

## FEEDING ECOLOGY OF THE BLACK-WHISKERED VIREO AND ASSOCIATED GLEANING BIRDS IN JAMAICA

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Although detailed studies have been conducted on many North American vireos, little information is available on the Black-whiskered Vireo (*Vireo altiloquus*) beyond Bent's (1950) brief description and Wetmore's (1916) account of its food habits in Puerto Rico. The Black-whiskered Vireo breeds from the southern coast of Florida to the Bahamas, Greater and Lesser Antilles to Aruba, and on Curaçao, Bonaire, and Margarita islands off Venezuela. Black-whiskered Vireo populations from southern Florida to the northern Lesser Antilles winter mainly in northern South America, whereas populations in Dominica and islands to the south are permanent residents (Bond 1971).

I studied the Black-whiskered Vireo in Jamaica during the spring and summer of 1970, and the summers of 1971 and 1972. This report considers the feeding ecology of the Black-whiskered Vireo and 4 associated gleaners: Jamaican White-eyed Vireo (*V. modestus*), Blue Mountain Vireo (*V. osburni*), Arrow-headed Warbler (*Dendroica pharetra*) and Bananaquit (*Coereba flaveola*) in a middle elevation forest in Jamaica. These 4 resident species were found to be most similar in their foraging behavior to the Black-whiskered Vireo. For information on the species of birds occurring in this region see Cruz (1972). The objectives of this investigation were to obtain quantitative information on: (1) the distribution and population densities of the Black-whiskered Vireo; (2) the food and foraging ecology of the Black-whiskered Vireo; and (3) ecological interactions between the Black-whiskered Vireo and these other species.

### STUDY AREA AND METHODS

*The study area.*—In order to get as complete a picture as possible of the biology of the Black-whiskered Vireo in Jamaica, I visited many distinct habitats, ranging from limestone scrub forest at sea level, to montane mist forest at an elevation of 1373 m. My principal study area of 40 ha was in Worthy Park (Lluidas Vale), St. Catherine Parish (ave. elev. 460 m). This area contained a mosaic of habitats, ranging from wooded pasture to dense wet limestone forest; the annual precipitation averaged 185 cm (Asprey and Robbins 1953). The canopy in the wet limestone forest is dense and contains trees up to 30 m or more. The dominant trees are broadleaf (*Terminalia latifolia*), Jamaican cedar (*Cedrela odorata*), sweetwoods (*Nectandra* spp.), bulletwoods (*Daphnopsis* spp.), prickly yellow (*Fagara martinicensis*), trumpet tree (*Cecropia peltata*), figs (*Ficus* spp.), cotton tree (*Ceiba pentandra*) and red birch (*Bursera simaruba*). In the wooded pasture, where some of the original vege-

tation has been removed, dominant trees also included guango (*Samanea saman*), pimento (*Pimento officinalis*), logwood (*Haematoxylum campechianum*), and citrus trees (*Citrus* spp.). Many of the trees in the area supported epiphytes and lianas.

I divided the main study area into 523 quadrats, each 30 × 30 m. Each quadrat was inspected for predominant vegetation and assigned to 1 of 3 major vegetation types: (1) wooded pasture (park-like in appearance with little or no understory present); (2) open wet limestone forest (well developed upperstory with little to moderate understory); and (3) dense wet limestone forest (closed canopy forest, understory moderate to dense).

*Population analysis.*—The population estimates were obtained from a combination of 3 techniques: (1) by the "spot-map" method of Williams (1936) and many others; (2) systematic observations of individual birds; and (3) capture-recapture analysis of netted birds. For each bird observed, its specific position, species identification, movements, etc., were recorded on gridded census maps. All mist-netted birds were examined for sex, age, fat and weight.

*Food and foraging ecology.*—Detailed observations on habitat use, foraging and feeding methods of the birds were made by adaptations of methods used by MacArthur (1958), Cody (1974) and Cruz (1977, 1978). The total number of feeding observations made on *V. altiloquus*, *V. modestus*, *V. osburni*, *C. flaveola* and *D. phareta* were 1087, 315, 118, 519 and 819, respectively. The specific technique involved walking a predetermined route until a bird was encountered. If the bird was foraging, information was recorded as to the foraging heights, zones and behavior. Each time a feeding bird moved more than 1.5 m these data were recorded. Any observation was terminated if a bird disappeared from view for more than 30 sec. The observation period of each individual was limited to 10 min. The foraging height intervals used were: ground, ground–15 cm, 15 cm–1 m, 1–2 m, 2–3 m, 3–6 m, 6–9 m, 9–12 m, 12–15 m, 15–25 m, greater than 25 m. These foraging height boundaries were chosen to approximate the major change in vegetation profile (ground, grassy areas and low shrubs, shrubs and low trunks, small trees and lower canopy, middle canopy, upper canopy, and emerging canopy, respectively). Ground, shrub, tree and aerial zones were identified. The trees were divided into 3 main feeding zones: trunk, inner branches and outer branches. Each of these main zones was in turn divided into 3 subzones: lower, middle and upper. Feeding behavior patterns of the birds in the study area were categorized as: gleaning (foliage, nectar, fruit, limb), hovering (foliage, fruit, limb), sallying, probing and pecking.

The degree of overlap in resource use for species pairs in various categories of the habitat and foraging matrix (height, zone and behavior) was calculated using the similarity index  $o_{ij} = 1.0 - 0.5(p_{ih} - p_{jh})$  where  $o_{ij}$  is the percent overlap and  $p_{ih}$  and  $p_{jh}$  are the proportions of species  $i$  and  $j$  associated with the resource category  $h$ . The index is standardized and varies from 0 (no overlap) to 1 (complete overlap). This index was first used as an overlap measure by Schoener (1970) and it was chosen because it is straightforward and easy to interpret mathematically. Frequency data were analyzed using the Chi-square test.

*Food analysis.*—I collected 17 adult Black-whiskered Vireos in similar habitats near the study area and examined stomach contents. The stomach and intestinal tracts were removed soon after death and preserved in 75% alcohol. Food samples were separated into animal and vegetable material; volume and frequency of occurrence of each food type were determined. Invertebrates that were essentially whole were keyed to the level of family. Fragmented insects could usually be identified to order, and often to family. Similar methods were used to identify fruit and other vegetable material. Stomach contents were directly compared to insects and fruits collected in the study area.

*Morphological analysis.*—Morphological measurements were obtained by standard mensural methods to see if differences in body structures of possible ecological significance existed among the species. Bill length (exposed culmen) was measured to the nearest 0.1 mm with vernier calipers, and weight was taken to the nearest 0.25 g with a Pesola spring

balance. Bill depth and width are measured at the level of the anterior end of the nares. Other measurements (including additional culmen measurements) are from Ridgway 1902 and 1904. All weights and measurements represent mean values.

#### RESULTS AND DISCUSSION

*Distribution, habitat preference and population densities.*—In Jamaica, most Black-whiskered Vireos arrived in mid-March and departed in early October. Extreme dates were 5 March 1972, at Rocklands, St. James Parish and 28 November 1972, at Port Henderson, St. Catherine Parish (Black 1972, 1973). The other species are permanent residents, although the Arrow-headed Warbler may move to lower elevations during the winter months (Osburn 1859, pers. obs.).

The Black-whiskered Vireo is a very common summer resident and, in fact, it may be the most common passerine species in certain (see below) habitats (Lack 1976, this study). It occurs from sea level mangrove and scrub forests to montane forests at approximately 1500 m in elevation. The Jamaican White-eyed Vireo and the Bananaquit also have a similar distribution, but the Blue Mountain Vireo and the Arrow-headed Warbler are confined mainly to mid-level and montane mesophytic forests.

The highest Black-whiskered Vireo densities were recorded in dry limestone forest (90/40 ha), and in the main study area, wet limestone forest (95/40 ha). The number of individuals was lowest in the mangrove woodlands (26/40 ha) and montane forests (22/40 ha) indicating that, at least in Jamaica, these areas are suboptimal for Black-whiskered Vireos. The high density figures for the Black-whiskered Vireo in the limestone forests are possibly related to the structural complexity of the forest. These forests have a well developed vertical stratification (more pronounced in the wet limestone forest) and high tree species diversity (including many fruiting trees) all of which increase the total area available for foraging.

Population densities of the Black-whiskered Vireo and associated gleaners in the main study area are shown in Table 1. They ranged from a mean of 13/40 ha for the Blue Mountain Vireo to 95/40 ha for the Black-whiskered Vireo. The number of individuals was reasonably constant from year to year.

Table 2 shows the percent occurrence of the different species in each of the different vegetation types present in the study area. When the percentage of time the bird spent in a vegetation type exceeds the percentage occurrence of that vegetation, some vegetation preference exists. The Blue Mountain Vireo and the Arrow-headed Warbler were found mainly in dense forests (89 and 87%, respectively), and were never found in more open areas. They were also the least common species in the area (Table 1). The Black-whiskered Vireo and the Bananaquit ranged from

TABLE 1  
POPULATION DENSITIES (INDIVIDUALS/40 HA) OF THE BLACK-WHISKERED VIREO AND  
ASSOCIATED GLEANERS IN THE MAIN STUDY AREA

	June 1970	June 1971	June 1972	$\bar{x}$ average
<i>Vireo altiloquus</i>	89	105	91	95 (42%) <sup>1</sup>
<i>Vireo modestus</i>	46	50	49	48 (21%)
<i>Vireo osburni</i>	13	12	15	13 (6%)
<i>Dendroica pharetra</i>	21	24	19	21 (10%)
<i>Coereba flaveola</i>	42	51	48	47 (21%)

<sup>1</sup> Percent of total number of individuals present.

wooded pasture to dense woodlands, but were more common in the open forest (41 and 39%, respectively). The Jamaican White-eyed Vireo was occasionally found in more open forest, but it was usually found in wooded areas with understory present (Table 2).

*Foraging ecology.*—The average overall overlap values (height, behavior, zone and habitat overlap) for each species pair are shown in Table 3. A more detailed view of the differences in overlap can be obtained by noting the amount of overlap in each specific microhabitat and foraging category (Tables 2, 3).

Fig. 1 summarizes the heights at which birds were seen foraging. Between species differences in foraging heights were significant ( $P < 0.01$ ). Black-whiskered Vireos foraged at a significantly greater height ( $P < 0.01$ ) than the other species, with 86% of its foraging being done in the middle and upper levels of trees (6 m or greater). Both White-eyed and Blue Mountain vireos foraged below 6 m (72% and 58%, respectively) and the

TABLE 2  
PERCENTAGE OF OBSERVATIONS OF THE BLACK-WHISKERED VIREO AND ASSOCIATED  
GLEANERS IN THE MAIN STUDY AREA IN EACH VEGETATION TYPE

Vegetation type	Wet limestone forest		Wooded pasture
	Open 22.8%	Dense 49.4%	27.8%
Percent occurrence			
<i>Vireo altiloquus</i>	43%	31%	26%
<i>Vireo modestus</i>	33%	53%	14%
<i>Vireo osburni</i>	11%	89%	—
<i>Dendroica pharetra</i>	13%	87%	—
<i>Coereba flaveola</i>	39%	36%	25%

TABLE 3  
 PERCENTAGE OVERLAP FOR SPECIES PAIRS ALONG VARIOUS ASPECTS OF A FORAGING  
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Species pairs	Foraging height	Foraging zone	Foraging behavior	Habitat overlap	Mean overlap
<i>Vireo altiloquus</i> <i>Vireo modestus</i>	0.52	0.72	0.56	0.78	0.65
<i>Vireo altiloquus</i> <i>Vireo osburni</i>	0.41	0.31	0.47	0.42	0.40
<i>Vireo altiloquus</i> <i>Dendroica pharetra</i>	0.72	0.63	0.46	0.44	0.56
<i>Vireo altiloquus</i> <i>Coereba flaveola</i>	0.68	0.68	0.49	0.95	0.70
<i>Vireo modestus</i> <i>Vireo osburni</i>	0.83	0.84	0.83	0.64	0.72
<i>Vireo modestus</i> <i>Dendroica pharetra</i>	0.79	0.59	0.70	0.66	0.69
<i>Vireo modestus</i> <i>Coereba flaveola</i>	0.80	0.55	0.39	0.83	0.64
<i>Vireo osburni</i> <i>Dendroica pharetra</i>	0.65	0.45	0.77	0.97	0.71
<i>Vireo osburni</i> <i>Coereba flaveola</i>	0.70	0.54	0.45	0.47	0.59
<i>Dendroica pharetra</i> <i>Coereba flaveola</i>	0.92	0.73	0.30	0.49	0.61

overlaps in foraging heights with the Black-whiskered Vireo were 0.52 and 0.41, respectively (Table 3). In some cases, the vertical feeding height overlap was high (e.g., 0.72 with the Arrow-headed Warbler and 0.68 with the Bananaquit), but the presence of 2 or more species at a particular height does not necessarily mean competition is occurring, since species may use different foraging zones, foraging behavior, or food items (see below). In addition, the food items may be abundant at certain times, and therefore, not a limited resource (Cruz 1974). For example, feeding assemblages of birds on 2 fruiting trees (*Ficus trigonata* and *Cecropia peltata*) in the same area were investigated (Cruz 1974). A total of 18 species, representing 12 genera and 10 families was recorded. The greatest number of birds observed feeding simultaneously on *Cecropia* was 9, representing 5 species, and on *Ficus* 28, representing 15 species. The large overlap in

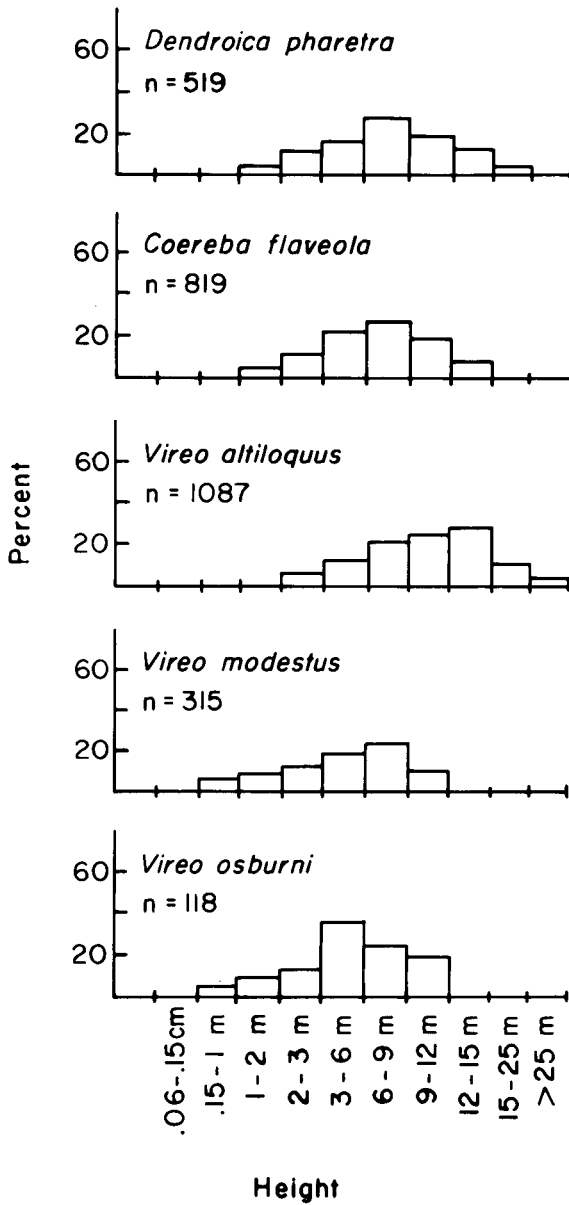


FIG. 1. Distribution of foraging heights of *Vireo altiloquus*, *V. modestus*, *V. osburni*, *Dendroica pharetra* and *Coereba flaveola* in wet limestone forest study area in Jamaica; N = number of observations.

food resource and the minimal degree of interspecific interference observed in that study were probably due to a superabundance of food.

Between species differences in foraging zone usage were significant ( $P < 0.01$ ). The data show that the 5 species did not segregate in an absolute way, but rather, in the frequency with which they used the various foraging zones. The birds differed with respect to the percent of foraging time in foliage (outer branches) and conversely, on stem substrates (inner branches). Thus, the Black-whiskered Vireo, Arrow-headed Warbler and Bananaquit foraged mostly in the middle and upper outer branches, whereas, the Blue Mountain Vireo foraged primarily in the lower and middle branches of trees. The birds also spent very different proportions of their time on shrubby plants, but the Black-whiskered Vireo was never recorded feeding on shrubs and the Arrow-headed Warbler spent only 2% of its time feeding there. Black-whiskered Vireo foraging zone overlap values with other species ranged from 0.31 with the Blue Mountain Vireo to 0.72 with the White-eyed Vireo (Table 3). Highest overlap value was recorded for the White-eyed Vireo and the Blue Mountain Vireo (0.84)—species that foraged mainly in the middle and lower branches of trees and in shrubs.

Between species differences in foraging behavior were also significant ( $P < 0.01$ ). The predominant foraging methods of the Black-whiskered Vireo were gleaning for fruits (50%), foliage gleaning for invertebrates (28%), foliage hovering for invertebrates (7%) and limb gleaning (6%). Hovering for fruits, probing and pecking into limbs and bromeliads accounted for the rest of the foraging procedure (8%).

The variety of fruits eaten by the Black-whiskered Vireo was large; I observed 21 different types of fruits being eaten. Fruits of Moraceae (*Ficus* and *Cecropia*) accounted for nearly 60% of the fruits observed eaten. The majority of fruits were taken from a perched position (gleaning—50%), but occasionally the birds took fruits by hovering (5%). Fruit-eating was also recorded in the other gleaners, ranging from 25% in the Bananaquit to 4% in the Arrow-headed Warbler.

Except for Bananaquits nectar was not a predominant food source. The Bananaquit is primarily a perching nectar feeder (51%), and as such occupies a completely different foraging habitat from the other species in this study. I observed Bananaquits feeding on 16 different species of flowering plants. Ten were large trees, 3 were small trees or shrubs, 2 were herbaceous plants and 1 was a vine. Feeding on fruits accounted for 25% of the total feeding records and these were taken from a perched position. When insect-searching (24%), Bananaquits examine leaves (mainly) and twigs, often hanging upside down to inspect the undersides.

Gleaning for invertebrates accounted for 34% of the total foraging behavior recorded for the Black-whiskered Vireo. This behavior involved

TABLE 4  
FOOD ITEMS FOUND IN THE STOMACHS OF THE BLACK-WHISKERED VIREO IN JAMAICA

Animal taxon	Percent		Plant taxon	Percent	
	Occurrence	Volume		Occurrence	Volume
Mollusca	11.7	5.3	Moraceae	94.1	26.4
Gastropoda	11.7	5.3	<i>Cecropia</i>	47.1	6.1
Pomatiasidae	11.7	5.3	<i>Ficus</i>	70.5	18.3
Arthropoda	88.2	43.3	<i>Trema</i>	5.8	2.0
Arachnida	41.1	3.2	Burseraceae	23.5	6.2
Undetermined	41.1	3.2	<i>Bursera</i>	23.5	7.3
Insecta	88.2	40.1	Butaceae	23.5	7.3
Orthoptera	47.0	13.1	<i>Fagara</i>	23.5	7.3
Blattidae	11.7	3.3	Euphorbiaceae	17.6	4.1
Gryllidae	5.8	4.5	<i>Sapium</i>	17.6	4.1
Tettigoniidae	17.6	5.3	Ulmaceae	5.8	2.3
Hemiptera	17.6	2.3	<i>Trema</i>	5.8	2.3
Pentatomidae	17.6	1.3	Melastomataceae	17.6	8.2
Undetermined	5.8	1.0	<i>Miconia</i>	17.6	8.2
Homoptera	17.6	1.3	Papaveraceae	11.7	1.8
Cicadidae	17.6	1.3	<i>Bocconia</i>	11.7	1.8
Coleoptera	47.1	6.2			
Curculionidae	23.5	4.8			
Cerambycidae	17.6	1.4			
Lepidoptera	70.5	17.2			
Noctuidae	35.2	6.5			
Geometridae	47.1	8.9			
Undetermined	11.7	1.8			
Total	88.2	48.6		94.1	51.4

slow and deliberate searching movements along the branches (6%) and foliage (28%) examining the undersides of leaves and branches above it and the uppersides of leaves and branches on its level, and darting forward or fluttering up to snatch its prey. In the 3 vireos, the manner of searching for food was slower-paced and more deliberate than that of the Arrow-headed Warbler and Bananaquit, and bouts of movements were punctuated with periods of searching surfaces of leaves and twigs. Gleaning for invertebrates in the White-eyed Vireo, Blue Mountain Vireo, Arrow-headed Warbler and Bananaquit accounted for 75, 80, 82 and 24% of the total foraging behavior, respectively. Identifiable invertebrates taken by Black-whiskered Vireos included spiders (Araneae) and Orthoptera, Coleoptera and Lepidoptera.

*Stomach analysis.*—Table 4 presents a list of all food items found in the



stomachs of the Black-whiskered Vireo, as well as percent frequency and percent by volume of each prey in the diet. In the Black-whiskered Vireo diet, both animal and vegetable matter are well represented, with an occurrence of 88.2 and 94.1%, respectively, and comprising 48.6 and 51.4%, respectively, of the total volume. These results are in agreement with the findings of Wetmore (1916) in Puerto Rico, where 84 stomachs of the Black-whiskered Vireo were examined and animal food was found to comprise 42.18% and vegetable, 57.82%.

Animal food included 3 classes, 7 orders, 12 families and a number of unidentified fragments. Insecta predominated in the Black-whiskered Vireo's diet, comprising 40.1% by total volume, with Orthoptera, Lepidoptera and Coleoptera, accounting for 13.1, 17.2 and 6.2% of the total volume, respectively. The proportion of the invertebrate prey found in the stomachs (43.7%) is in close agreement with observation of foraging methods, where gleaning, hovering and probing for invertebrates accounted for 45% of the total foraging.

Fruits and seeds of 7 families and 8 genera were identified with Moraceae, accounting for 26.4% of the total volume. *Cecropia* and *Ficus* spp. predominated with 18.3 and 6.1% of the total volume. Also found were Butaceae (7.3%), Burseraceae (6.2%) and Euphorbiaceae (4.1%). The large and diverse numbers of animal and plant species found in the stomachs of Black-whiskered Vireos suggest that it is exceedingly diverse and opportunistic in its feeding habits, taking nearly all the animal and fruit material that it encounters while foraging.

*Community coexistence.*—The number of species living together in a community depends on several interrelated factors: the range of resources used by each species (its niche width), the tolerable amount of overlap in the use of resources (the limits to similarity) and the total range of resources available to the community (MacArthur 1958, 1972; Hespenheide 1971a). Differences in foraging microhabitat and in diet have been used by other authors as evidence for reduced competition, which makes coexistence possible for closely related species (MacArthur 1958, Crowell 1968, Johnston 1971, and others). Hespenheide (1971b) found that 3 species of eastern flycatchers, which all breed in deciduous forest, actually had different microhabitats. In this study, differences in preferred habitat within a community, in foraging ecology and in the food items consumed are shown, or suggested, to be important factors permitting coexistence.

Hamilton (1962) felt that habitat co-occupancy was seldom found in species of *Vireo*, but when it does occur, the species occupy spatially separated portions of the habitats. That is, 1 species will be primarily a thicket and lower tree branch forager, and another will be primarily an

arboreal crown forager of the same habitat. He has further indicated that such species usually are members of different subgenera that occupy different niches and have different combinations of plumage characters. Examples in North America are the arboreal foraging Red-eyed Vireo (*V. olivaceus*, subgenus *Vireosylva*: wingbars and eye-rings absent) and the thicket foraging White-eyed Vireo (*V. griseus*, subgenus *Vireo*: eye-rings and wingbars usually present). In this study, illustrating the above phenomenon, the arboreal foraging Black-whiskered Vireo (subgenus *Vireosylva*) was found with the lower branch and thicket foraging Jamaican White-eyed Vireo and Blue Mountain Vireo (both in subgenus *Vireo*). However, Lack (1976) and I (present study) also found members of the same subgenus (*Vireo*, Jamaican White-eyed Vireo and Blue Mountain Vireo) occupying similar habitats. Barlow (pers. comm.) feels that *V. osburni* and *V. modestus* do not belong to the same subgenus. He notes that "*V. osburni* is probably a very primitive vireo surviving as a relict on Jamaica—from a time when shrike-vireos (*Vireolanus*) and the Vireonidae were separating from early protovireo populations. Or, *V. osburni* is an early, but surviving, *Lanivireo* (i.e., *V. solitarius* and *V. flavifrons*, which have been in their own subgenus, *Lanivireo*, from time to time). Morphology, behavior (vocal and physical), ecology and multivariate phenetic studies all support this latter hypothesis."

In the case of the Blue Mountain and the Jamaican White-eyed vireos, there was a large overall overlap (0.77), but differences in habitat preferences were noted (0.64 overlap). In addition, the difference in body size (48%) and bill size (31%) (Table 5) suggests that these birds could be using food resources differing on the basis of size. Schoener (1965) has shown theoretically that sympatric, congeneric or closely related species of nearly the same body weight, or bill size, would be likely to subdivide food by feeding on similar-sized prey in different microhabitats. When differences in body and bill size are larger it is probable that coexistence (assuming that food is in limited supply) in the same microhabitat is achieved through selection of different sizes of prey. Schoener (1965) compared the ratios of character differences, defined as the ratio of bill lengths of the larger to the smaller species, of groups of species in several families of birds, and he was able to define a zone of transition from small to large ratios, at approximately 1.14, about which it becomes feasible for 2 species to partition food by size, rather than by microhabitats. Schoener's (1965) formulation assumed that body size is correlated with size of prey taken, and that this assumption would likely hold for bill size. Using the data in Table 5, I calculated ratios of character differences for bill dimensions and body weight for the Blue Mountain Vireo and the Jamaican White-

TABLE 5  
WEIGHTS AND MEASUREMENTS OF BLACK-WHISKERED VIREO AND OTHER JAMAICAN CLEANERS<sup>a</sup>

Species	Weight (g)	(N)	Exposed culmen (mm)	(N)	Bill depth <sup>b</sup> (mm)	(N)	Bill width <sup>b</sup> (mm)	(N)	Wing (mm)	(N)	Tail (mm)	(N)	Tarsus (mm)	(N)
<i>Vireo altiloquus</i>	17.9	(27)	16.4	(27)	4.9	(7)	4.1	(8)	82.8	(7)	57.6	(7)	18.9	(7)
<i>Vireo modestus</i>	10.1	(6)	9.0	(10)	3.9	(3)	4.0	(3)	56.4	(10)	48.5	(10)	18.7	(10)
<i>Vireo osburni</i>	19.2	(2)	13.0	(1)	6.4	(2)	5.0	(2)	72.0	(1)	58.0	(1)	21.0	(1)
<i>Dendroica pharetra</i>	10.9	(4)	10.8	(6)	3.8	(4)	4.0	(4)	62.5	(6)	52.1	(6)	18.7	(6)
<i>Coereba flaveola</i>	8.1	(10)	12.0	(6)	4.1	(6)	4.2	(6)	58.0	(6)	36.9	(6)	16.4	(6)

<sup>a</sup> The weights and bill measurements are from the author's unpublished data, and represent mean values. Other measurements (including additional culmen measurements) are from Ridgway 1902 and 1904.

<sup>b</sup> Bill depth and width are measured at the level of the anterior end of the nares.

eyed Vireo, following Schoener's method. As predicted by Schoener's model, it is feasible for the Blue Mountain and the Jamaican White-eyed vireos to feed on different sized insects in the same habitats when they occur together because the ratio of bill length (1.4) and body weight (1.9) is larger. Hespentheide (1971b) confirmed Schoener's assumption by demonstrating a strong correlation between size of insect prey and both body size and bill size of their avian predators, although the former is the more strongly correlated of the two in several families of birds, including Vireonidae. However, Hespentheide (1974) in a reanalysis of his data, notes that although mean prey size increases with predator size within each foraging guild, prey size is not as strongly correlated either with body size, or bill size, as it is with foraging method. Foraging differences which affect the choice of prey type and prey size seem the most likely explanation for the close correlation of prey size and prey type in the absence of close correlation of either with bird size.

#### SUMMARY

This study considers the feeding ecology of the Black-whiskered Vireo and 4 associated gleaners: Jamaican White-eyed Vireo, Blue Mountain Vireo, Arrow-headed Warbler and Bananaquit in a middle elevation forest (460 m) in Jamaica. In Jamaica, the Black-whiskered Vireo is migratory, the majority arriving in mid-March from northern South America and departing in early October. The Black-whiskered Vireo is perhaps the most common passerine in certain habitats. This species occurs from sea level mangrove and scrub forests to montane forests, up to 1500 m.

Differences in foraging ecology of the Black-whiskered Vireo and associated gleaners were observed. The Black-whiskered Vireo foraged at a significantly greater height than the other vireo species, with 86% of its foraging being done in the middle and upper levels of trees. In some cases, the vertical feeding height overlap was high, but differences in the foraging behavior were noted. The Arrow-headed Warbler fed primarily by foliage and stem gleaning and the Bananaquit fed mainly by nectar gleaning, whereas the Black-whiskered Vireo fed largely on fruit and by foliage gleaning. For the Black-whiskered Vireo and associated gleaners, differences in their preferred habitat within a community and differences in their food and foraging ecology were shown, or suggested, to be important factors permitting coexistence.

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