

# FORAGING BEHAVIOR AND HABITAT SELECTION OF THREE SPECIES OF VIREOS IN SOUTHERN ONTARIO

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The Red-eyed Vireo (*Vireo olivaceus*), the Warbling Vireo (*V. gilvus*) and the Yellow-throated Vireo (*V. flavifrons*) have completely overlapping ranges in southern Ontario. The Red-eyed and Warbling vireos generally occupy different habitats, but the Yellow-throated Vireo is reported to occupy the range of habitats occupied by the other two species (Sutton 1949, Bent 1950).

Hamilton (1962) has categorized all vireos as gleaners from foliage, although Kendeigh (1945) has indicated that the Solitary Vireo (*V. solitarius*), which is closely related to the Yellow-throated Vireo, searches branches for food. However, in the literature, the Yellow-throated Vireo is repeatedly characterized as a forager of the uppermost or crown-layer of trees, apparently supporting Hamilton's (1962) contention that they glean from leaves. Hamilton further indicates that, as a crown-layer forager, the Yellow-throated Vireo is able to share successfully the same habitat with the Red-eyed Vireo to the extent that the 2 forms forage in the same parts of trees.

The present report gives the results of a study in which I examined foraging behavior, habitat choice, the extent of sympatry, and some of the factors which facilitate sympatry in the genus *Vireo* in southern Ontario.

## METHODS

Most observations were made between sunrise and noon, when the birds were most active. I spent about 500 hours observing in the field in the summers of 1966 and 1967. Observations were made with the aid of a 7 × 35 binocular.

This study was conducted in southern Ontario, in Toronto city, and surrounding regions within a general area having forest communities dominated by broadleaved trees. However, in southern Ontario the natural vegetation has been mostly reduced to farm woodlots, hedgerows, and remnant stands on soils too poor to farm (Rowe 1959:44).

Within this general region, vireos were studied in 5 specific localities: (1) Pickering-Ajax area 30 km E Toronto, Ontario Co., (2) north of Toronto, 8 km NW King City, York Co., (3) Don River Valley in Toronto (Glendon College Campus), York Co., (4) Campbellville district, 48 km W Toronto in the Halton Co. forest tracts and environs atop the Niagara escarpment, (5) Galt area, 96 km W Toronto (Dryden tract 6.5 km W Galt, and Wrigley Lake), Waterloo Co.

*Foraging study.*—When I saw a vireo foraging, I followed its progress until it flew out of sight, and for every successful foraging event, recorded the following:

- (1) I categorized the method used to approach and secure the food item as (a) *Hawking*—where both the birds and prey were in flight, (b) *Hovering*—where a bird in

flight removed prey from a plant, or (c) *Stalking*—where both bird and prey were clutching a plant surface.

- (2) The source of food I identified as a leaf or branch. A leaf source included the ends of small twigs bearing leaves, as well as any buds present. Branches comprised all tree parts from small twigs to large limbs, or all cases where no leaves were near the food source, including the trunk of the tree.
- (3) The zone of the tree, in which an insect was caught I categorized as peripheral (the outer, or terminal portions, of the limbs where most of the leaves were concentrated), or central (the area from the trunk or center of a tree, radially outward, exclusive of the outer portions of branches, and characterized mainly by bare or dead limbs).
- (4) The perch upon which a bird stood as it searched for food immediately prior to catching an insect I categorized as a dead or live branch, and, in the latter case, whether foliated (bird within or adjacent to leaves) or unfoliated.
- (5) The height of the tree in which the bird was foraging and the height above the ground at which the bird was foraging when it secured a food item, I estimated to the nearest meter.
- (6) The species of tree in which the bird was foraging was recorded.

When I observed foraging, but the source of food could not be determined, I only recorded the height of foraging, tree height, and the species of tree.

*Habitat Study.*—I regarded nest location as strongly indicative of habitat preference, since it was always within the habitat used by the vireos for all their activities throughout the nesting cycle. Data were collected on the habitat surrounding 8 Red-eyed, 9 Warbling, and 9 Yellow-throated vireo nests. The pairs of vireos associated with these nests were studied for sufficient periods of time to enable me to obtain a good approximation of the territory used for foraging throughout the nesting cycle.

In order to distinguish among the habitat types, I recorded the following criteria: (a) tree species present, (b) percentage of dead limbs on tree near the nest, (c) presence or absence of understory, and (d) percent of tree or canopy cover on a territory. In determining percentage of dead limbs on trees, I assessed as many as 5 trees which were used extensively for foraging in each territory, regardless of the tree species. The total number of major limbs were counted and the proportion of dead limbs noted. I estimated canopy cover with the aid of sketches, plotting the locations of all trees within the area. All continuous forests were recorded as 90% canopy cover (Park 1931).

I also compared the heights and positions of all nests, and the species of tree in which the vireos nested.

*Interspecific reactions.*—Tape recorded songs were used to compare responses of each species to congeneric and conspecific song. Songs were recorded in the field on a Uher 4000 Report-L tape recorder with the microphone affixed to a 60 cm aluminum parabolic reflector, at a tape speed of 19.05 cm per sec. I used a J. B. Lansing Signature Hi-fidelity speaker in field playback experiments.

During playback the speaker was placed on the ground below and within 15 m of a nest tree. Songs were played in the vicinity of 2 to 5 active nests of each species, in both the nest building and incubation phases of the nesting cycle. In the case of the Warbling Vireo additional experiments were performed when young birds were in the nest. For all experiments, songs of the 2 sympatric vireos were played for 1 min each, followed by a maximum of 1 min of conspecific song. The interval between songs was never less than 1 min or as long as 5 min. In addition, I observed several naturally occurring interspecific encounters.

TABLE 1  
FORAGING, NESTING, AND HABITAT DIFFERENCES AMONG VIREOS IN SOUTHERN ONTARIO

	Red-eyed	Warbling	Yellow-throated
<b>Foraging Method (%)</b>			
Stalking	28.0	32.0	69.0***
Hovering	61.0	59.0	28.5***
Hawking	11.5	10.0	4.5
n	150	132	64
<b>Food Source (%)</b>			
Leaf	99.0	97.0	16.0***
Branch	1.0	3.0	84.0***
n	150	132	64
<b>Tree Zone (%)</b>			
Peripheral	93.5	88.0	19.5***
Upper	38.5	40.0	5.5
Middle	42.0	40.0	12.5
Lower	13.0	8.0	1.5
Central	6.5	12.0	80.5***
Upper	1.5	6.0	26.5
Middle	5.0	6.0	48.5
Lower	—	—	5.5
n	76	64	78
<b>Foraging Perches (%)</b>			
Unfoliated	65.0	51.5	21.5
Foliated	22.0	39.0	2.0
Dead	14.0	9.5	76.5***
n	150	132	64
<b>Nest Height (m)</b>			
Average	4.9	8.2	13.4
Range	2–15	6–15	9–15
n	10	10	10
<b>Nest Placement</b>			
Peripheral			
Upper	3	4	1
Middle	4	3	—
Lower	2	1	—
Central			
Upper	1	2	6
Middle	—	—	3
Lower	—	—	—

\*\*\* Significant differences ( $P < .001$ ) between this and the other 2 species.

TABLE 1  
(Continued)

	Red-eyed	Warbling	Yellow-throated
Canopy Cover (%)			
Average	78	34	62
Range	50-90+	10-70	30-90
n	8	9	9
Dead Limb Counts			
Average	11.1	9.3	19.8
Range	5-20	5-30	5-35
n (Trees)	22	29	25
n (Territories)	7	8	8

*Bill morphology.*—I measured bill length, from the anterior margin of the external nares to the tip of the bill, and depth and width of the bill at the anterior margin of the external nares on study skins. Ten males were measured for each of the 3 species as were 10 Red-eyed Vireo females but only 9 each of Warbling and Yellow-throated vireo females. All specimens were from existing Royal Ontario Museum collections and were taken in Ontario between the months of May and August.

*Statistical analysis.*—A statistical test of the equality of percentages (Sokal and Rohlf 1969:608) was used (unless otherwise indicated) to test foraging differences among the vireos. In all cases where a significant difference was indicated between percentages, I tested the percentages to determine what sample sizes would be required to detect a true difference between them (Sokal and Rohlf 1969:609). In all cases my sample sizes were sufficiently large to be 90% certain of detecting a true significant difference at the 5% level.

## RESULTS

*Foraging differences.*—A breakdown by method of 346 successful foraging bouts for the 3 species is given in Table 1. Hovering was used to about the same extent by the Red-eyed and Warbling vireos to secure the major portion of their food. The Yellow-throated Vireo on the other hand took significantly more food by stalking. None of the species used hawking to any extent to obtain food.

The Red-eyed and Warbling vireos, clearly using the same source, took their food almost entirely from leaves. Although they secured a large proportion of their food by hovering, some food was obtained by hanging from the end of a branch and picking an invertebrate from a leaf. This method was included under stalking. In contrast, the Yellow-throated Vireo gleaned most of its food from the bark of trees.

The Yellow-throated Vireo foraged largely within the central zone of trees.

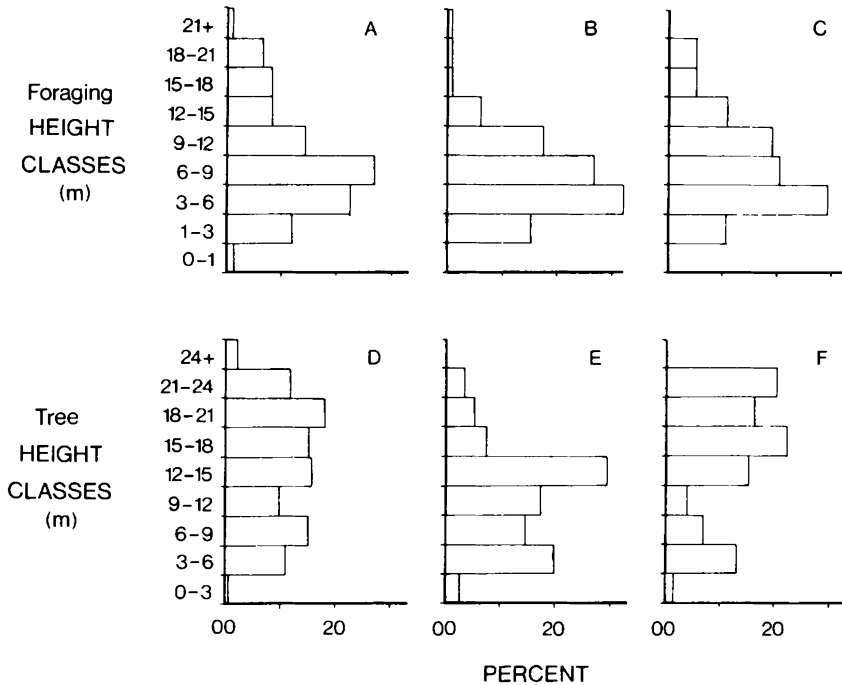


FIG. 1. A-C. The percentage of the total number of foraging actions recorded at different heights above the ground. A. *V. olivaceus* (n = 211; mean = 7.83 m); B. *V. gilvus* (n = 131; mean = 7.74 m); C. *V. flavifrons* (n = 228; mean = 9.26 m). D-F. The percentage of the number of trees of different height classes in which foraging actions were recorded. D. *V. olivaceus* (mean = 15.1 m); E. *V. gilvus* (mean = 10.0 m); F. *V. flavifrons* (mean = 16.2 m).

The Red-eyed and Warbling vireos, however, foraged significantly more in the peripheral areas. Yellow-throated Vireos often spent a protracted period in a tree before moving on to another. As it foraged on the basal portions of limbs, moving near and around the trunk in a spiral fashion, this vireo searched a higher percentage of dead limbs than the other species. Warbling Vireos like the Yellow-throated Vireos spent much time foraging in individual trees. Moving through the outer foliage Warbling Vireos restricted foraging largely to the tips of live branches. Red-eyed Vireos on the other hand moved rapidly from tree to tree in mature dense forest perching mainly on smaller live branches. Both Warbling and Red-eyed vireos searched peripheral leaves from perches on nearby twigs.

Figure 1 (a, b, c) shows the foraging heights of 570 foraging bouts for the species. The mean foraging heights for Red-eyed, Warbling, and Yellow-

throated vireos were respectively 7.8, 7.7, and 9.3 m. No significant differences are apparent in foraging height ( $P < .05$  using a single classification anova with unequal sample sizes, Sokal and Rohlf 1969:219) or in the heights of the trees in which these foraging bouts were recorded (Fig. 1: d, e, f). Mean tree heights for Red-eyed, Warbling and Yellow-throated vireos are respectively 15.1, 10.0, and 16.2 m.

The amount of foraging done in the lower, middle, or upper third of the peripheral or central zones of tree by each species is summarized in Table 1. Both Red-eyed and Warbling vireos foraged similarly in the peripheral zone and upper  $\frac{2}{3}$  of trees, different from Yellow-throated Vireos which largely foraged centrally although in the upper  $\frac{2}{3}$  of trees.

Average nest height for 10 nests of each species was 4.9, 8.2 and 13.4 m for the Red-eyed, Warbling and Yellow-throated vireos respectively. While these bear no relationship to mean foraging heights, the placement of nests in trees (Table 1) corresponds closely to preferred foraging positions ( $r = .94$  for Red-eyed, .89 for Warbling and .89 for Yellow-throated using product-moment correlation coefficient for small samples, Sokal and Rohlf 1969:509).

*Habitat differences.*—In general, the vireos foraged in any tree within their territories (Table 2). However, over half the Yellow-throated territories had oaks (*Quercus* sp.) present and this was the only vireo to forage in conifers. The Red-eyed was the only species to make significant, and repeated, use of understory (Table 2b). The Warbling occasionally forages in short trees, but I did not consider these understory because of the open nature of the habitat this vireo occupied.

A comparison of the percent canopy cover on the territories of Red-eyed and Warbling vireos (Table 1) shows that Warbling Vireo habitat was significantly more open ( $P < .001$ ) than that of the Red-eyed Vireo, consistent with reported habitat preferences (Bent 1950, James 1971). The percent canopy cover on Yellow-throated Vireo territories averaged between the values for the other species and is significantly different from either of them ( $P < .05$ , using a t-test for small samples).

Average figures for the dead limb estimates on territories of the different vireo species (Table 1), reveal a significantly higher value for the Yellow-throated Vireo over the other 2 species ( $P < .05$ ). As much as 10% of the limbs on any tree were dead, and the increase shown in the Yellow-throated Vireo habitat indicates a preference for completely dead trees or trees such as oaks and aspens (*Populus* sp.) which often have large numbers of dead lower limbs.

In 1965 and 1966, pairs of Yellow-throated Vireos nested less than 100 m from a Warbling Vireo nest of 1967. Because of an open marsh to the north, and a young pine (*Pinus* sp.) plantation to the south which converged to the

TABLE 2  
RELATIVE TREE SPECIES USE BY VIREOS\*

(a) Overstory	Red-eyed (n = 7)			Warbling (n = 8)			Yellow-throated (n = 8)		
	(A)	(B)	(C)	(A)	(B)	(C)	(A)	(B)	(C)
Sugar maple ( <i>Acer saccharum</i> )	6	6	4	5	5	2	5	5	1
White elm ( <i>Ulmus americana</i> )	3	3	2	5	5	1	5	5	1
Red oak ( <i>Quercus rubra</i> )	3	2		2	1		5	5	3
Balsam poplar ( <i>Populus balsamifera</i> )	2	1	1	4	3	2	3	3	2
Trembling aspen ( <i>Populus tremuloides</i> )				5	2	3	5	5	1
White birch ( <i>Betula papyrifera</i> )	3	2		1	1		1	1	
Beech ( <i>Fagus grandifolia</i> )	4	3	1	1			3	1	
Silver maple ( <i>Acer saccharinum</i> )	2	1		2	2	2	1	1	1
Ash ( <i>Fraxinus</i> sp.)	3	1		4	3		1		
Apple ( <i>Malus</i> sp.)	1	1		4	2		2	1	
Basswood ( <i>Tilia americana</i> )	1	1		3	3		1	1	
Ironwood ( <i>Ostrya virginiana</i> )	1	1		2	2				
White pine ( <i>Pinus strobus</i> )	1			3			3	3	
Hickory ( <i>Carya ovata</i> )	2	2	1				2	1	
Hawthorn ( <i>Crataegus</i> sp.)	1	1	1	1	1		2	1	
Walnut ( <i>Juglans</i> sp.)	1			2	1		3	1	1
Cherry ( <i>Prunus</i> sp.)				2	1				
Willow ( <i>Salix</i> sp.)				3			1	1	
Spruce ( <i>Picea glauca</i> )	1			1					
Cedar ( <i>Thuja occidentalis</i> )	1						1		

\* Tree species recorded in vireo territories, the number of territories each species was recorded in (Column A), the number of these territories in which the vireos were seen foraging in these trees (Column B) and the number of times each type of tree was used as a nest tree in 10 nestings of each species (Column C).

TABLE 2  
(Continued)

(b) Understory	Red-eyed (n = 7)			Warbling (n = 8)			Yellow-throated (n = 8)		
	(A)	(B)	(C)	(A)	(B)	(C)	(A)	(B)	(C)
Maple ( <i>Acer</i> sp.)	6	5							
Ironwood ( <i>Ostrya virginiana</i> )	4	4							
Beech ( <i>Fagus grandifolia</i> )	3	3							
Elm ( <i>Ulmus americana</i> )	3	1							
Willow ( <i>Salix</i> sp.)					2		1		
Dogwood ( <i>Cornus</i> sp.)					4				
Poplars ( <i>Populus</i> sp.)					3		1		

east of the Warbling Vireo nest, the Warbling and Yellow-throated vireos foraged in the same area, although in successive years.

In 1967, a Yellow-throated Vireo nested within 75 m of a Warbling Vireo with some observed overlap of foraging areas. In 1963 and 1965 a Yellow-throated Vireo nested in a tree whose branches intertwined with a tree in which a Warbling Vireo nested in 1967. In 1966, a Yellow-throated Vireo nested less than 50 m from Warbling Vireo nests of 1966 and 1967. Again, I observed overlap of foraging by these vireos in 1966.

In 1967, I observed 3 instances of Yellow-throated Vireos nesting within 100 m of Red-eyed Vireo nests, and in one case, not more than 25 m separated the nest trees. In all cases, where Yellow-throated Vireos nested near Warbling Vireos, the habitat was open. Where nests were near Red-eyed Vireos, twice they were in a mature forest, and once in a more open river valley with mature trees. From these observations it is evident that Yellow-throated Vireos can nest in a habitat similar to either of the other species. Several tree species used as nest trees are common to all 3 vireos (Table 1). The seeming preference for sugar maples (*Acer saccharum*) by the Red-eyed Vireo was probably a function of availability rather than preference. Yellow-throated Vireos seemingly demonstrated a proclivity for oaks, which were not plentiful in the study area.

*Interspecific reactions.*—None of the vireos responded strongly to playback of congeneric song. Playing of a congeneric vireo song resulted in a temporary



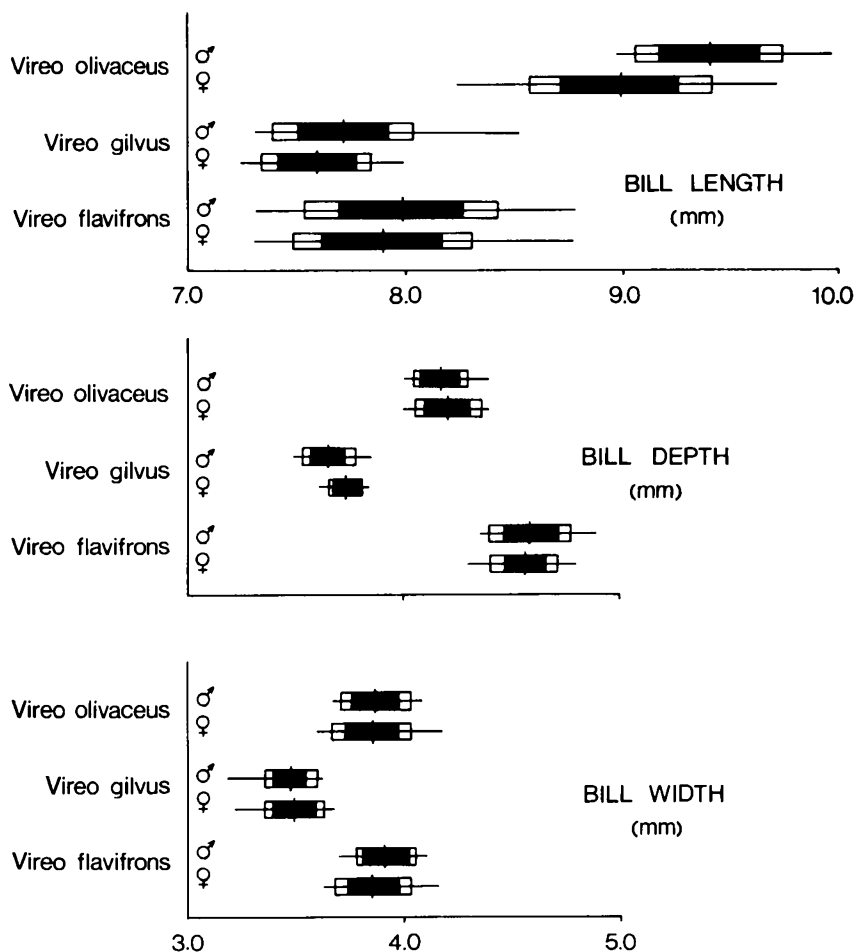


FIG. 2. Comparison of length, width, and depth of bill of the 3 vireos. Horizontal line represents the range, vertical line the mean, open bar 1 standard deviation on either side of the mean, and solid bar 2 standard errors on either side of the mean.

increase in the rate of song or a return to the nest tree by the male in whose territory tape recorded song was played. But never in 2 to 5 trials at any stage of the nesting cycle, did a vireo approach the speaker after 1 min of playback of a congeneric vireo song. On the other hand, a conspecific song invariably drew the bird to within 3 m of the speaker within 30 sec, and in as little as 5 sec, regardless of the stage of the nesting cycle.

On 2 occasions Red-eyed Vireos sang in areas used for foraging by Warbling Vireos, and on one occasion in an area used by Yellow-throated Vireos. On

these occasions, and once when a Yellow-throated Vireo sang in the nesting area of a Warbling Vireo, there was no aggressive interaction between species. However, in all these cases the intruding bird was at some distance from the nest of the resident bird. Twice a Warbling Vireo passed through a Yellow-throated Vireo nest tree after having been attracted by tape recorded song. On these occasions the Warbling Vireo was chased immediately from the nest tree but continued to sing unmolested a short distance (within 30 m) from the nest tree. Other small passerines, such as warblers, were frequently chased from a nest tree by vireos. It appeared that the presence of a bird of any species was a greater stimulus for defense than a congeneric vireo song. The strongest stimulus for defense was, however, the conspecific song which rapidly drew a bird some distance from its nest.

*Bill morphology.*—Warbling and Red-eyed vireos have bills of similar proportions but all dimensions of Warbling Vireo bills are smaller than those of Red-eyed Vireos (Fig. 2). Yellow-throated Vireos have bills similar in length to that of Warbling Vireos but are both deeper and wider than either Warbling or Red-eyed vireo bills.

#### DISCUSSION

My observations support statements by others that the Red-eyed Vireo is a gleaner of arthropods from foliage (Kendeigh 1945, Bent 1950) and that its foraging encompasses not only the canopy but also the shrubby understory (Sutton 1949, Hamilton 1962). Although I did not color band birds, I noted no sexual differences in the foraging heights of male and female Red-eyed Vireos as demonstrated by Williamson (1971). However, she also points out that habitat configuration can promote much of this divergence and most of the forest in which my observations were made was second growth with a more uniform vertical distribution of foliage.

The Warbling Vireo has also been considered a gleaner of arthropods from foliage (Bent 1950, Root 1967), but one that prefers to forage in the tree tops (Sutton 1949, Hamilton 1962). I noted a significant use of the upper-most strata for feeding by Warbling Vireos; however, this vireo also forages in the lower parts of trees, and occasionally places a nest in the lower branches of tall trees.

My observations show Yellow-throated Vireos to be neither habitual treetop foragers nor habitual gleaners from foliage as suggested by Bent (1950), Hamilton (1962), or Williamson (1971). This vireo not only foraged on the lower limbs of trees but also showed as great a vertical foraging amplitude as the other 2 species. Again habitat characteristics may explain many of the differences. Williamson (1971) worked in mature climax forests. When Yellow-throated Vireos were observed in such habitat in Ontario, where trees

reached 30 m in height, the birds tended to forage higher in the trees. But, much of the habitat was not climax forest but shorter, dispersed, second growth. I even noted Yellow-throated and Red-eyed vireos on the ground and Warbling Vireos within 15 cm of the ground. Sutton (1949) reported Yellow-throated Vireos nesting near the ground. Moreover, my study has indicated that the Yellow-throated has a foraging niche distinct from that of Warbling and Red-eyed vireos. The Yellow-throated Vireo forages in a manner similar to that suggested for the Solitary Vireo, searching the bases of horizontal branches and the numerous dead stubs that occur in a forest (Kendeigh 1945, 1947:56). It is not surprising to find such a resemblance between these 2 vireos when the suggested evolutionary origin of Yellow-throated from Solitary vireos is considered (Hamilton 1958). The habit of Yellow-throated Vireos, of spiralling upward about the trunk on the bases of branches, is also reminiscent of the actions of Bell Vireos (*V. bellii*), when foraging in large trees (Barlow 1962). The presence and importance of such distinct foraging niches has been clearly demonstrated among numerous other sympatric species (Hartley 1953, MacArthur 1958, Gibb 1960, Stallcup 1968).

Nine of 10 Red-eyed Vireo nests in my study area were placed in forests with abundant understory. This is consistent with the reported habitat requirements of this bird (Sutton 1949). One nest was placed in a small bush near a grove of taller trees, more typical of nest placement in more northern areas (Lawrence 1953) where they may nest in mixed forest, but still require a high percentage of broadleaved trees to which they largely confine their activities (Kendeigh 1945, 1947:56).

The Warbling Vireo was found nesting in open habitat ranging from open parkland with isolated trees and small groves where flights of up to 100 m might be made between foraging sites, to the open edge of forest inhabited by Red-eyed Vireos. The amounts of understory and canopy cover distinguished the habitats of Red-eyed and Warbling vireos on my study area, consistent with the reported preferences of these species (Bent 1950). The choice of habitat by Red-eyed and Warbling vireos appears to be on the basis of general habitat configuration, (similar to that reported by James, 1971, for these species), rather than tree species composition.

Yellow-throated Vireos occupied a greater range of habitat type than either of the other species. Bent (1950) and Sutton (1949) indicated that the Yellow-throated Vireo may forage and nest in habitats preferred by either of the other species. I recorded territorial overlap between Yellow-throated and both Warbling and Red-eyed vireos, although I noted no instance of Red-eyed or Warbling vireos nesting closely enough to overlap one another. An examination, then, of some of the factors facilitating this ecological overlap seems appropriate.

The habitat of Yellow-throated Vireos is usually somewhat different, although overlapping that of the other species. Yellow-throated Vireos generally occupy more open parts of woods (Sutton 1949) or areas with little understory when nesting near Red-eyed Vireos. The Yellow-throated Vireos were the only species to show a preference for large oak trees which were nesting sites or present in large numbers in 6 of 10 territories. The only species I saw foraging in white pines (*P. strobus*) and rarely in tamarack (*Larix laricina*) and norway spruce (*Picea abies*) was the Yellow-throated Vireo. On one territory white pines made up nearly 50% of the mature trees and such conifers are occasionally used for nesting sites by Yellow-throated Vireos (Bent 1950). Red-eyed Vireos have been reported nesting in conifers (Williams 1946) or making limited use of spruce trees for foraging (Kendeigh 1947:56), but the Solitary Vireo, more closely related to the Yellow-throated Vireo, is the only species which regularly nests in conifers. Tree species composition then may also be important in the habitat choice of Yellow-throated Vireos, as is the general habitat configuration.

Visual characteristics have been considered of lesser importance as isolating mechanisms than habitat separation, because vireos as a group have been considered to show little difference in coloration (Hamilton 1962). Vireos do possess distinct plumage patterns and the bright yellow breast and eye ring, and the white wing bars of Yellow-throated Vireos, must not be overlooked as possible recognition marks serving to reduce interspecific strife, as in other species (Kroodsma 1974).

The songs of vireos, however, seem to be far more important in interspecific recognition. Playback experiments with vireo song strongly suggest that the vireos were able to differentiate readily between songs, responding only to a conspecific song. Sutton (1949) considered song an adequate isolating mechanism in vireos because he had never seen fights between vireo species in 14 years of observations, although he had several times seen Yellow-throated Vireos in the same tree as one of the other vireos.

Just as playback of recorded congeneric song aroused little or no reaction, a territorial male vireo singing near the nest of another species provoked no defensive action on the part of the nesting vireo. Aggression resulted only if the intruding vireo actually landed in a nest tree. But the intruder was then chased from the nest tree as was any other small passerine entering the nest tree.

Food selection is apparently one of the most important single factors involved in competitive situations (Lack 1966). Many of the ways related species avoid competition seem to have a direct bearing on allowing the differential taking of foods (Lack 1961:55-72). The bills of these vireos show definite differences in size and proportion sufficient to suggest different prey

selection (see Root 1967). The bills of male and female Red-eyed Vireos show considerable divergence in length and even this difference has been correlated with distinct foraging patterns of the sexes (Williamson 1971).

Chapin (1925) in his analysis of vireo stomach contents indicated little difference in the diet of the 3 vireos, except to point out that Yellow-throated Vireos took a large number of adult moths. Most moths (*Lepidoptera*) are nocturnal, concealing themselves during the day against a dark background such as the bark of trees. Hence, it is not surprising that a vireo searching the bark of trees, would find more moths than vireos searching leaves.

As birds are not dependent upon any specific food, as long as it belongs to a general type (Kendeigh 1947:56), little difference in insect species may be evident. However, arthropods of different sizes or different stages of growth might be chosen by the different vireos. It is unfortunate that Chapin (1925) did not differentiate adult or larval forms or the size of items he found in vireo stomachs.

I seldom observed 2 of these vireo species in the same tree. When observed, they were usually in the nest tree of one of the species, and antagonism was evident. Nevertheless, Yellow-throated Vireos have been observed in the same tree as one of the other species, both apparently unconcerned with the other. This response or lack of it, suggests that ecological isolation is functionally operative, and that territorial exclusion among congeners applies only to the immediate nest area as noted in the genus *Parus* in Europe (Hinde 1952 in Hamilton 1962).

#### SUMMARY

Three sympatric vireos, the Red-eyed, the Warbling, and the Yellow-throated, were the objects of this foraging and habitat study conducted in southern Ontario in the summer of 1966 and 1967.

The foraging behavior of Red-eyed and Warbling vireos was found to be very similar, both species hovering to obtain most of their food from leaves about the periphery of trees. Yellow-throated Vireos foraged in the interior of trees, stalking insects along the branches. A large vertical foraging range is displayed by all 3 vireos. The Yellow-throated Vireo avoids competition with the other species by lateral separation within trees, whereas the Red-eyed and Warbling vireos avoid overlap through habitat selection. Red-eyed prefer shady forests while Warbling Vireos inhabit more open areas, with a scattered assemblage of trees. The Yellow-throated Vireo may overlap both of the other species in habitat choice, and has been observed occupying at least parts of territories occupied by one or the other species. Data on interspecific reactions, and bill morphology tend to support the above results.

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