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# FRUGIVORY AND COEXISTENCE IN A RESIDENT AND A MIGRATORY VIREO ON THE YUCATAN PENINSULA<sup>1</sup>

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**Abstract.** The White-eyed Vireo (*Vireo griseus*) and the Mangrove Vireo (*V. pallens*) are two of the most common species of insectivorous bird on the Yucatan Peninsula. Mangrove Vireo pairs maintain year-long territories primarily in scrub, whereas individual White-eyed Vireos defend territories in a broad range of terrestrial habitats. The two species show a strong reciprocal distribution along a successional gradient from regenerating pasture and old field to mature dry forest. Within second growth scrub, White-eyed Vireos are primarily associated with patches of trees. Despite minor morphological differences typical of migrant-resident comparisons, we found no significant differences in the rates of different locomotory movement, in the relative proportion of attack type used, nor in foraging substrate. The major foraging differences were a lower reduced attack rate and greater use of fruit (primarily *Bursera simaruba*) in the White-eyed Vireo. Playback experiments failed to draw significant interspecific responses to song playback and elicited weak responses to conspecific and heterospecific chatter calls. Simultaneous call-in experiments and opportunistic observations failed to provide evidence of interspecific aggression. White-eyed Vireos, however, consistently chased Mangrove Vireos out of fruiting *Bursera*. We hypothesize that the extensive use of *Bursera* fruit allows White-eyed Vireos to over-winter in mature forest on the Yucatan Peninsula, a habitat that apparently cannot support breeding by vireos in the White-eyed Vireo complex.

**Key words:** *Vireo; frugivory; Neotropical migrant; foraging; aggression.*

## INTRODUCTION

Competition forms the backbone of most theories regarding the winter distribution of migratory birds. Competition hypotheses have focused on interactions between closely-related migratory species (Salamonson 1957, MacArthur 1958, Cox 1968, Chipley 1980) or between migratory and resident components of a local avifauna (Willis 1966, Leck 1972, Waide 1980, Ricklefs 1992) with little attention given to ecological interactions between closely-related sympatric resident and migratory species (or populations within a species, but see Barlow 1980). However, the period during or immediately following speciation is when selection for separation by macro-habitat or geography may be most intense (Lack 1944, Cox 1968). Therefore, potential interactions with congeners may have a particularly im-

portant role in the distribution of overwintering migrants.

The Mangrove Vireo (*Vireo pallens*) and White-eyed Vireo (*Vireo griseus*) are closely-related (Hellmayr 1935, Paynter 1955, Hamilton 1958, Blake 1968, Parkes 1990). A few authors have considered them conspecific because of their allopatric breeding distribution and morphological similarity (Hellmayr 1935, Paynter 1955, Hamilton 1958, Smithe and Paynter 1963). However, most workers familiar with both species in the field consider them to be very closely-related species, part of a larger complex including several West Indian species (Chapman 1896, Miller et al. 1957, Hamilton 1962, Russell 1964, Monroe 1968).

Both species are among the most common in terrestrial habitats of the Yucatan Peninsula (Paynter 1955, Lynch 1989). Mangrove Vireos occur throughout the year in early stages of second growth and White-eyed Vireos can be found

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throughout the winter (October–mid April) in a variety of habitats.

This paper summarizes the habitat distribution, ecological morphology and foraging ecology of the two species of vireos. We also report experiments testing for response to playback song and chatter (both White-eyed Vireo and Mangrove Vireo are territorial and sing in the non-breeding season) and to the close approach of heterospecific territory holders.

## STUDY SITE

The research was conducted as part of a project on the ecology of migrants in and around the Sian Ka'an Biosphere Reserve, on the road to Vigia Chico, northeast of Felipe Carrillo Puerto, Quintana Roo. The vegetation is a mosaic of mature and regenerating tropical dry forest (approximately 1.2 m rainfall/year), which has two distinct phases: a low canopy subdeciduous forest and a medium canopy subperennial forest (Olmsted et al. 1983). The forest types differ in overall stature (Greenberg 1992) as well as degree of leaf loss during the long dry season (January–June). Although forest covers most of the area, there are small areas of recently cleared cattle pasture and milpa, and larger areas of regenerating cattle pasture and burns, mostly 5–7 years of age at the time of the study.

## METHODS

### ECOLOGICAL MORPHOLOGY

We compared the external morphology of the two species by measuring study skins in the U.S. National Museum of Natural History collection. To reduce possible confounding effects of sexual dimorphism, we compared measurements of males. We measured 21 specimens each from Mangrove Vireos from the Yucatan Peninsula and Peten and White-eyed Vireos from scattered localities in the eastern United States. Because we found no statistically significant difference in the measurements of *Vireo griseus griseus* and *V. g. noveboracensis*, we pooled White-eyed Vireo measurements to compare to Mangrove Vireos. One of us (DN) measured the following to the nearest 0.1 mm using dial calipers: bill length, width and depth (at anterior edge of nares); unflattened wing cord; tarsus; and tail length. In addition, we obtained an index of wing pointedness (Gaston 1974) based on the difference between the length of the longest primary and

primary no. 1. Body mass was obtained from specimens netted in northern and central Quintana Roo. We found no significant difference in fat scores for the two species, so the masses are directly comparable.

### HABITAT DISTRIBUTION

We established six one-km census transects as part of a broader study of the distribution of birds in the Sian Ka'an Biosphere Reserve and Vicinity (Greenberg 1992). The transects were established in a partially active and partially abandoned farm and included: a one year-old cattle pasture (cleared, but with no planted grass); an area of 5–7 year-old grazed second-growth habitat (grazed acahual); an area of 5–7 year-old ungrazed second-growth habitat (ungrazed acahual); a semi-deciduous (short) forest (canopy ht. =  $10.2 \pm 0.2$  m SE); and a medium stature subperennial (tall) forest (canopy ht. =  $13.2 \pm 0.3$  m). Transects were censused weekly between 1 October 1987 and 30 March 1988, and 25 October 1988 and 30 March 1990. We conducted censuses by walking the transect and counting all birds heard or seen within 20 m of the transect. We recorded the location of each vireo to the nearest  $50 \times 40$  m transect unit. Repeated censuses were used so that a profile of the distribution of vireos could be compared to the pattern of vegetation structure. The distribution along the ungrazed acahual transect, where both species were common, was compared with values for several vegetation variables measured for each  $5 \times 40$  m unit. Measurements were taken for 10 evenly spaced circular plots (2 m radius) per unit and include the number of stems of varying dbh (0–1.0 cm, 1.1–2.0 cm, 2.1–5.0 cm, 5.1–10.0 cm, 10.1 + cm dbh), maximum plant height, estimated ground cover (to nearest 10%) and total number of trees greater than 5 m ht./transect unit.

### FORAGING DATA

We gathered foraging data by observing in appropriate habitat and recording the location, locomotory movements, and foraging attack methods of vireos. Individual vireos were followed for variable periods and only sequences greater than 30 sec were used for analysis. Average sequences lasted 77 sec for White-eyed Vireos and 66 sec for Mangrove Vireos. Additional data on foraging attack methods were gathered on 150 additional White-eyed and 45 additional Man-

grove Vireos. We spent a disproportionate amount of time at ecotones and intermediate habitats so that individuals of either species could be followed. Because of this, foraging variables that reflect habitat use (tree height, plant type) can be used to compare the relative habitat use by species, but not to generate estimates of absolute habitat use. The location variables, recorded once per individual, include height of bird, height of plant, leaf size of plant, and perch branch angle and diameter. Locomotory variables include the number and estimated length of hops (branches changed without the use of wings), creeps (branch not changed) and flights (branch changed, wings used). For a subset of the sequences, we recorded the vertical direction of flights (up, down, horizontal, approximately 45°). Foraging maneuvers were classified based on a system modified from Remsen and Robinson (1990). The following attack maneuvers were recognized: glean, where a perched bird plucks food item from substrate; reach, where bird cranes upward from a perch to grab prey item; leap, where a bird attacks upward propelled by legs or wings (includes upward strike and leap of the Remsen and Robinson system [1990]); hover, where bird strikes upward and remains stationary with rapid wing beating; lunge, bird rushes horizontally or downward; and hang, bird grabs on side or undersurface of substrate while gleaning or probing. Other tactics were rare. The taking of large prey items or fruit were recorded as well.

#### FRUGIVORY

To explore in detail interactions at fruiting trees, we examined data gathered during a study of the use of the fruit of *Bursera simaruba* by White-eyed Vireos (Greenberg et al., in prep.). We also watched two fruiting trees in small patches of trees of the grazed acahual, recording all visits, fruit consumed, and aggressive interactions. We watched each tree between 05:30–09:30 at least five days (one in October and one in March). All local White-eyed Vireos and several Mangrove Vireos were color-banded. In addition, we watched a fruiting *Bursera* at the Uxmal archaeological site for six hours which also received visits by both White-eyed and Mangrove vireos.

#### PLAY-BACK RESPONSE EXPERIMENTS

We conducted playback trials 13–23 October 1989 during the first 3 hr after sunrise. Based on

censusing during the prior year, this represents the peak period of arrival of White-eyed Vireos at Sian Ka'an. Trials were conducted by systematically selecting points within the most appropriate habitat for each species based on two years of census work. Playback points were established along transects at approximately 200 m. If we heard a member of the target species before we began a trial, the playback point was advanced an additional 100 m.

A Sony TCM 5000 EV recorder was placed on the ground with the speaker directed upward. Observers (SH and CB) positioned themselves 5 m on either side of the recorder. Stimuli tapes were constructed to include baseline, playback, and residual periods during which the observers recorded the number of chatterbursts, the number of songs, approaches (bird observed or heard moving in direction of speaker), approaches within 5 m of the speaker, latency to approach within 5 m of the speaker, and number of flights over the speaker.

At each playback point, we presented either chatterburst or song playbacks. One of the three types of chatter were presented in a particular trial: White-eyed Vireo, Mangrove Vireo, or a non-vireo control consisting of the chatter of the Carolina Wren (*Thryothorus ludovicianus*) or White-bellied Wren (*Uropsila leucogastra*). In the song trials, each trial presented songs from one of the vireo species. Categories of both song and chatter were alternated between playback points to minimize the indirect arousal of neighboring individuals. Chatter and song trials were not conducted in the same areas within 72 hr. Chatter and song trials were mixed over an 11-day period.

From bioacoustic libraries and private collections, we obtained recordings of eight different songs and two different chatters of Mangrove Vireo recorded on the Yucatan Peninsula. We selected an equal number of different songs and chatter segments from our recordings of White-eyed Vireos from southwestern Virginia. Recordings of one chatter segment each were used for the two wren species.

All recordings were band-pass filtered at 500–800 kHz, digitized using a 16 kHz sampling rate, rescaled so that the peak amplitudes in all stimuli were matched, reconverted through the D-to-A and input to a cassette deck for reconstructing playback tapes.

For the song trials, we constructed tape segments consisting of 2 min of silence, 30 repeti-

tions of the song in 6-sec onset-onset intervals (3 min), then 2 min more of silence. At the beginning/end of each of the three segments, we inserted a 250 ms, 4 kHz tone to signal timing during field trials.

To prepare the chatter stimulus tapes we extracted a 3-sec segment of chatter and used repetitions of that segment for the entire presentation. Each tape began with 2 min of silence, 30 repetitions of chatter in 4-sec onset-onset intervals (2 min), followed by a 2-min residual period. All other details of chatter tape presentation were as described above for the song tape. We used two different 3-sec segments from each of the original recordings, giving four chatter playback tapes for each of the Vireo species and four total control tapes.

#### SEQUENTIAL PLAY-BACK AT ECOTONES

We presented 2-min playbacks of songs of each species sequentially within forest and acahual 10 m from the same point along the ecotone. The experiment was conducted at a total of eight points along the ecotone, located at least 100 m apart. The order of habitat was alternated between points, and the order of species presentation was alternated between presentations for a particular habitat. For up to 3 min after song presentation, we recorded when a bird approached within 5 m of the speaker or another vireo. We also recorded all interactions between vireos. The purpose of this experiment was two fold: to determine how far into the less preferred habitat individuals of each species will approach the simulated encroachment of a conspecific, and to see how vireos that are stimulated to approach a potential encroaching conspecific, respond to the presence of a responding heterospecific on their territory.

### RESULTS

#### ECOLOGICAL MORPHOLOGY

Although morphologically similar, White-eyed and Mangrove vireos differ significantly in several mensural characteristics (Table 1) resulting in virtually no overall overlap (a DFA based on specimen measurements correctly classified, *a posteriori*, 98% of the specimens [Wilkinson 1987]). The tail, wing chord and wing pointedness of the Mangrove Vireo all measure lower than those of the White-eyed Vireo (tail 12%, wing cord 10% and wing pointedness 29%), but the tarsii are 4% longer. Based on field measure-

TABLE 1. Measurements of Mangrove Vireo and White-eyed Vireo (mm,  $\bar{x}$  + SE).

Characteristic	Mangrove Vireo	White-eyed Vireo
Bill length	73.1 (1.23)	70.9 (0.06)
Bill width	36.4 (0.08)	36.1 (0.04)
Bill depth	40.0 (0.11)	40.1 (0.04)
Tarsus	196.4 (0.21)	188.4 (0.11)** <sub>a</sub>
Length of tail	436.3 (0.95)	499.2 (1.66)**
Unflattened wing	537.2 (0.96)	603.4 (0.30)***
Roundness of wing	71.7 (0.48)	109.3 (0.26)***
Weight (g)	9.2 (0.15)	11.0 (0.19)***

<sup>a</sup> Significance of difference based on student's *t* test corrected for multiple comparisons \*\*  $P < 0.005$ ; \*\*\*  $P < 0.001$ .

ments, we found that body mass was 15% smaller in the Mangrove Vireo. Based on a 4.5% reduction in the cube root of body weight compared to White-eyed Vireo, the Mangrove Vireo has a disproportionately long tarsus, short tail and short and more rounded wing.

#### HABITAT DISTRIBUTION

The two species show a strongly complementary distribution pattern along the successional gradient represented by the census transects (Fig. 1). Mangrove Vireos are restricted to the pasture, farm and scrub habitats with a few individuals in *tintales* (seasonally flooded depressions within the forest that support a lower stature vegetation type [Olmsted et al. 1983]). White-eyed Vireos are less specialized, but largely restricted, nonetheless, to forest. A more fine-scaled analysis of the ungrazed acahual, the scrub transect with moderate numbers of White-eyed Vireos, also shows a negative correlation between the number of sightings of the two species within the 40 × 50 m transect units ( $r = -0.40$ ,  $n = 267$  sightings in 20 units). White-eyed Vireo sightings were positively correlated with the total number of trees per transect unit ( $r = 0.50$ , 71 sightings) and plant stems greater than 5 cm ( $r = 0.45$ ) showed no significant correlation with other vegetation variables (ground cover, mean canopy height). Stem density greater than 5 cm and total trees were the only two vegetation variables that were significantly correlated ( $r = 0.62$ ). Mangrove Vireos sightings showed a weak, but significantly negative correlation with total trees/unit ( $r = -0.44$ ) and a positive correlation with percent ground cover ( $r = 0.42$ ).

#### WINTER SOCIAL ORGANIZATION

Based on the observation of 15 color-marked birds (seven in acahual and eight in forest) we

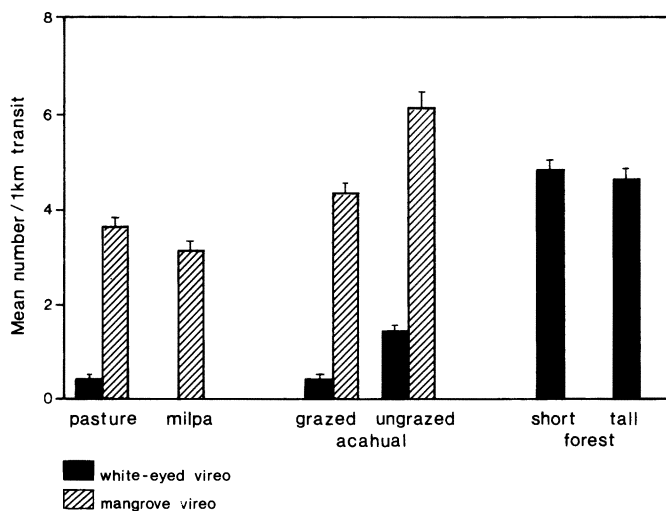


FIGURE 1. Mean and standard error of sightings of White-eyed and Mangrove vireos per 1 km transects ( $n = 37$  counts/transect over two years).

found that White-eyed Vireos were consistently territorial (average territory size was approximately  $\frac{1}{2}$  ha). All birds were found to be resident on territory for at least two weeks and seven of the eight birds monitored through the winter remained on territory. Trespassing to *Bursera* trees on neighboring territories was commonly observed when conducting focal watches of these trees (Greenberg et al., ms.). These individuals were almost invariably chased back into their territories. Mangrove Vireos occur primarily in

pairs throughout the winter and although we had only a few color-banded, their behavior was consistent with year-long territories. Both species commonly sing during the winter months.

#### FORAGING BEHAVIOR

We found no significant difference in the locomotion of foraging vireos (Table 2). The two species made an average of approximately 13 moves per minute of which a majority were hops. This is considerably lower than the 17 moves/

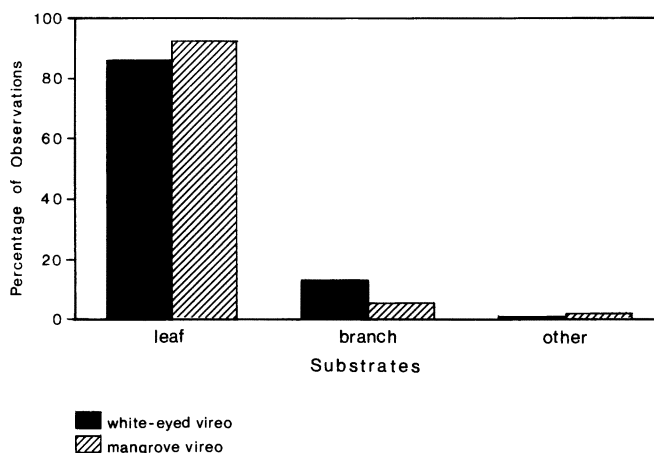


FIGURE 2. Proportion of observed insectivorous foraging attacks directed to different substrates ( $n = 109$  for White-eyed Vireo and 207 for Mangrove Vireo). Within foliage insectivory both species showed a similar preference for leaf under surfaces ( $75.2 \pm 2.3\%$  for White-eyed Vireo;  $77.8 \pm 3.4\%$  for Mangrove Vireo).



TABLE 2. Mean and standard error of major foraging variables recorded during focal watches.

	Mangrove Vireo	White-eyed Vireo
Foraging rate <sup>a</sup>	1.54 + 0.21	1.01 + 0.14 <sup>*b</sup>
Creep rate	1.94 + 0.29	1.34 + 0.18
Hop rate	7.46 + 0.44	7.08 + 0.52
Flight rate	2.92 + 0.20	3.37 + 0.39
Total rate	13.87 + 0.58	12.79 + 0.67
Creep distance <sup>c</sup>	13.44 + 2.22	11.02 + 1.80
Hop distance	92.43 + 8.35	87.26 + 12.24
Flight distance	320.71 + 41.09	306.57 + 32.52
Flight orientation (% up, level, down)	19:59:21 (708)	23:61:16 (813)
Total distance	426.58 + 43.40	404.86 + 36.19
Feeding height (m)	2.91 + 0.17 (88) <sup>d</sup>	5.20 + 0.31 (86) <sup>**</sup>
Relative height (m)	0.65 + 0.02 (86)	0.67 + 0.05 (81)
Leaf area (cm <sup>2</sup> )	25.50 + 3.74 (73)	32.07 + 3.89 (61)
Branch diameter	8.7 + 0.31 (178)	9.2 + 0.38 (293)
Branch angle	42.3° + 2.7 (173)	37.5 + 3.2 (293)

<sup>a</sup> All rates denote number of maneuvers/minute. Sample sizes are: Mangrove Vireo,  $n = 143$ ; White-eyed Vireo,  $n = 144$ .

<sup>b</sup> Significance of difference between species based on student's  $t$  test corrected for multiple comparisons \*  $P < 0.05$ , \*\*  $P < 0.001$ .

<sup>c</sup> All distances denote cm/minute. Sample sizes are: Mangrove Vireo,  $n = 104$ ; White-eyed Vireo,  $n = 102$ .

<sup>d</sup> All  $n$  values are in parentheses.

min found by Williamson (1971) for White-eyed Vireos during the breeding season. The estimated distance moved was similar (4.27 m/min vs. 4.06 m/min) for Mangrove and White-eyed vireos and there was no significant difference between species in the distance moved by creep, hop or flight. In terms of distance moved, flights accounted for over 75% of the distance moved. There was a small, but significant difference in the vertical orientation of flights (Table 2). The only rate difference was found in the frequency of prey attacks which was 50% greater in Mangrove Vireo than in White-eyed Vireo ( $P < 0.05$ ). The value of 1.0 prey attacks per min in the White-eyed Vireo is similar to the 1.2 attack/min found by Williamson (1971) on the breeding grounds. The type of foraging attack used and the substrate attacked was not significantly different between the two species (Fig. 2 and 3). The similarity index (Schoener 1968) are 0.90 and 0.93 (index range = 0–1) respectively.

The two largest differences in foraging between the two species were found in location variables and probably reflect gross habitat differences in where individuals were located. White-eyed Vireos fed higher off the ground. The higher foraging height reflects the White-eyed Vireo's preference for forest and patches of trees in second growth. The relative foraging height (bird height/tree height) was nearly identical for the two species (0.65 vs. 0.67, Table 2). The mean foraging height

for White-eyed Vireos of 5.1 m is probably a low estimate for the population as a whole. We gathered foraging data in areas where both species could be found (edges between forest and second growth). The high density of White-eyed Vireos in forest suggests that the actual mean may be

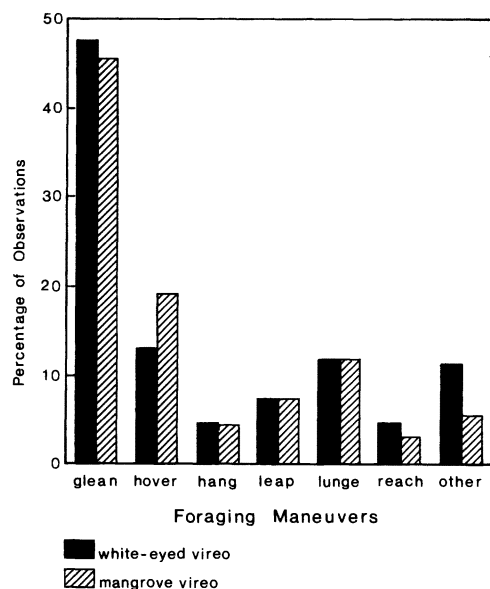


FIGURE 3. Proportion of foraging attacks using different techniques (see Fig. 2 for sample sizes).

TABLE 3. Responses of the White-eyed Vireo and the Mangrove Vireo to a playback of stimulus species' song.

Stimulus species Target species	Flyover		Approach		Increase/decrease <sup>a</sup>	
	% Trials	Median #/trial	% Trials	Median latency	Call rate	Song rate
White-eyed Vireo						
White-eyed	60	1.5	90	45	80/20	40/30
Mangrove	0	0	0	NA <sup>b</sup>	30/0	20/0
Mangrove Vireo						
White-eyed	10	0	10	NA	30/10	10/20
Mangrove	60	1.5	70	40	70/0	70/20

<sup>a</sup> Percent of trials where there was an increased or decreased rate of vocalization during presentation and post presentation compared to presentation period.

<sup>b</sup> NA = No Approach within 5 m.

closer for data taken for White-eyed Vireos foraging along the transects in the forest (mean foraging height =  $10.1 \pm 0.3$  mm SE,  $n = 140$ ).

#### FRUGIVORY

The two species differed significantly in the percentage of birds observed eating fruit. White-eyed Vireos ate fruit significantly more often than Mangrove Vireos ( $\chi^2$ ,  $P < 0.001$ ). Twenty-five percent of the White-eyed Vireos ( $n = 247$ ) versus six percent of the Mangrove Vireos ( $n = 158$ ) were observed eating fruit. This difference is based primarily on the differential use of *Bursera simaruba*, since 96% of all frugivorous observations in vireos involved consuming capsules of this species (Greenberg 1992).

White-eyed Vireos visited the three focal *Bursera* trees in scrub habitat on the average of 0.9 vs. 0.3 times per hr ( $n = 47$  hr) for Mangrove Vireo. The success rate (arils consumed per visit) was almost 10 times greater as well ( $1.17 \pm 0.21$ , vs.  $0.11 \pm 0.07$ ,  $t = 4.6$  df 59, 1.  $P < 0.001$ ). Mangrove Vireos visits were less than half as long as those of White-eyed Vireos ( $43 \pm 3.2$  vs.  $102 \pm 4.7$ ,  $t = 4.6$ ,  $P < 0.001$ ). It was during observations of *Bursera* trees that we observed the only overt aggression between the species; Mangrove Vireos were chased out of the trees by the resident White-eyed Vireo during 45% (9/20) of the visits.

#### PLAY-BACK RESPONSE

Both species responded more strongly to conspecific than heterospecific song. Responses to conspecific song were generally the most intense of all the presentations including frequent flyovers (median = 1.5/trial, 60% of trials Table 3) and rapid approach to within 5 m (median latency = 40 sec, 80% trial frequency). Approaches

were far less common (5%) and slower (median = no approach) for heterospecific songs.

Responses to homo- versus heterospecific vireo calls were similar (Table 4). Flyovers occurred in 30% of both the homo- and heterospecific presentations, close approaches occurred in 50% of both trial types, and latencies averaged approximately 200 sec for both. None of these comparisons involved significant differences. The only significant difference was in the proportion of presentations that elicited increased calling in the presentation and post-presentation parts of the experiment. Vireos increased their calling significantly ( $\chi^2$   $P < 0.01$ ) more in response to homospecific versus heterospecific calls. Vireos were more responsive to vireo than to wren chatter. They approached vireo chatter twice as frequently as wren chatter (50% versus 25%,  $\chi^2$   $P < 0.01$ ) and also flew over significantly more often (30% versus 10%). Vireos did respond to wren chatter by increasing their rate of chatter bursts during 70% of the trials.

#### SEQUENTIAL PLAY-BACK AT ECOTONES

White-eyed Vireos approached within 5 m for seven out of eight of the forest play-back trials. Similarly, Mangrove Vireos responded to six of eight *acahual* trials. White-eyed Vireos also approached in seven of eight of the *acahual* trials, whereas Mangrove Vireos never entered the forest to approach the speaker in the forest trials. During eight trials, Mangrove Vireos approached to the absolute edge of the forest and sang in response to the conspecific playback. The habitat edge was apparently an absolute territory boundary to the Mangrove but not White-eyed Vireos.

During six *acahual* playback trials, individuals of both species approached the speaker and were present within 5 m of the speaker (and each oth-



TABLE 4. Responses of White-eyed and Mangrove vireos to playback of stimulus species' chatter call.<sup>a</sup>

Stimulus species Target species	Flyover		Approach		Increase/decrease <sup>a</sup>	
	% Trials	Median #/trial	% Trials	Median latency	Call rate	Song rate
White-eyed Vireo						
White-eyed	30	0	50	230	50/30	30/10
Mangrove	20	0	70	93	10/10	60/50
Wren	10	—	30	NA	70/0	70/0
Mangrove Vireo						
White-eyed	30	0	30	NA	40/20	50/30
Mangrove	40	0	50	192	80/10	60/20
Wren	10	—	20	NA	70/10	40/10

<sup>a</sup> See notes for Table 3.

er) at the same time. Although vireos remained in the vicinity for several minutes actively flying back and forth and apparently searching for intruders, we recorded no interactions between individuals. On two occasions, Mangrove and White-eyed Vireos perched within 1 m of each other on the same branch.

## DISCUSSION

### COMPLEMENTARY HABITAT DISTRIBUTION

Complementary habitat distribution is supported by the transect census results. Additionally, these results show fine-tuned differences in distribution in transitional habitat (shrubby field with patches of trees). The transects provide relatively little replication for the censusing effort, but the degree of complementarity is supported by the response to play-back experiments. We observed no responses by White-eyed Vireos to White-eyed Vireo songs in scrub habitats and no response by Mangrove Vireos to Mangrove Vireo song in the forest habitat.

Strongly complementary habitat distribution between ecologically similar species can result, in a proximate sense, from aggressive interactions, including interspecific territoriality. Interspecific territoriality has also been reported for at least one pair of Vireo species (Rice 1978). However, playback experiments did not provide any evidence for aggressive interactions between these two species. The strongest responses in both species were to homospecific song. Vireos responded to song with rapid approach to within 5 m of the speaker and low flyovers. These approach behaviors probably reflect a high level of potential aggression. Responses to call notes were weaker (fewer flyovers, longer latency to ap-

proach). It is in the weaker responses to call notes that we failed to find consistent differences in how vireos responded to homospecific and heterospecific calls (although they did respond stronger to vireo than to wren calls). The simultaneous playback experiments demonstrated that vireos called into conspecific songs, ignored nearby individuals of the other species. This lack of response is particularly telling considering that the vireos are approaching the tape recording with aggressive fly-overs and therefore might be sensitized to attack a wider range of stimuli.

### SIMILARITY OF MORPHOLOGY AND FORAGING BEHAVIOR

White-eyed and Mangrove vireos are morphologically and ecologically similar species with complementary habitat distribution. The longer and more pointed wings of the White-eyed Vireo may be related to migratory status (Chapman 1940, Leisler and Winkler 1985) or its use of more open microhabitats for foraging (Poole 1938, Morrison 1982). In most aspects of foraging behavior and location, the two species were indistinguishable. This includes locomotory behavior, attack type and foraging substrate. The degree of similarity, particularly in the type and distance of movement, is surprising given the differences in branch density and arrangement and foliage structure in forest and second growth habitats. This result suggests that despite differences in wing shape, the two species share a particular locomotory stereotypy (Klopfer 1967). However, reduced wing and tail size could allow Mangrove Vireos to perform similar movements to White-eyed Vireos while minimizing feather wear.

*Use of fruit.* The major ecological difference

between the two species is the use of fruit. White-eyed Vireos feed heavily upon the fruit of *Bursera simaruba* throughout the winter. A similar system has been described for the Gray Vireo (*Vireo vicinior*) in western Mexico (Bates 1992). In the forests of Sian Ka'an, *Bursera* produces a crop of up to a few thousand capsules which ripen slowly for a 7–8 month period primarily during the stay of White-eyed Vireos (September–early April). Individual White-eyed Vireos visit trees with fruit on their territory daily. During these visits, they test the indehiscent capsules and swallow the seeds when the capsules fall away from the ripe arils. The importance of the tree to White-eyed Vireos (Greenberg et al., ms.) is suggested by the persistence of vireos visiting the trees, the frequency (25%) of vireos observed visiting trees during foraging observations, and the correlation between the occupancy of small forest patches in agricultural areas and the presence of a territorial White-eyed Vireo (size of patch and canopy height were not correlated).

We observed Mangrove Vireos feeding on *Bursera* capsules, however such events are rare for two reasons. The abundance of *Bursera* and per capita fruit crop is much lower in the scrub habitat. We found *Bursera* fruit to be almost an order of magnitude more dense in forest than second growth habitats (Greenberg et al., unpubl. ms.). The second probable cause is the aggression the White-eyed Vireos' display towards Mangrove Vireos at fruiting *Bursera*. Besides being chased out of the trees, Mangrove Vireos visited for short periods and were less successful at locating ripe fruit during visits than the local White-eyed Vireo. The rate of chasing probably underestimates the importance of dominance, since the short and unsuccessful visits also may result from the overall dominance relationship.

The migrant status of the White-eyed Vireo raises the issue of what limits the distribution of vireos during the period of the year when only the scrub-breeding Mangrove Vireo is present. During the temperate zone winter, virtually all terrestrial habitats on the Yucatan Peninsula support one or the other of the two small vireo species. During the summer months, the presumed breeding season for the Mangrove Vireo, only scrub habitats support a member of the White-eyed Vireo group although the much larger and distantly related Yellow-green Vireo (Johnson et al. 1988) breeds in dry forest.

It is unclear why no member of the White-

eyed Vireo complex breeds in the Yucatan forests. Perhaps vireos cannot compete for arthropod resources in mainland forests with their diversity of foliage gleaning birds. Cox (1985) suggested that migrants can often occur in tropical areas under situations that resident populations cannot, because migrants can use food sources that are poor sources of protein for feeding young. By this argument, the forests of the Yucatan provide appropriate food that can be used by vireos for overwintering, but not for breeding. Fruit is protein poor and therefore a poor resource for raising young (Morton 1973). Furthermore, the particular fruit involved, *Bursera*, is only available during the winter months.

The use of fruit versus insects appears to involve trade-offs. We observed Mangrove Vireos attacking arthropod prey at a considerably higher rate than did White-eyed Vireos. Foliage arthropods are more common in scrubby habitats than in forest understory (Greenberg 1992). Small body size, short tail, and short rounded wings might allow Mangrove Vireos to maneuver through dense foliage with minimum plumage wear. Larger body size and pointed wing in the White-eyed Vireos may be primarily related to its migratory status, but it could also favor its ability to dominate a fruit crop by increasing the speed and force of an aggressive chase. Thus, White-eyed Vireos are able to control a critical non-breeding resource against its resident counterpart.

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## LITERATURE CITED

- BARLOW, J. 1980. Patterns of ecological interactions among migrant and resident vireos in the wintering grounds, p. 79–107. In A. Keast and E. S.

- Morton, [eds.], Migrant birds in the neotropics. Smithsonian Institution Press, Washington, DC.
- BATES, J. 1992. Frugivory on *Bursera microphylla* (Burseraceae) by wintering Gray Vireos (*Vireo vicinior*, Vireonidae) in the coastal deserts of Sonora. Southwest. Nat. 37:252–258.
- BLAKE, E. R. 1968. Family Vireonidae, p. 103–138. In R. A. Paynter, Jr. [ed.], Checklist of birds of the world, vol 14. Museum of Comparative Zoology, Cambridge, MA.
- CHAPMAN, F. 1896. Notes on birds observed in the Yucatan. Bull. Am. Mus. Nat. Hist. 8:271–290.
- CHAPMAN, F. 1940. A post-glacial history of *Zonotrichia capensis*. Bull. Am. Mus. Nat. Hist. 77: 381–438.
- CHIPLEY, R. M. 1980. Nonbreeding ecology of the Blackburnian Warbler, p. 309–317. In A. Keast and E. S. Morton [eds.], Migrant birds in the Neotropics. Smithsonian Institution Press, Washington, DC.
- COX, G. 1968. The role of competition in the evolution of migration. Evolution 22:180–192.
- COX, G. 1985. The evolution of avian migration systems between temperate and tropical regions in the New World. Am. Nat. 126:451–474.
- GASTON, A. J. 1974. Adaptation of the genus *Phylloscopus*. Ibis 116:432–450.
- GREENBERG, R. 1986. Competition in migrant birds in the nonbreeding season, p. 281–307. In R. J. Johnston, [ed.], Current ornithology, vol. 3. Plenum Press, New York.
- GREENBERG, R. 1992. Forest migrants in non-forest habitats in Quintana Roo, Mexico, p. 273–287. In J. Hagan and D. Johnston [eds.], Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.
- HAMILTON, T. H. 1958. Adaptive variation in the genus *Vireo*. Wilson Bull. 70:307–346.
- HAMILTON, T. H. 1962. Species relationships and adaptations for sympatry in the avian genus *Vireo*. Condor 64:40–68.
- HELLMAYR, C. E. 1935. Catalogue of birds of the Americas and the adjacent islands, part 8. Field Mus. Nat. Hist. Zool. Ser. 13.
- JOHNSON, N. K., R. A. ZINK, AND J. A. MARTIN. 1988. Genetic evidence or relationships in the avian family Vireonidae. Condor 90:428–445.
- KLOPPER, P. 1967. Behavioral stereotypy in birds. Wilson Bull. 79:29–300.
- LACK, D. 1944. Ecological aspects of species formation in passerine birds. Ibis 86:260–283.
- LECK, C. 1972. The impact of some North American migrants at fruiting trees in Panama. Auk 89:842–850.
- LEISLER, B., AND H. WINKLER. 1985. Ecomorphology, p. 155–186. In R. F. Johnston [ed.], Current ornithology, vol. 2. Plenum Press, New York.
- LYNCH, J. F. 1989. Distribution of overwintering nearctic migrants in the Yucatan Peninsula: 1. General patterns of occurrence. Condor 91:515–545.
- MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.
- MILLER, A. H., H. FRIEDMAN, L. GRISCOM, AND R. T. MOORE. 1957. Distributional check-list of the birds of Mexico, Part II. Pacific Coast Avifauna 33.
- MONROE, B. L. 1968. A distributional survey of the birds of Honduras. Ornithol. Monogr. 7.
- MORRISON, M. 1982. The structure of western warbler assemblages: ecomorphology of the Black-throated Gray and Hermit Warblers. Auk 99:503–513.
- MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit-eating in tropical birds. Am. Nat. 107:8–22.
- OLMSTED, I. C., A. LOPEZ ORNAT, AND R. DURAN. 1983. Vegetacion, p. 41–64. In Sian Ka'an, estudios preliminares. Puerto Morelos, Quintana Roo, Mexico. SEDUE.
- PARKES, K. C. 1990. A revision of the Mangrove Vireo (*Vireo pallens*) (Aves: Vireonidae). Ann. Carnegie Mus. 59:49–60.
- PAYNTER, JR., R. A. 1955. The ornithogeography of the Yucatan Peninsula. Peabody Mus. Nat. Hist., Yale Univ. Bull. 9.
- POOLE, E. L. 1938. Weights and wing area of North American birds. Auk 55:511–517.
- REMSEN, J. V. AND S. K. ROBINSON. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Stud. Avian Biol. 13:144–160.
- RICE, J. 1978. Ecological relationships of two inter-specifically territorial Vireos. Ecology 59:526–538.
- RICKLEFS, R. 1992. The megapopulation: a model of demographic coupling between migrant and resident populations, p. 537–548. In J. Hagan and D. Johnston, [eds.], Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.
- RUSSELL, S. M. 1964. A distributional survey of the birds of British Honduras. Ornithol. Monogr. 1:1–195.
- SALAMONSON, F. 1957. The evolutionary significance of bird migration. Dan. Bol. Medd. 22:1–61.
- SCHOENER, T. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49:704–726.
- SMITHE, F. B., AND R. A. PAYNTER, JR. 1963. Birds of Tikal, Guatemala. Bull. Mus. Comp. Zool. 128.
- WAIDE, R. 1980. Resource partitioning between migrant and resident birds: the use of irregular resources, p. 337–352. In A. Keast and E. S. Morton [eds.], Migrant birds in the neotropics. Smithsonian Institution Press, Washington, DC.
- WILKINSON. 1987. SYSTAT manual. Winston, IL.
- WILLIAMSON, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. Ecol. Monogr. 41:129–152.
- WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5:187–231.