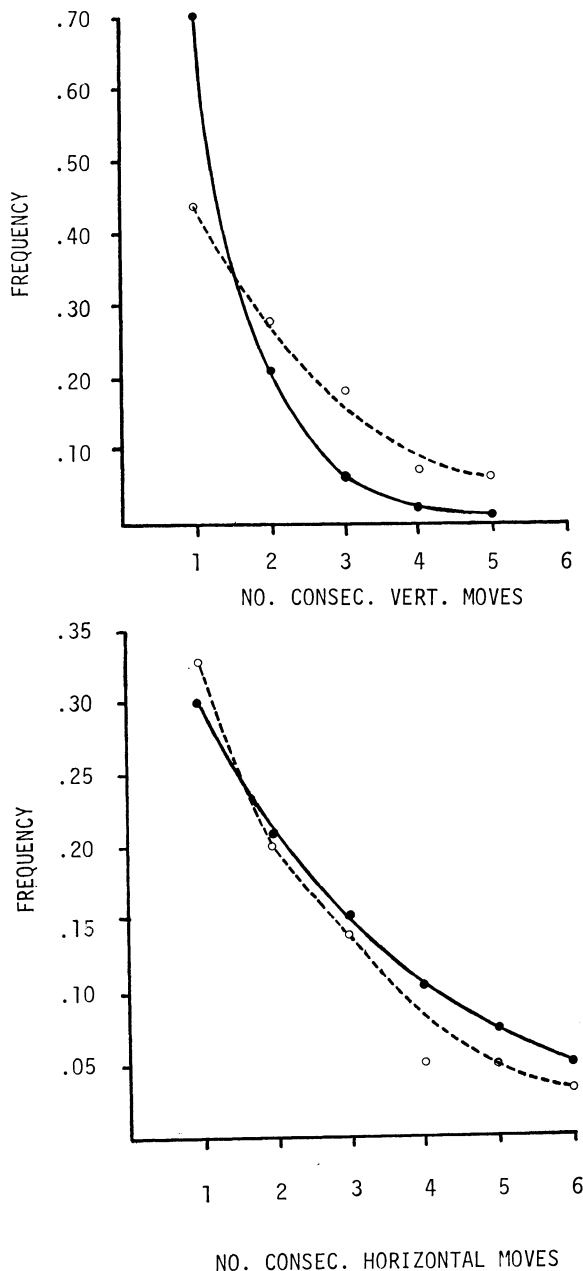


FIG. 13. (Top) The frequency of numbers of consecutive vertical moves for foraging Yellow-throated Vireos. The solid line represents the expected frequencies of consecutive vertical moves (based on the 0.30 frequency of vertical movement); the dashed line represents the frequencies observed. The numbers of consecutive vertical moves observed differed significantly from the expected geometric distribution (χ^2 , $P < .01$). (Bottom) The frequency of numbers of consecutive horizontal moves for foraging Yellow-throated Vireos. The solid line represents the expected frequencies of consecutive horizontal moves (based on the 0.70 frequency of horizontal movement); the dashed line represents the frequencies actually observed. Sequences of horizontal moves were random (followed the expected geometric distribution).

of trees and shrubs (Fig. 3), a preference shown throughout the breeding season. The choice of foraging perches did not vary, and branches were used most frequently. Food was taken less often from twigs, but still to a significant extent (Table 2). During the breeding season White-eyed Vireos had a vertical foraging range of 1.5–47 ft. Apparently feeding occurred at higher levels as the season progressed (Table 10).

Two-minute observations of approximately 10 individual White-eyed Vireos revealed that gleaning was the principal foraging tactic and that hovering and pecking were less common (Table 3). A White-eyed Vireo was never seen performing a hawking maneuver, although this was reported by Crowell (1962), who also noted this species occasionally foraging on the ground. On several occasions large arthropods were anchored by a foot while being eaten, instead of being swallowed directly. This was also observed by Nolan and Wooldridge (1962).

Patterns and timing of movements.—Foraging movements for the White-eyed Vireo, like the Red-eyed and the Yellow-throated Vireos, were divisible into two non-overlapping size classes: hops (0–6 inches) and flights (1–10 ft). The total frequencies of hopping and flying, 0.51 and 0.49, remained stable throughout the breeding season, but shifted markedly in winter (see below). Whether the winter population is the same group as the summer one is not known, however. The frequency distribution of hop and flight distances was not significantly different from that of the Red-eyed Vireo (Fig. 7). Both hops and flights occurred in random order throughout the season, although there was a slight trend ($P < .10$) for more flights to be made in a sequence.

The White-eyed Vireo had a 0.57 frequency of vertical movements. Sequences of such moves occurred randomly (Fig. 14, top). On the other hand, longer sequences of horizontal moves occurred than were predicted for this species (Fig. 14, bottom). When vertical and horizontal shifts in position were grouped into categories of “hop” or “flight,” hops were found to be significantly associated with upward moves, and flights with horizontal and downward shifts, throughout the breeding season ($P < .02$).

Plotting individual foraging sequences revealed a consistent pattern of foraging for this species: a stepwise series of upward hops and horizontal flights alternated with larger downward flights. Searching for prey was associated primarily with the upward and horizontal shifts, whereas downward movements did not usually result in exploration for food items.

The capture of prey.—White-eyed Vireos (unknown sex) had a rate of foraging generally similar to Red-eyed Vireos (17.8 moves/min; $n = 93$; $SE = 0.9$). The mean capture rate (1.2 items/min;

TABLE 9. Measurements of the Yellow-throated Vireo (ranges in parentheses)

Mean wing area ^a (cm ²) (n = 2)	Mean wing length ^a (mm) (n = 10)	Bill (mm) ^b			Foot (mm) ^b		Leg (mm) ^c		
		Length	Width (n = 5)	Depth	Mid toe (n = 5)	Hallux	Femur	Tibio-tarsus (n = 6)	Tarso- metatarsus
36.7	75.7 (73–78)	8.6 (8.2–9.2)	4.2 (3.8–4.5)	4.9 (4.7–5.2)	15.3 (14.5–16.0)	14.4 (14–15.5)	14.7 (14.3–15.3)	25.7 (25–26.8)	18.6 (18.2–19.6)

^aBreeding birds, Patuxent Center.^bBreeding birds, Patuxent Center, and specimens from Tower kill at Leon, Florida.^cFrom skeletal material; birds collected in Florida.

TABLE 10. Seasonal changes in the distribution by height of foraging White-eyed Vireos

Month	Mean height (ft)	Range (ft)	Number of observations	SD	SE
April–May	13.5	15–25	38	6.0	0.9
June	19.3	2–47	31	5.7	1.0
July–August	23.0	15–35	9	0.4	2.6

$n = 30$; range = 0.6 – 4.0; $SD = 0.9$) was significantly lower than that of female Red-eyes and similar to male Red-eyes. These rates for Red-eyed and White-eyed Vireos were measured at the same times of year, but represent behaviors in different habitats.

The moves leading to captures were predominantly in the upward direction (62%, $n = 30$). Moves after feeding (for 30 attacks) tended to be both downward and horizontal (42% and 52%, respectively). Examination of the three moves preceding and following feeding revealed a trend (significant at the 7% level) for White-eyed Vireos to move in hops before finding prey and to fly following a capture. This strategy is also used by, and more marked in, the two sympatric vireos (significant at a higher level).

Winter observations.—Observations of White-eyed Vireos on their winter range in northern Florida showed that the foraging patterns of these birds in winter and summer differ markedly (Table 11). During breeding there was a marked horizontal emphasis (ascending steps with prominent plateaus and sharp descents), whereas in winter the emphasis was a conspicuous vertical one (longer sequences of upward hops, less prominent plateaus, and again, sharp descents). The overall frequency of hopping was significantly higher in winter.

Analysis of measurements.—Measurements of structures possibly related to foraging were made from specimens collected in Florida and from skeletons. The methods used were the same as those for Red-eyed Vireos. The White-eyed Vireo is smaller than the Yellow-throated Vireo in all dimensions measured. With the exception of the hallux, middle toe, and tarso-metatarsus, the White-eyed Vireo is also smaller than the Red-eyed Vireo in all structures measured (Tables 12 and 13).

EXPLOITATION PATTERNS OF THE AMERICAN REDSTART AND THE ACADIAN FLYCATCHER

Data were collected on the foraging strategies of the American Redstart and Acadian Flycatcher, two of the several insectivorous species which occur regularly in deciduous woodlands in Maryland together with the Red-eyed and Yellow-throated Vireos. Although a large proportion of the foraging maneuvers of both of the former species are aerial, they also glean and can be considered members of the “foliage-gleaning guild” (Root 1967). Since the niche relations of species with such adaptations overlap those of the vireos, and they utilize a common space, knowledge of them is germane to this study.

American Redstart

The Redstart is a small wood warbler weighing approximately 9 g. It breeds commonly in deciduous woods near water (Bent 1953) where, at the Patuxent Center, at least eight individuals were observed during the 1968 breeding season. The foraging pattern of this species is one of rapid, continuous movement. Long periods of searching of the surrounding foliage, characteristic of the vireos, are absent. Redstarts spend more time actively exploring single trees before flying to a neighboring one to continue the same pattern. They showed no obvious preference for certain portions of trees (inner, middle, and outer). Insects were rarely taken from trunks or limbs; the twigs and branches were the primary foraging sites. The vertical range of foraging was 2–50 ft (mean = 26.7 ft, $n = 38$, $SD = 9.0$, $SE = 1.4$). These general features remained stable throughout the season.

The Redstart bill is wide and flat surrounded by well-developed rictal bristles, and thus it is suited for capturing flying insects. The distribution of foraging tactics is similar to those of the Red-eyed and Yellow-throated Vireos (Table 3), but the broad, flat bill and small size suggest that Redstarts select different foods.

The two size classes of foraging movements of the Redstart are the same as those of the three vireos: hops, 0–6 inches; and flights, 1–10 ft. The frequency of hopping (0.63 vs. 0.48–0.57) was greater, however. Analysis of the patterns of hopping, based on

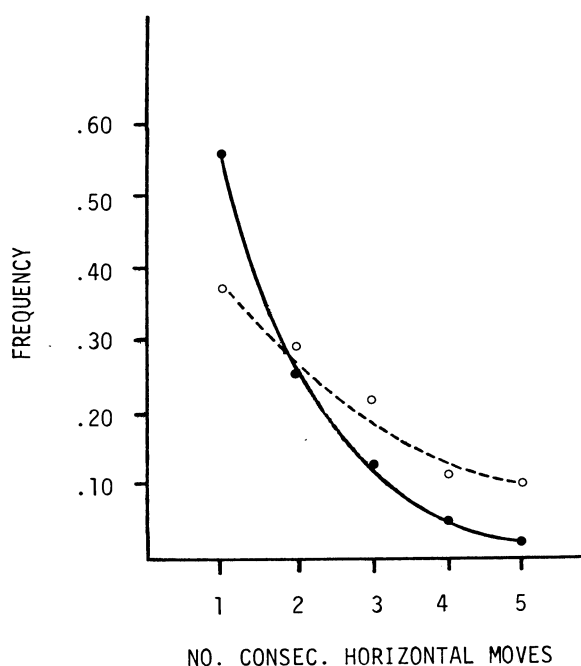
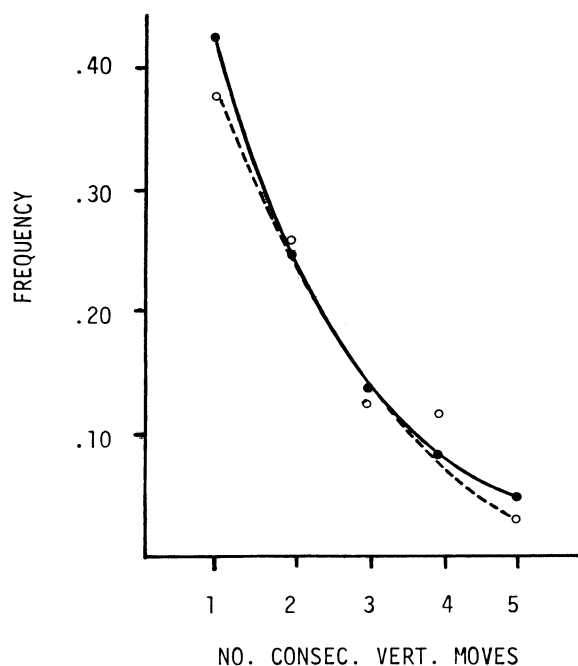


FIG. 14. (Top) The frequency of numbers of consecutive vertical moves for foraging White-eyed Vireos. The solid line represents the expected frequencies of consecutive vertical moves (based on the 0.57 frequency of vertical movement); the dashed line represents the frequencies actually observed. Sequences of vertical moves were random (followed the expected geometric distribution) for this species. (Bottom) The frequency of numbers of consecutive horizontal moves for foraging White-eyed Vireos. The solid line represents the expected frequencies of consecutive horizontal moves (based on

TABLE 11. Summer and winter foraging behavior of the White-eyed Vireo

Behavior	Summer (Maryland)	Winter (Florida)
Mean foraging height in feet (range)	17.3 (1.5-47.0)	16.7 (0.5-64)
Frequency of hopping	0.51	0.70
Size of hops	0 - 6 inches	0 - 6 inches
Long sequences of consecutive hops	Not significant	Not significant
Frequency of flying	0.49	0.30
Length of flights	1 - 10 ft	1 - 10 ft
Long sequences of consecutive flights ($p < .10$)	Slight trend	Not significant
Frequency of vertical moves	0.57	0.55
Long sequences of consecutive vertical moves	Not significant	Significant ($p < .01$)
Frequency of horizontal moves	0.43	0.45
Long sequences of horizontal moves	Significant ($p < .02$)	Not significant
Association between distance and direction of movements	Hops correlated with upward moves; flights, with downward and horizontal	Hops correlated with upward moves; flights, with downward and horizontal
Rate of foraging	17.8 moves/min ($n = 93$ sequences; $2 SE = 1.8$)	18.8 moves/min ($n = 39$ sequences; $2 SE = 3.0$)

the 0.63 frequency of such movements, revealed that significantly more hops were taken in sequence than would be expected by chance (χ^2 , $P < .001$). This observation was consistent throughout the season. Redstarts moved vertically 52% of the time, and horizontally the remainder. Both vertical and horizontal moves occurred non-randomly (χ^2 , $P < .01$ for each). Longer runs of both horizontal and vertical moves occurred than were predicted (see Appendix for method of analysis). The grouping of horizontal and vertical shifts into categories of "hop" or "flight" revealed no significant associations. There was no consistent correlation between the length of a movement and its direction.

Data from many individual foraging sequences revealed an overall pattern of ascending or descending spirals in single trees. The irregular spirals were comprised of continuous moves toward either the trunk or outer branches, but had a steady vertical emphasis. Redstarts foraged rapidly, 29.4 moves/min ($n = 32$ sequences), with no specific direction associated with pre- and post-feeding movements. However, when the three moves preceding and following feeding were examined (60 sets for each), pre-feeding moves were associated with hops, and post-feeding shifts with flights ($P < .05$). These tendencies agreed with those seen in the vireos.

the 0.43 frequency of horizontal movement); the dashed line represents the frequencies actually observed. The numbers of consecutive horizontal moves actually observed differed significantly from the expected geometric distribution (χ^2 , $P < .02$).

TABLE 12. Measurements of White-eyed Vireos collected in Gainesville, Florida (all values are means; ranges in parentheses)

Sex	Number	Wing length (mm)	Bill			Foot		Weight (g)
			Length (mm)	Width (mm)	Depth (mm)	Mid toe (mm)	Hallux (mm)	
Males	16	58.2 (54-62)	7.1 (6.3-7.8)	4.1 (3.8-4.4)	3.8 (3.6-4.1)	14.3 (13-16)	12.1 (11-13)	12.1 (11.5-13.3)
Females	11	57.6 (56-60)	7.1 (6.0-8.1)	4.2 (3.8-4.6)	3.9 (3.3-5.0)	14.2 (13-15)	12.1 (11-13)	12.2 (10.9-12.8)

TABLE 13. Skeletal measurements of White-eyed Vireos collected in Florida (ranges in parentheses)

Sex	Age	Number	Mean femur length (mm)	Mean tibio-tarsus length (mm)	Mean tarsus-meta- tarsus (mm)
Mixed	Adult	11	13.5 (13.2-13.9)	24.3 (23.9-24.9)	19.0 (18.5-19.5)

Acadian Flycatcher

The Acadian Flycatcher is a common breeding bird in the eastern United States in moist deciduous woodlands, usually remaining beneath the canopy (Bent 1949). It was abundant at the Patuxent and Chesapeake Bay Centers, where approximately 20 individuals were observed. This species is slightly larger than the White-eyed Vireo, weighing approximately 13 g. During the breeding season it is the only small tyrannid in the deciduous woods, and its manner of foraging, like that of the Pewee (*Contopus virens*) and Great Crested Flycatcher (*Myiarchus crinitus*), was characteristically flycatcher-like.

Several perches, usually bare branches or twigs, were used repeatedly by the Acadians. From these perches they surveyed the surrounding area and initiated the characteristic foraging pattern: silent perching, often for many minutes; sudden foraging activity; and return to the same or another perch. Although aerial foraging was the most conspicuous tactic of this species, many captures were made by gleaning and hovering, and a few by pecking (Table 3). For the population, the mean foraging height was 21 ft, and the vertical range up to 50 ft ($n = 93$; $SD = 12.9$; $SE = 1.3$). Individuals, however, remained at or near the same level for extended periods, day after day.

An estimation of the distance of each movement comprising many foraging sequences revealed that the moves of the Acadian could be grouped into two non-overlapping size classes, not unlike those of the species previously discussed. The occasional hops (frequency 0.12) were only 0-6 inches; but the long flights were 1-15 ft, indicating a greater searching radius and a very different foraging strategy. The directions of foraging movements were about evenly distributed: 47% vertical and the remainder hor-

izontal. Analyses of foraging behavior showed that the movements of the Acadian were consistently random throughout the season; sequences of hops, flights, vertical moves, horizontal moves, and the association of distance and direction did not differ significantly from the predicted random values. Examination of different aspects of the foraging pattern of flycatchers might reveal non-random parameters.

The rate of foraging was slow, 7.8 moves/min, emphasizing the tendency of this flycatcher to remain in one place for long periods. Food-getting maneuvers were associated with upward and horizontal moves (35% and 50% respectively; $n = 133$), and post-feeding moves were primarily downward and horizontal (35% and 50% respectively; $n = 133$).

DISCUSSION

Sexual divergence in the Red-eyed Vireo

Male and female Red-eyed Vireos feed at different levels over 64% of the time. This difference is maintained by a consistent pattern of movement for each sex. The following questions have biological significance: (1) What are the possible advantages of height differences in foraging patterns? (2) Why do these patterns result in a bimodal feeding distribution? (3) What is the selective pressure responsible for them? (4) How are the exploitation patterns of males and females similar? and (5) How are they different?

Advantages of sexual divergence.—Females forage close to their nests (Table 1) and thus expend less energy obtaining food. During incubation and the period of nestling care, the proximity of the nest to the foraging area allows maximal efficiency in energy allotment. For the males, singing perches overlap their foraging stations, again allowing minimal expenditure of energy for foraging and the simultaneous defense of a territory. By utilizing this spacing mechanism, both sexes have likely increased the resources cropped per unit area. Similar correlations concerning the relative positions of nest height, singing perch, and foraging heights, with overall efficiency in exploitation, were reviewed by Morse (1968) for members of the genus *Dendroica*.

The bimodal feeding curve.—A frequency dis-

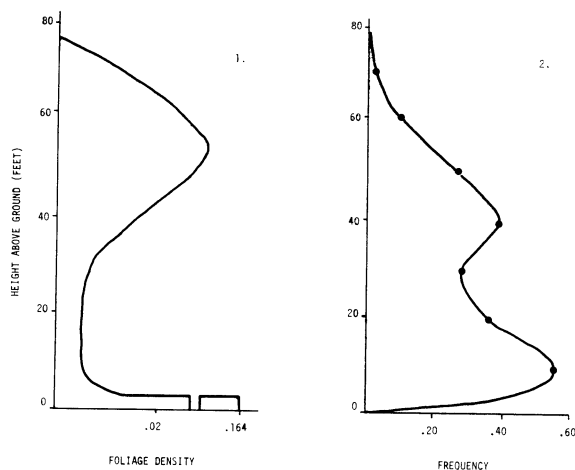


FIG. 15. A comparison of a foliage density profile for a Maryland deciduous woodland with the bimodal frequency distribution (height) of foraging activity in the Red-eyed Vireo (data for the former from MacArthur and MacArthur 1961).

tribution of the height of foraging males and females (Fig. 15) shows two distinct peaks and a large trough. Two possible explanations for this distribution are as follows:

(1) The observed feeding frequencies at different heights of males and females may reflect a bimodal density of foliage (from the canopy to the forest floor) and the arthropods associated with the foliage. MacArthur and MacArthur (1961) show that foliage density profiles for such woods can be bimodal; foliage density may also be uniform or decrease from the ground to the tree tops, or vice versa. It is not known, however, whether the observed sexual divergence in behavior of the birds is a general phenomenon that is independent of these differences. If Red-eye foraging activity is a real correlate with forest structure, then it is possible that local populations of birds shift their frequency of foraging in accordance with the foliage/arthropod densities at various locations. Lawrence's (1953) observation that Red-eyed Vireos were absent from forests where undergrowth was totally lacking would appear to support this speculation.

(2) The observed trough in the curve of male and female foraging heights might additionally reflect the "cost" of sexual feeding displacement. As long as more energy is gained by females foraging closer to nest sites, and males closer to display sites, the sexes can be expected to move apart. (Energy can be gained by finding the same amount of food (in calories) in less time, or an increased amount of food in the same time.) At the point beyond which a further restriction in foraging areas would not "pay off," that is, where less food per unit time is discovered, the peaks should stabilize.

It seems probable that a combination of both factors (i.e., sexual differences in behavior and food distribution due to foliage profile) generates the observed exploitation curve and that it will shift to meet local variation in distribution of foliage/prey.

Evolution of sexual divergence of behavior.—Territoriality may increase feeding efficiency and nesting success (Nice 1941, Hinde 1956). Within the territory the smaller foraging area of each sex resulting from displacement is of selective value if it reduces the time expended in searching for prey. A population whose size is density-dependent and within which there is intense intraspecific pressure could have a smaller territory (volume) per bird as a result of displacement of the sexes. The more efficient exploitation of food within small territories perhaps allows Red-eyed Vireo populations to be larger and, therefore, closer to the carrying capacity of the environment.

Similarities in male and female exploitation patterns.—The exploitation patterns of male and female Red-eyes share many common elements. Some of these would seem to be imposed on any species of similar size and structure. Both sexes have the same length hops (0–6 inches) and flights (1–10 ft), features that logically relate to the absence of any significant difference in sizes of feet and legs (Tables 7 and 8). Similar frequencies of prey-seeking movements were observed during autumn migration, although the structure of the vegetation differed markedly from the mature deciduous woodlands occupied during breeding (i.e., thickets of young deciduous trees, roadside margins, or other "edge" situations). Further support was thus provided for an imposed relation of a common morphology to a common behavior (prey-seeking movements).

Also, as foliage-gleaning insectivorous predators, both males and females must execute that role in similarly structured parts of a common habitat. It follows that some non-random components of the species' exploitation pattern are shared by the sexes. Exploitation of a dispersed food source by both males and females may in part account for selection for similar foraging behavior. Thus a basic searching technique has emerged for the Red-eyed Vireo: a sequence of hops, and the discovery and procurement of a food item, followed by a flight. While the bird is foraging, hops are in the upward and horizontal direction, and flights tend to be downward. This non-random searching behavior is consistent in both sexes as the method of procuring food and persists whenever a Red-eyed Vireo is foraging.

Differences in male and female exploitation patterns.—The differences between the foraging of males and females probably relate in part to the stratal variation in the habitat, and to the one significant

structural difference, the length and area of the wing. Behavior specific to each sex may also modify foraging patterns. Thus, the moves of the defensive territorial male are frequent and conspicuous. In conjunction with territorial defense, the pattern of male movements has a horizontal emphasis, which is lacking in that of the female. This emphasis appears to be incorporated into the foraging pattern (Fig. 11).

Just as males remain conspicuous in defense of territories, females remain inconspicuous when attending nests. This behavior is associated with an up-down pattern of movement to which the vertebrate eye (predator) is less responsive (Walls 1942), rather than to one of continued horizontal movement. The tendency to habituate to things seen repeatedly (Marler and Hamilton 1967), such as falling leaves or twigs, is reflected by the downward component of female movements.

Females hover more than males, and this may be a consequence of the vertical moves that predominate in female foraging (Fig. 11 B). Moreover, vertical moves may expose certain prey that are most easily captured by hovering. Wing shape may influence the female's tactics. Bats with short, broad wings are best adapted for hovering, whereas those possessing wings with a high aspect ratio (long and narrow) are adapted for rapid prolonged flight (Vaughan 1959). These principles hold for birds as well. It follows that female Red-eyed Vireos, whose wings are significantly shorter and broader than those of the males, are better adapted for hovering and use this foraging tactic more than males.

It has been hypothesized that wing length in birds relates to migratory tendencies and, additionally, that the length of the wing is proportional to the distance of migration (Chapman 1940, Kipp 1958). It is not known whether male Red-eyed Vireos migrate farther than females. If so, the above foraging preferences might be construed as secondary adaptations resulting from an imposed morphology.

Red-eye foraging behavior observed during fall migration strengthens the thesis that some major elements of a species' exploitation pattern are influenced by habitat structure, food type and distribution, and the seasonal repertoire of activities. The maintenance of behavior specific to males or females during the breeding season might not exist at other times of the year. The edge vegetation where most Red-eyed Vireos were seen during autumn migration provided a single dense layer of foliage with the tallest trees about 35 ft in height. Although sex and age of individuals were unknown, the flocks moved as a unit and it seems reasonable to assume that females and males foraged together. Migrating Red-eyed Vireos fed largely on clusters of berries, as well as more distributed arthropods. The switch to tightly

clumped and highly visible food accounts satisfactorily for the observed changes in certain non-random elements of the feeding pattern.

Female Red-eyed Vireos foraged (significantly) faster than males throughout the breeding season, with the greatest difference in July and August, at the peak of the incubation, nestling, and fledgling periods. Also, females captured significantly more prey per unit time. It would seem likely that males have the capability to forage as rapidly and as efficiently as females. It appears that in those breeding seasons when food is abundant and weather favorable, the young can be raised by only one rapid, efficient forager. This is naturally the female, for she is already solely responsible for incubation and is not involved in defense of territory. In a critical season, when food is less abundant or bad weather prevails, or both, males can probably contribute as much as females to the rearing of young.

The rate of foraging for all Red-eyed Vireos during migration was slow (13.3 moves/min), which further indicates that such rates are subject to various environmental and internal stimuli.

Use of space by vireos

Avian territory has classically been defined as "any defended area" (Noble 1939). Nice (1941), using this definition, distinguished six types of such areas. Only one is pertinent and applicable to this study, the "type A" category defined by both Hinde (1956) and Nice as one used for mating, nesting, and feeding. Many passerine species, including the vireos, wood warblers, and tyrant flycatchers, defend this type of territory.

With regard to the type A territory of the vireos, it is useful to look at the relationship between the defended area and the actual volume of space used for foraging. The denotation of territory size (e.g., 3 acres) is used to indicate that only one male of a particular species occupies that area. However, he also occupies a volume of space limited by the height of the foliage within the 3 acres. That is, the defended area is three-dimensional; territories do not usually overlap horizontally or vertically. However, the volume actually utilized for feeding may be much smaller than might be indicated by a particular vertical foliage profile. The space utilized by the Red-eyed Vireo can be visualized as a cylinder extending from the canopy nearly to the forest floor; this space-conserving shape might account for the small territory of less than 2 acres. The Yellow-throated Vireo is more restricted vertically, especially from the peak of breeding through the end of the season, and its large defended territory of about 10 acres is compressed, like a pancake, and high in the canopy. The foraging space occupied by a pair of Red-eyed Vireos

TABLE 14. The relationship of territory size to foraging volume in three species of vireos

Species	Territory size (acres)	Vertical range (ft)	Foraging volume (ft ³ /pair)	Foraging volume (ft ³ /bird)	Foraging volume index/bird (or pair)
Yellow-throated Vireo	10	40	17.3×10^6	8.7×10^6	3
White-eyed Vireo	3	40	5.2×10^6	2.6×10^6	1
Red-eyed Vireo	1.5	80	5.2×10^6	2.6×10^6	1

is one-third that of a pair of Yellow-throated Vireos, and equal to that of a pair of White-eyed Vireos (Table 14).

The separation of male and female Red-eyed Vireos results in a foraging volume per bird approximately only one-half that of the pair. Presuming similar separation of the other vireos, the foraging volume indices are 3:1:1 per bird for the Yellow-throated, White-eyed, and Red-eyed Vireos, respectively (Table 14). Thus, although the defended territory and feeding areas occur in the same place, the actual "volume of space" in which the bird forages does not necessarily equal the "volume" of defended area. Foraging volume indices for species permit comparisons of efficiency and behavior not possible with knowledge of the territory size alone.

Foraging patterns of insectivorous birds

Comparison of the exploitation patterns of the three vireos reveals a marked similarity in basic strategy. All have slightly different, non-random patterns of foraging movements, separated by intervals of observation of the adjacent foliage and branches. All demonstrate a similar sequence of behaviors surrounding the capture of prey, i.e., hopping, discovery, capture, and flight. These vireos have evolved adaptations as stalking predators exploiting a class of similar food items (Chapin 1925), i.e., largely caterpillars (30–42%) and other arthropods that move slowly and are detected from some distance by their shapes or colors, or both, rather than by sudden movements after flushing.

The Redstart exhibits responses similar to those of vireos surrounding the discovery and capture of prey—hopping before and flying after. However, the total pattern of movement, many sequential hops and prolonged periods of foraging in single trees, is more rapid than in the vireos. Both Redstarts and vireos exploit dispersed food sources; however, rapid movements in a single tree (restricted space) probably promote insect flight from leaves and further enhance the Redstart's hunting strategy. A basically different *modus vivendi* results.

The Acadian Flycatcher, on the other hand, is a "passively searching" predator of flying arthropods. In this species the roles between prey and predator

take a new tack. In general, the initiation of a foraging maneuver of this flycatcher depends upon the movements of small visible prey in that volume of space within sight. Movements to capture such prey follow expected geometric distributions, correlated with the presumably randomly occurring flights of arthropods.

The behaviors of all these birds are in accord with their particular adaptations and structures and result in species-specific modes of foraging. For the foliage gleaners, these are consistent and non-random. Figure 16 is a diagrammatic portrayal of the characteristic elements of movement and positions in the woods for the five species examined.

Foraging patterns and coexistence of species

The species considered here are important components of the "guild" of insectivorous birds in the deciduous woodland of the central Atlantic states. Twelve species of birds derive at least part of their food by gleaning arthropods from the foliage in this habitat. It is reasonable to assume that their evolution has involved a long period of coexistence in such woodlands, and that this has resulted in the adjustments in structure and behavior that are reflected in the niche specializations observed. The specific foraging movements, including differences in the height and particular location of birds, indicate that each species (and perhaps, each sex) is exposed to only a particular portion of the available habitat. The inferences to be derived from these observations include: (1) that each species has evolved responses to cues established by the repetitive presentation of specific configurations of foliage and associated prey, and (2) that this group of foliage-gleaners forms an integrated group that exploits insects in a common space.

The species-specific patterns of foraging movements described above delineate one parameter of the niche, and together with the other quantitative measures used, provide an exact means of discerning total "pictures" of habitat utilization.

During the past 15 years there have been an increasing number of studies delineating the foraging behaviors of taxonomically and ecologically related species of birds. In his detailed work on tits (*Parus*

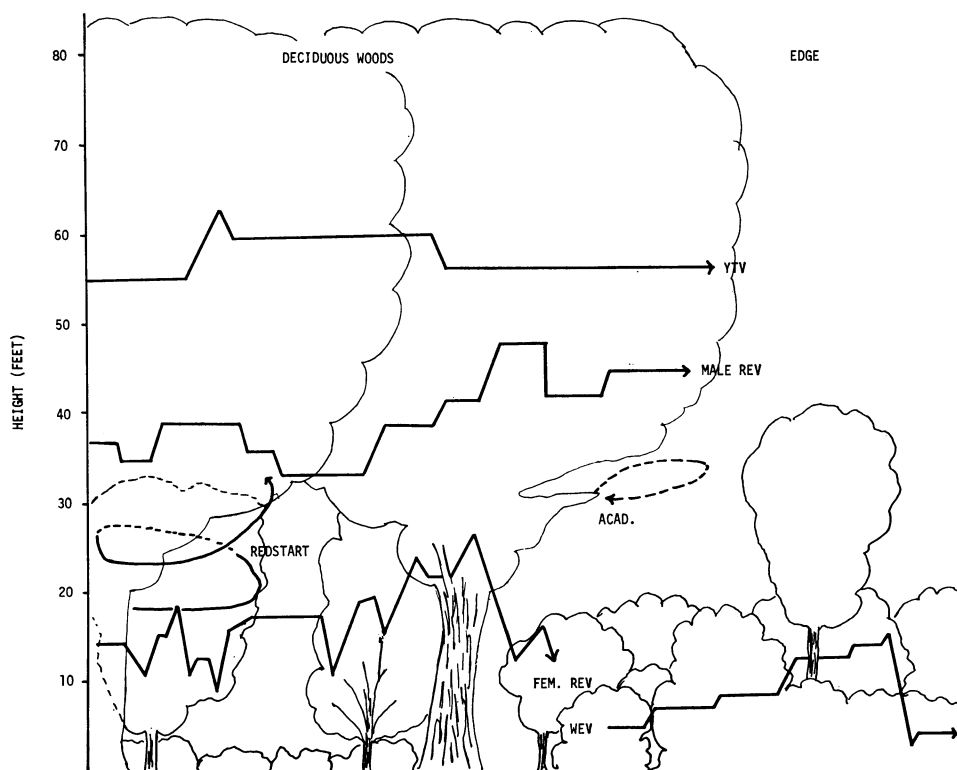


FIG. 16. A diagrammatic representation of the foraging patterns of five sympatric, insectivorous passerine birds in the deciduous woodland of Maryland. Uppermost is the Yellow-throated Vireo (YTV), showing a conspicuous horizontal trend. The male Red-eyed Vireo (REV) is more central, and the horizontal movement is in shorter segments. The female Red-eyed Vireo (FEM. REV) shows a marked interspersion of vertical movements. The edge-dwelling White-eyed Vireo (WEV) moves in a predictable step-wise fashion interspersed with long downward moves. The Redstarts' pattern of movement tends to result in either ascending or descending "spirals." The Acadian Flycatcher (ACAD.) sallies forth in predominantly hawking maneuvers from several perches in the territory.

spp.) Gibb (1954, 1960) considered the portions of trees utilized, the frequencies of use of foraging maneuvers, and the body weights of the species studied, and thus determined several species-specific feeding niches. Hartley's (1953) work paralleled that of Gibb in making nearly identical sorts of determinations for the English tits (*Parus*). More recently, the data collected by MacArthur (1958) allowed him to make comparisons of the feeding ecology of five species of wood warblers in a way that considered different, perhaps subtler, aspects of their interrelationships. His observations showed that the behavior of congeneric and sympatric species of the parulid genus *Dendroica* includes movements with distinctive directional components and decided preferences for specific areas of trees. In his words, the "birds behave in such a way as to be exposed to different kinds of food. They feed in different positions, indulge in hawking and hovering to different extents, move in different directions through the trees, vary from active to sluggish, and probably have the

greatest need for food at different times corresponding to the different nesting dates."

The detailed study of the exploitation pattern of the Blue-grey Gnatcatcher (*Polioptila caerulea*) (Root 1967) emphasized those changes in feeding behavior which correspond with the differing demands of feeding young and self-maintenance feeding during different seasons and in different habitats. There emerged from Root's study a presentation revealing the effects of a changing environment on the feeding behavior and preferences of a small insectivorous bird.

The present study delineates patterns of foraging movements for five species of foliage-gleaning insectivorous birds. These patterns, for the Red-eyed Vireo, provide suitable documentation for behavioral differences separating the sexes during foraging. For all five species the findings are similar to those of MacArthur and Root, i.e., that patterns of foraging movements are species-specific, reveal to the bird different parts of the environment, likely result in

the exposure of different kinds of food, and are responsive to environmental changes.

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LITERATURE CITED

- Baldwin, S. P., H. C. Oberholser, and L. G. Worley. 1931. Measurements of birds. Sci. Publ. Cleveland Mus. Natur. Hist. 2: 1-165.
- Bent, A. C. 1949. Life histories of North American flycatchers, larks, swallows, and their allies. Smithsonian Inst., U.S. Nat. Mus. Bull. 179. 555 p.
- . 1953. Life histories of North American wood warblers. Smithsonian Inst., U.S. Nat. Mus. Bull. 203. 734 p.
- Brewer, R. 1955. Size of home range in eight species in a southern Illinois swamp-thicket. Wilson Bull. 67: 140-141.
- Chapin, E. A. 1925. Food habits of the vireos; a family of insectivorous birds. U.S. Dep. Agr. Bull. 1355. 44 p.
- Chapman, F. A. 1940. A post glacial history of *Zonotrichia capensis*. Bull. Amer. Mus. Natur. Hist. 77: 381-438.
- Crowell, K. L. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology 43: 75-88.
- Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London. 488 p.
- Feller, W. 1950. Introduction to the theory of probability and its applications. Vol. 1. John Wiley & Sons, New York.
- Gibb, J. 1954. Feeding ecology of tits, with notes on treecreeper and gold crest. Ibis 96: 513-543.
- . 1960. Populations of tits and goldcrests and their food supply in pine plantations. Ibis 102: 163-208.
- Hamilton, T. H. 1962. Species relationships and adaptations for sympatry in the avian genus *Vireo*. Condor 64: 40-68.
- Hartley, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. J. Anim. Ecol. 22: 261-288.
- Higman, D. 1968. An ecologically annotated check list of the vascular flora at the Chesapeake Bay Center for Field Biology, with keys. Smithsonian Institution, Washington, D. C. 234 p.
- Hill, A. B. 1961. Principles of medical statistics. Oxford Univ. Press, New York. 367 p.
- Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis 98: 340-369.
- Hoiberg, A. J. 1954. Breeding bird census; oak-pine stream bottomland. Audubon Field Notes 8: 369.
- Hotchkiss, N., and R. E. Stewart. 1947. Vegetation of the Patuxent Research Refuge, Maryland. Amer. Midland Natur. 38: 1-75.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415-427.
- James, R. D. 1967. Comparative foraging behavior and habitat selection of three species of *Vireo* (Aves: Vireonidae) in Southern Ontario. M.S. Thesis. Univ. Toronto, Toronto, Ont. 73 p.
- Johnson, N. K. 1966. Bill size and the question of competition in allopatric and sympatric populations of dusky and grey flycatchers. Systematic Zoology 15: 70-87.
- Keast, A. 1966. Trophic interrelationships in the fish fauna of a small stream. Univ. Michigan, Great Lakes Res. Div. Publ. 15: 51-79.
- Kilham, L. 1965. Differences in feeding behavior of male and female Hairy Woodpeckers. Wilson Bull. 77: 134-145.
- Kipp, F. A. 1958. Zur Geschichte des Vogelzuges auf der Grundlage der Flügelanpassungen. Die Vogelwarte 19: 233-42.
- Kolman, W. A. 1960. The mechanism of natural selection for the sex ratio. Amer. Natur. 94: 373-378.
- Lawrence, L. de K. 1953. Nesting life and behavior of the Red-eyed Vireo. Can. Field-Natur. 67: 46-77.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.
- . 1961. Population effects of natural selection. Amer. Natur. 95: 195-199.
- MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42: 594-600.
- Marler, P. R., and W. J. Hamilton, III. 1967. Mechanisms of animal behavior. John Wiley and Sons, Inc., New York. 771 p.
- McAttee, W. L. 1926. The relation of birds to woodlots in New York State. Roosevelt Wildl. Bull. 4: 157 p.
- Mengel, R. M. 1965. The birds of Kentucky. Ornithol. Monogr. No. 3. Allen Press, Lawrence, Kansas. 581 p.
- Morse, D. 1968. A quantitative study of foraging of male and female spruce wood warblers. Ecology 49: 779-784.
- Nice, M. M. 1941. The role of territory in bird life. Amer. Midland Natur. 26: 441-487.
- Noble, G. K. 1939. The role of dominance in the social life of birds. Auk 56: 263-273.

- Nolan, V., Jr., and D. P. Wooldridge. 1962. Food habits and feeding behavior of the White-eyed Vireo. *Wilson Bull.* **74**: 68-74.
- Root, R. B. 1967. The niche exploitation pattern of the Blue-grey Gnatcatcher. *Ecol. Monogr.* **37**: 317-350.
- Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* **155**: 474-477.
- . 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704-726.
- Selander, R. K. 1966. Sexual dimorphism and different niche utilization in birds. *Condor* **68**: 113-151.
- Southern, W. E. 1958. Nesting of the Red-eyed Vireo in the Douglas Lake region, Michigan. *Jack Pine Warbler* **36**: 105-130.
- Stewart, R. E., and C. S. Robbins. 1958. The birds of Maryland and the District of Columbia. U.S. Gov. Printing Office, No. 62- N. Amer. Fauna. 401 p.
- Storer, R. W. 1966. Sexual dimorphism and food habits in three North American accipiters. *Auk* **83**: 423-436.
- Sutton, G. M. 1949. Studies of the nesting birds of the Edwin S. George Reserve. Part 1. The vireos. Misc. Publ. Univ. Mich. Mus. Zool. **74**: 5-36.
- Vaughan, T. A. 1959. Functional morphology of three bats: *Eumops*, *Myotis*, *Macrotus*. Univ. Kansas Publ. Mus. Natur. Hist. **12**: 1-153.
- Walls, G. L. 1942. The vertebrate eye and its adaptive radiation. Hafner Publ. Co., New York. 785 p.

APPENDIX

The following method of analysis was used to determine the goodness of fit of sequences of movements of the birds to a geometric distribution. By this method it was possible to determine whether a particular pattern or sequence of movements departed from the expected.

Given: For the type of movement there is a probability p of hopping and a probability q of flying. Thus, $p + q = 1$ because the bird either hops or flies. For the direction of movement, there is a probability p' of horizontal movement and a probability q' of vertical movement. Similarly, then, $p' + q' = 1$ for the bird moves either vertically or horizontally.

Hypothesis: The sequence of hops follows a geometric distribution; i.e., the number of hops before the first flight and preceded by a flight is n and it has a distribution $p^n q$ (Feller 1950), where $n = 1, 2, 3$, etc. Thus, the expected value for a sequence of 1 hop, flight-hop-flight, = the probability q ; that for a sequence of 2 hops, flight-hop-hop-flight, = pq ; that for 3 hops, flight-hop-hop-hop-flight, = $p^2 q$ etc.

Assumed: This geometric distribution is based upon the assumption that the probabilities of hopping and flying (p and q) remain constant, and that each move is independent of every other one.

Example: In Fig. 11, curves were presented to demonstrate the seasonal changes in the number of consecutive hops during the foraging of the Red-eyed Vireo. The following example tests the hypothesis that the number of consecutive hops follows the expected geometric distribution for the females (Fig. 11 B) from April to mid-June.

$p = 0.57$ (p = frequency of hopping) $q = 0.43$ (q = frequency of flying)				
No. of hops in a row (n)	Expected (e) ($p^n q \times \text{total}$)	Observed (o)	$o - e$	$(o - e)^2 / e$
1	55.9	48	7.9	1.10
2	32.2	31	1.2	.04
3	18.3	20	1.7	.16
4	10.9	9	1.9	.33
5	6.2	6	0.2	.01
6	3.5	5	1.5	.65
7	2.6	4		
8	1.4	2		
9	0.8	1		
10	0.4	1		
11	0.3	2		
12	0.1	1		
	total	130		
Chi square (Hill 1961)		$[(o-e)^2 / e] = 7.19$ $P < .30$ (6 d.f.)		

In this example the sequence of hops does not depart significantly from the expected geometric distribution.