

COMPETITION BETWEEN TWO WEST INDIAN FLYCATCHERS, *ELAENIA*

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SIBLING species whose ranges overlap generally exhibit some measure of ecological and morphological displacement in the area of sympatry. This presumably results from competition for common limiting factors, but as such a process is self-effacing it has seldom been observed, and its reality must be adduced from its consequences. The thesis is strengthened by the finding that differences are often less marked in regions of allopatry. Several such cases are reviewed by Lack (1944).

Few of these studies have been extended to determine the effects of interspecific competition on population density. The greater density of passerine populations in Bermuda (Crowell, 1962) suggests that competition in the larger North American communities limits the populations of these species there, but relationships between particular species are not clear. A quantitative study of competition between congeneric species thus seemed desirable. Islands are ideal for such a study because areas of sympatry and allopatry are sharply defined, while the fact that each family is represented by fewer species makes competitive relationships between these species more evident. Such a situation is reported here.

The ranges of the Yellow-bellied Elaenia (*Elaenia flavogaster*), a species of Central and South America, and the Caribbean Elaenia (*E. martinica*), a West Indian species, overlap in the Windward Islands (Figure 1). The area of sympatry includes the islands of Grenada and St. Vincent; the two species occupy different habitats on Grenada, but coexist on St. Vincent (Bond, 1948). *E. flavogaster* occurs alone on Trinidad, and *E. martinica* alone on St. Lucia. I studied the distribution and ecology of the two species on their respective islands during the spring of 1961, visiting St. Lucia in late March and mid-April, St. Vincent in early April, Grenada in late April, and Trinidad in early May.

DISTRIBUTION AND NOMENCLATURE

Elaenia is a widespread tyrannid genus of tropical America represented by some twenty species. The range of *E. martinica* includes virtually all the islands of the Caribbean with the exception of the Greater Antilles (Bond, 1956). Seven subspecies are currently recognized (Hellmayr, 1927). *E. martinica martinica* Linnaeus occupies all the Lesser Antilles including and south of Saba, except Antigua and Barbuda. A similar race, *E. m. riisii* Sclater is found on the latter two islands and the more northern Lesser Antilles. Apparently it is still extending its range westward. Robertson (1962) cites evidence that it invaded the Virgin Islands shortly after

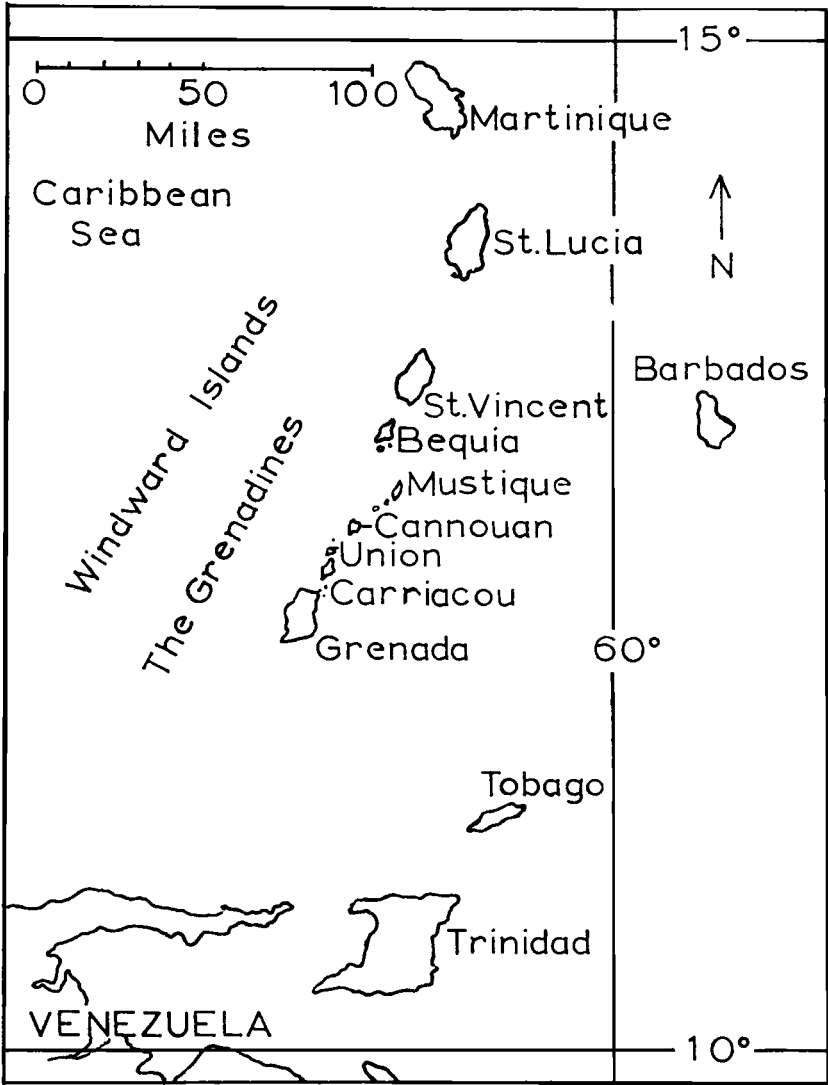


Figure 1. Map of the southern Caribbean Sea showing the Windward Islands and Trinidad.

1900. Danforth (1935) found it abundant there, but absent or rare in eastern Puerto Rico where it is now established; and Lanyon (1966) reports it from western Puerto Rico. However, Bond (pers. comm.) points out that until recently the avifauna of eastern Puerto Rico has received little attention, and *martinica* might have been overlooked previously.

The northernmost race, *E. m. remota* Berlepsch, occurs on the islands of Cozumel and Mujeres. It has not been found resident on the adjacent mainland, with the exception of specimens taken by Gaumer (1917 *in* Paynter, 1955). At least one of these is *martinica*, but both the dates (Paynter, 1955) and place (Salvin, 1889) of their collection are questionable. A. Phillips reported *martinica* from mainland Yucatan, and one specimen of *E. m. remota* was taken at Belize, British Honduras (Bond, pers. comm.).

E. flavogaster is a mainland species ranging from Veracruz to northern Argentina. At least two subspecies are recognized—*E. f. subpagana* Sclater & Salvin north of Panama, and *E. f. flavogaster* Thunberg, a southern race. In the Caribbean *flavogaster* occurs on Trinidad, Tobago, Grenada, St. Vincent, and the Grenadines; but on no other islands with the possible exception of those off the Yucatan Peninsula. Its status there rests on specimens allegedly taken by Gaumer from the islands of Cozumel, Mujeres, and Holbox, the latter two being 3 to 5 miles off the coast. Paynter (1955: 204) states "it is possible that one bird and possibly two from Isla Mujeres must be identified as *E. flavogaster*. Thus it appears that *E. martinica* and *E. flavogaster* exist sympatrically on Isla Mujeres and at least contiguously on the mainland."

The present distributions of *martinica* and *flavogaster* in the southern Lesser Antilles are apparently of long standing. When the first collections were made in the late 19th century, *E. flavogaster* was recorded on Grenada (Lawrence, 1878). It was found on St. Vincent and throughout the Grenadines—Bequia and Mustique (Clark, 1905), Bequia, Union, Petit Martinique, Carriacou (Ridgway, 1907).

E. martinica was recorded from St. Vincent by Lawrence (1879). Its status on Grenada and the Grenadines has been less certain. One specimen from Grenada in the American Museum was taken in 1893, and four at Harvard taken by Allen in 1910 are apparently mislabelled as *flavogaster* (Paynter, pers. comm.). Bond observed it at the Grand Etang in 1929 (pers. comm.). He did not find it in 1956, but it was observed in 1961 by both myself and Schwartz (pers. comm.). Thus *martinica* persists in remnants of mountain forest on Grenada. (Schwartz (pers. comm.) recently took a possible specimen from arid Point Salina.) It has been recorded from only the most northerly Grenadines—Mustique (Clark, 1905), Isle Quatre, a key of Bequia (Kennedy, 1912 *in* Bond, 1956), and on Bequia by myself in 1961. It has been reported absent from these islands by Thayer (1923), Bond and Danforth (*in* Bond, 1956), Bond (1962), and Schwartz (1960–1966, pers. comm.).

DESCRIPTION AND VOICE

Because of their similarity, the taxonomic status of the two species has varied (Peters, 1926; Hellmayr, 1927), and some museum specimens appear mislabelled, but field notes often make it clear which species is involved in early records.

In the field the two are readily distinguished by appearance, voice, and behavior; *flavogaster* is a noisy, active bird with a conspicuous crest, while *martinica* is more shy and displays its white crown patch only when aroused.

Museum skins of the two are extremely difficult to separate as discussed later, but the following criteria prove useful: The lower breast and abdomen of *flavogaster* are a rich lemon-yellow contrasting with the gray-brown upper breast and light gray throat. In *martinica* the middle breast is darker and the abdomen is only faintly washed with yellow. The secondaries and wing coverts of *flavogaster* are more broadly edged with cream or buff, although this character varies considerably. The bill is more triangular in *flavogaster* and the wing less pointed (Peters, 1926), that is, the primaries do not extend so far beyond the secondaries. The white crown patch is more truncate in *martinica*, and Bond (pers. comm.) suggests that the feathers of the crown may be shorter. Lastly, the marginal wing coverts of *flavogaster* are yellow and contrast noticeably against the darker sides where they overlap the wrist in the specimen as viewed ventrally.

Both call and song of *E. martinica* distinguish it from *flavogaster*. Lanyon (1966) describes the call of *martinica* as "a single note that rises sharply and then falls off in pitch just as abruptly," and I would give it as a sharp *pee-ur*. The typical song of the eastern races (*martinica*, *riisii*, and *barbadensis*) is a *pee-whitler*. Song and a sharp *chip* are often alternated at 2-second intervals (Figure 2). The dawn song is more com-

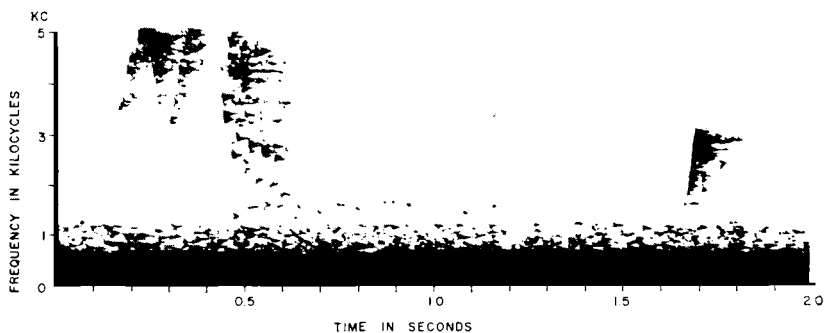


Figure 2. Song of *E. martinica* on St. Vincent.

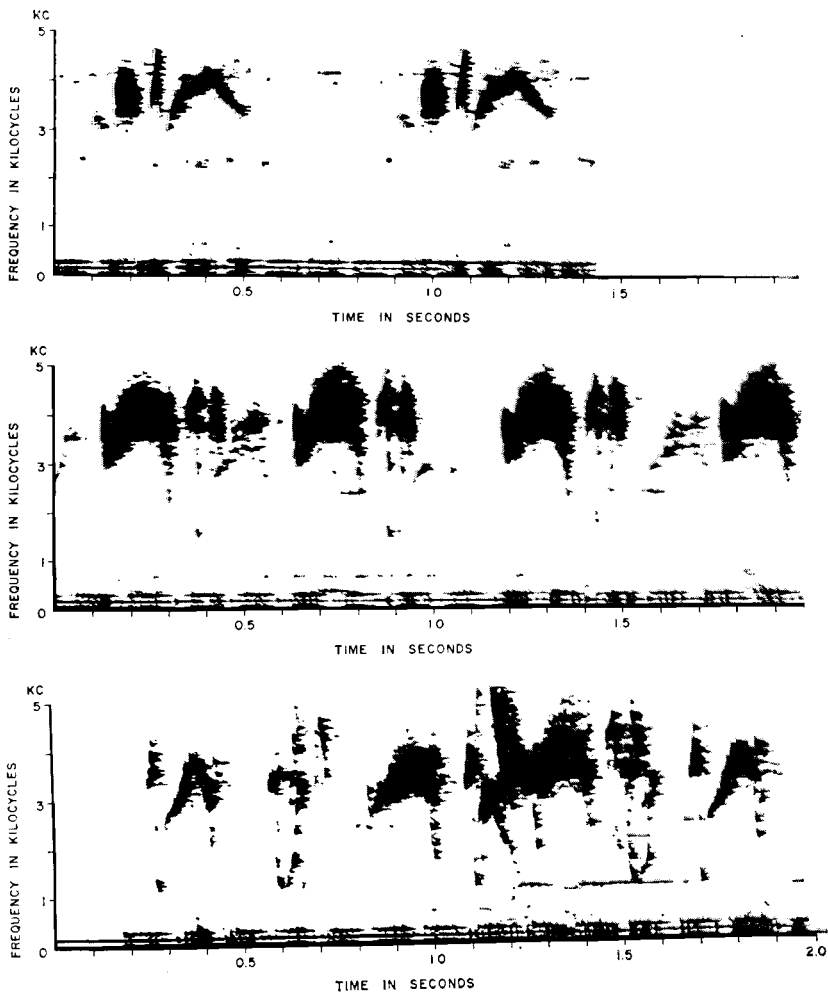


Figure 3. Songs of *E. flavogaster* on St. Vincent. Dawn song (top) and usual song (middle and bottom).

plex, resembling Lanyon's (1966) spectrograms 9-10. The dawn song of *flavogaster* (Figure 3, top) could be confused with that of *martinica*, but the typical song is most distinctive, and is often sung in chorus. Bond (1961) characterized it as "a harsh *creup-creup-wi-creup*."

PHYSIOGRAPHY, CLIMATE AND VEGETATION

The Windward Islands are remarkably similar in topography and vegetation. Grenada, St. Vincent, and St. Lucia are 120, 130, and 233 square

miles in area respectively (Beard, 1949), and range from 18 to 28 miles in length and 10 to 12 miles in width. Each has a forested central massif with peaks reaching 2,000 to 3,500 feet. Much of the present topography dates from the Miocene, although St. Vincent was formed by volcanic activity in the Pleistocene (Beard, 1949). During the Pliocene Grenada and the Grenadines formed one land mass while to the north the Leeward Islands were connected with Puerto Rico and Hispaniola.

Mean maximum and minimum temperatures for Soufrière, St. Lucia are 86° and 72° respectively (Great Britain Meteorological Office, 1958). Annual rainfall varies from over 100 inches at high elevations with more than 200 rainy days to less than 30 inches in coastal areas which have a 3- to 5-month dry season (Beard, 1949). Temperatures in Trinidad run higher with greater extremes, while rainfall is lower with a longer dry season.

Zonation of vegetation formations is complicated by rainfall decreasing not only with elevation, but from interior to coast and from east to west. Beard (1949) distinguishes the following formations: In lowland and coastal areas are seasonal and dry evergreen forests and their secondary derivatives such as dry brush woodland in which thorny trees and some cactus are prevalent. At mid-elevations seasonal forest formations grade into rain forest. Both are highly disturbed by transient agricultural practices, and secondary forests are widespread, with *Cecropia* spp. being common. At higher elevations rain forest is replaced by montane rain forest, and eventually by palm brake (at 1,600 feet on St. Vincent), montane thicket, and elfin woodland.

These formations differ slightly in extent on the respective islands. Poorly-drained soils on St. Lucia prevent the growth of true rain forest, but there is a well-developed montane rain forest; conversely on St. Vincent well-drained youthful soils support rain forest and there is no montane formation. On Trinidad rain forest is replaced by lower montane rain forest and evergreen seasonal forest because of reduced moisture (Beard, 1946). The Grenadines are drier and support only seasonal forest and dry brush woodland.

While the vegetation formations of the Windward Islands, and even of Trinidad, are extremely similar in physiognomy, they differ floristically in that the number of species declines progressively from Guadeloupe to Grenada. This reflects the Pliocene connections of the northern islands with the greater Antilles on the one hand, and the recent origin of St. Vincent on the other. However, two-thirds of the plant species of the Lesser Antillean seasonal woodlands are also found in Trinidad (Beard, 1949); and in spite of differences, the overwhelming impression is one of great similarity.

FIELD STUDIES—METHODS

Habitat preference.—Density of resident pairs in representative habitat types was determined on the respective islands. For this purpose the following classification proved satisfactory:

Brush—vegetation predominately (80%) under 10 feet in height. This was largely found in xeric sites, interspersed with xerophytic scrub.

Scrub—trees and shrubs 10–25 feet in height.

Xerophytic: found in dry coastal regions, approximates Beard's dry brush woodland.

Mesophytic: not xerophyllic or thorny, generally a pioneer stage for evergreen seasonal or rain forests.

Second growth—Dominant trees 25 to 60 feet in height and up to 15 inches dbh. open: canopy broken, often in disturbed areas with much edge. Many trees are naturalized species such as breadfruit (St. Vincent) and nutmeg (Grenada). dense: trees are evenly spaced and form a closed canopy.

Forest—Dominant stratum of trees taller than 60 feet and larger than 15 inches dbh, includes seasonal, rain, and montane formations.

Listed below are localities where the respective habitat types were found, and corresponding vegetation formation (Beard, 1949) when applicable:

St. Lucia.

Dense second growth (montane rain forest): Forestière, Barre de l'Isle, Fond d'Assor.

Open second growth: Migny, Paix Bouche, Gros Morne.

Mesophytic scrub: Talvern.

Xerophytic scrub: Anse Pileri, Choc, Reduit, Marisule, Marigot Mongiraud.

Grenada.

Forest (rain forest): Grand Etang, Minorca.

Dense second growth: Minorca.

Xerophytic scrub: vicinities of St. George's and Grand Anse.

Trinidad.

Forest: Arima (evergreen seasonal), road above Spring Hill Estate (lower montane).

Dense second growth, open second growth (evergreen seasonal): Simla, Spring Hill.

Mesophytic scrub: Cumato reserve.

St. Vincent (numbers of *E. flavogaster* : *E. martinica* given).

Forest: King's Hill (semideciduous seasonal), (2:5), Symon's Bow (evergreen seasonal or rain), (0:0), Lowrt (rain forest), (0:1), Mt. St. Andrew (0:1).

Dense second growth: Camden Park Experiment Station (0:1).

Open second growth: Lowman's (4:7), Dalaway (1:5).

Mesophytic scrub: Camden Park (4:1), Rilland Hill (4:1).

Xerophytic scrub and brush: Cane Grove to Layou (7:2), Brighton (6:0), Montrose and Monte Bello (4:1).

Censuses were made by counting singing males. The rough terrain and the necessity of visiting many sites in a limited time made it impractical to apply the Williams method (Kendeigh, 1944) to mapped plots. Instead habitats were traversed by a road or path, the distance traveled was paced, and the distance for which birds were

clearly visible on either side estimated. Results were then expressed in customary terms of pairs per 100 acres (Figure 4). In obtaining an average density for each habitat type, the respective plots were weighted in proportion to both their size (acre-visits) and the number of times visited (plot-visits). Relative numbers per linear distance walked were comparable to estimated densities per unit area.

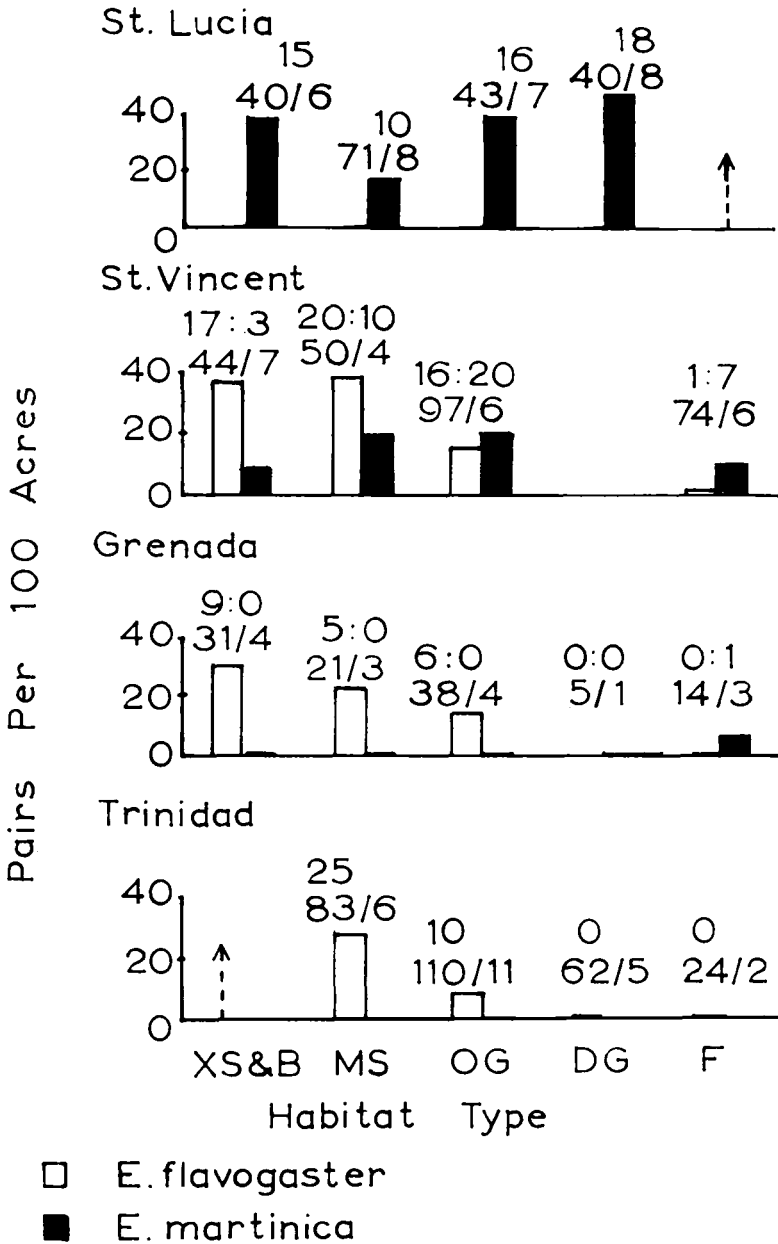
This method might well underestimate the area utilized by the birds observed, making estimates of absolute density too liberal, but selected plots that were mapped and censused in the conventional manner yielded results close to those obtained by the walk method.

FIELD STUDIES—RESULTS

Figure 4 shows that on St. Lucia *martinica* is common in all habitats (the small sample from mesophytic scrub is probably not representative). These observations are corroborated by reports from others. Lanyon (pers. comm.) found *martinica* common in "semi-arid open country" on Martinique and in "forest clearings" of Dominica and St. Kitts. Danforth (1930) reports it in "hilly, xerophytic brushy type of vegetation" on St. Martin, and in both "semi-arid" and "dense forest" on St. Eustatius. Voous (1955) found it mainly in the lowlands of Saba and not in cloud forest above 400 meters. Likewise, in 76 hours of observation in dry scrub and forest and 57 hours in moist forest on St. Johns, Robertson (1962) found 56 and 14 individuals respectively. Thus *E. martinica* is found in all habitats, but may be somewhat more common in lowland scrub. It does not show a preference for mountain forest, the habitat to which it is restricted in Grenada.

Observations of *flavogaster* on St. Vincent, Grenada, and Trinidad (Figure 4) show it to be most common in open habitats and absent from mountain forest. Skutch (1954) states that in Costa Rica *flavogaster* is found to elevations of 6,000 feet in open country including plantations, shady pastures, and hedgerows, but never in dense forest. Similarly, I observed it in roadside clearings in the mountains of Trinidad, but not in adjoining forest. On Grenada I found *flavogaster* in roadside scrub at the Grand Etang (elev. 1,700 feet) where Bond (pers. comm.) did not find it previously. It may have entered after hurricane Janet decimated the forest in 1956, when *martinica* apparently declined in the area. The forest in which I found *flavogaster* on St. Vincent was a remnant of the semideciduous formation on the coast. I did not visit arid coastal scrub in Trinidad, but Snow (pers. comm.) reports it common there.

The habitat preferences of *flavogaster* for Grenada and St. Vincent shown in Figure 4 do not differ significantly ($X^2 = 2$, $P > .50$), but the preferences shown by *martinica* on St. Vincent differ significantly both from those of *flavogaster* ($X^2 = 287$, $P < .001$), and from those of *martinica* on St. Lucia ($X^2 = 10$, $P < .02$). Granting the errors involved in such data, the density of *martinica* in open habitats on St. Vincent is



Key: XS, xeric scrub; XB, xeric brush; MS, mesophytic scrub; OG, open second growth; DG, dense second growth; F, forest.

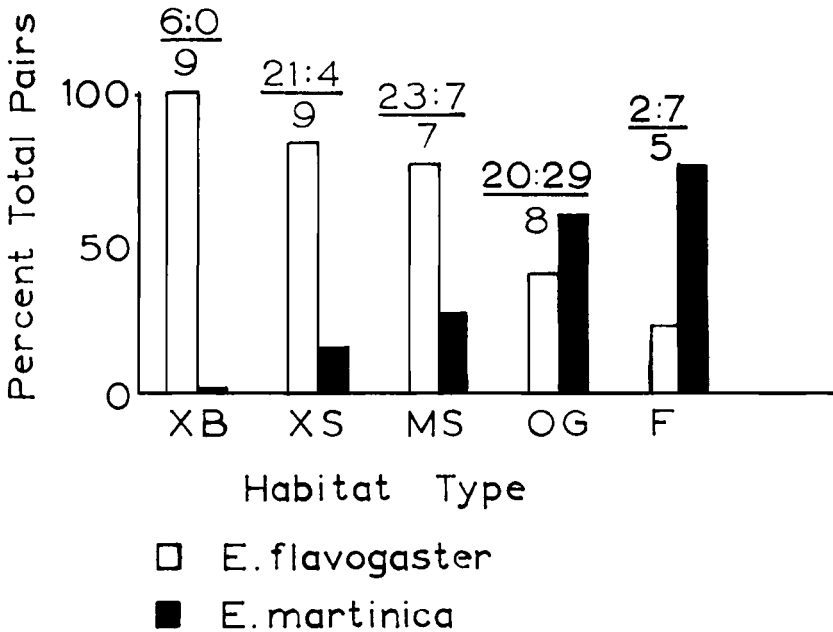


Figure 5. A comparison of the relative densities of *E. martinica* and *E. flavogaster* in several habitats on St. Vincent. Figures show observed number of pairs of each species above the line, and number of plot-visits below the line. Symbols as in Figure 4.

lower than in those on St. Lucia, but total numbers of elaenias in these habitats appears greater.

Feeding habits.—On St. Vincent I recorded feeding heights and methods in the two species. Apportionment of feeding time in relation to height (Figure 6) was based on 55 separate observations totaling 1,750 seconds for *flavogaster* and 34 observations totaling 2,140 seconds for *martinica*. The two species differed significantly in feeding height ($X^2 = 107$, $P < .001$). As these data were not weighted according to the distribution of foliage, they may reflect differences in habitat preference as well as any height preference per se.

Four feeding methods were distinguished: feeding directly on fruits;

←

Figure 4. A comparison of the densities of *E. martinica* and *E. flavogaster* in several habitats, expressed in pairs per 100 acres. Arrows indicate reported presence in habitats not visited personally. The upper numbers give the number of pairs of each species observed, the lower numbers show the number of acre-visits and the number of plot-visits.

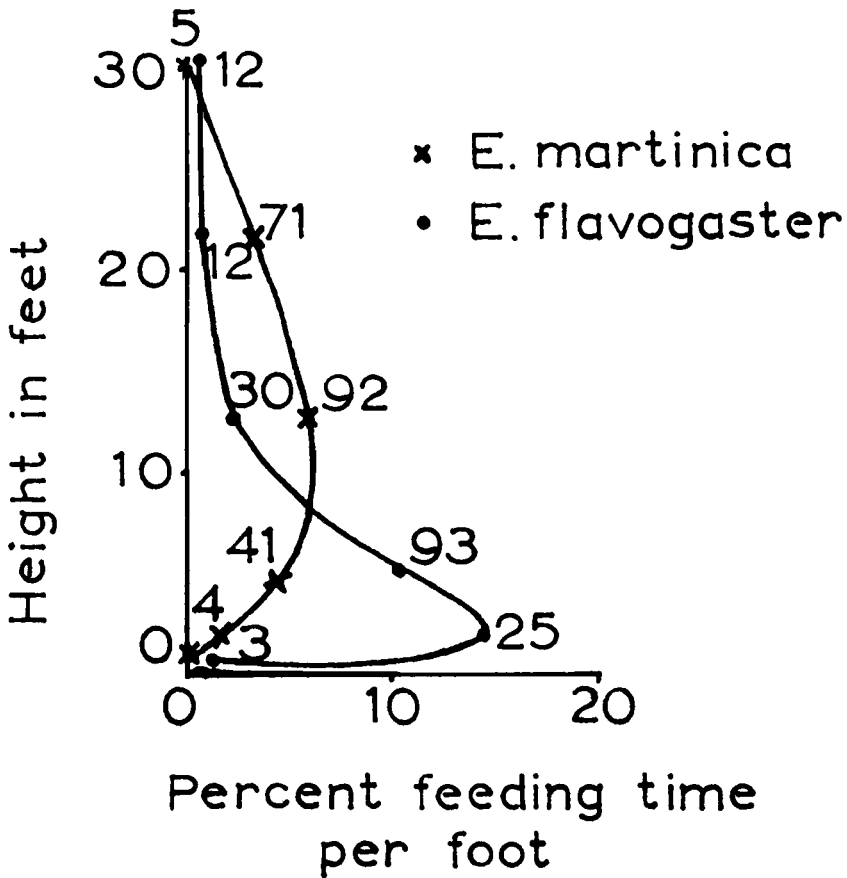


Figure 6. Frequencies of feeding heights in *E. martinica* and *E. flavogaster* on St. Vincent. Numbers show total time recorded for each height zone in 10-second units.

feeding among vegetative or flowering parts (this usually meant taking insects from the plant, but in some instances the birds appeared to eat the flowers themselves); taking food while the bird is in flight; and taking flying insects. These categories are designated respectively as fruit, foliage, hover, and hawk in Figure 7. A total of 980 seconds representing 44 observations for *flavogaster* and 1,260 seconds from 37 observations for *martinica* were allocated between these methods, and differences were again highly significant ($X^2 = 17.3, P < .001$).

These results agree with reported observations on both species. Skutch (1954) reports that *flavogaster* hawks for insects and feeds on berries, and that it feeds the young berries and minute insects. Similarly I saw

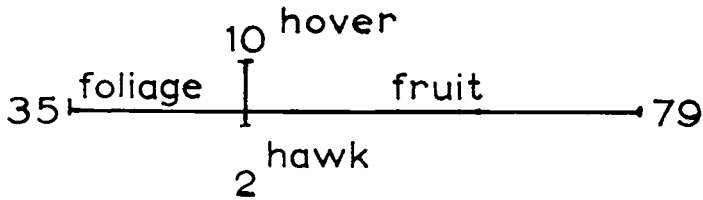
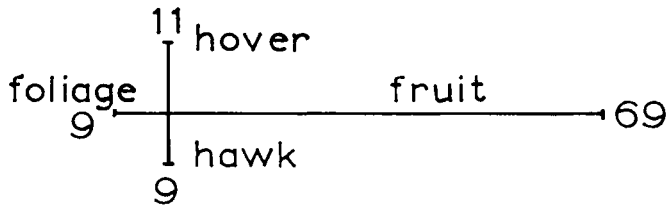
E. martinica*E. flavogaster*

Figure 7. Frequencies of feeding methods in *E. martinica* and *E. flavogaster* on St. Vincent. Length of each arm indicates number of 10-second units observed for that category.

martinica feed fledged young the large resinous berries of the gumbolimbo (*Bursera simaruba*). Over 50 stomach analyses on *martinica* by several workers throughout the Lesser Antilles show 90–100 per cent vegetable matter, largely berries and drupes (Wetmore, 1916; Danforth, 1930, 1934, 1935, 1937, 1939*a*, 1939*b*; Pinchon, 1953; Voous, 1955). In all Danforth's analyses the fruits of Solanaceae predominated. *Cecropia* fruits are also a favorite food.

In summary, feeding observations show that both species feed primarily on fruit, but *flavogaster* takes more insects by hawking, and *martinica* feeds more in foliage, presumably taking insects much of this time.

TABLE 1
AGGRESSIVE ENCOUNTERS OF *E. martinica* AND *E. flavogaster*¹

	<i>E. martinica</i>			<i>E. flavogaster</i>		
	<i>n</i>	<i>t</i>	Encounters	<i>n</i>	<i>t</i>	Encounters
Intraspecific	61	215.5	1	56	750	10
Interspecific	51	198.5	+1, -4	51	198.5	+4, -1
Intergeneric	10	17	+3, ±2, -2	4	3	+1, ±1

¹ Number of instances (*n*) and their duration (*t*) when at least one individual is present for intraspecific or when two individuals are within 100 feet of each other for interspecific and intergeneric encounters. Outcome of resulting interactions is signified by (+) win, (-) lose, or (±) mutual threat.

Aggressive interactions.—I spent some 36 hours studying aggressive behavior of the two elaeenias and recorded the number and duration of instances when I could clearly see individuals of each species and they were within 100 feet of each other. These and the number of resulting encounters are shown in Table 1. The number of times when more than one male or pair of the same species were near each other were not recorded, but in the locations where I made the observations more than one pair of each species held adjoining territories. Nonetheless, the greater number of intraspecific encounters for *flavogaster* must to some extent reflect its greater population density. Occasions when other species were within 100 feet of elaeenias should be regarded as a minimum estimate only.

The data suggest that *flavogaster* is dominant over *martinica*, although statistical treatment is not appropriate. However *flavogaster* was seen to tolerate *martinica* in a tree with its nest, while a *martinica* tolerated *flavogaster* near its fledged young. The possibility of aggressive behavior implementing competition between these two species thus requires further study.

MORPHOLOGICAL VARIATION

To find reliable criteria for separating the two species, I analyzed several morphological characters for character displacement. Results are shown in Figure 8 and Table 2. Wing length was measured as an indication of body size. The average of both wing lengths was taken, measuring on the arc with a ruler reading to 0.5 mm with an estimated error of ± 0.25 mm. In each species wing length of males was greater than that of females, but $P > 0.10$. There were no significant differences between species or islands, although body weights show *flavogaster* to be somewhat larger. Paynter (1955) found 1 male *flavogaster* to weigh 24.7 g and 2 females to weigh 23.6 and 25.3 g; while in 7 male *martinica* Danforth (1937) found a range of 18.1–19.6 with a mean of 18.8 g.

Wing shape, the difference between the longest primary and longest secondary, was measured to the nearest 0.1 mm, with an estimated error of ± 0.5 mm. Although this character is highly variable and difficult to take on prepared skins, the difference between the two species proved highly significant by the t-test ($P < .001$). Mean ± 2 S. E. for *martinica* and *flavogaster* from all populations were 15.3 ± 0.33 mm and 11.3 ± 0.24 mm respectively. There was no correlation between wing shape and wing length.

Confidence limits based on standard deviations at the 0.10 level are ± 3.21 and ± 3.72 respectively, and the lower limit for *martinica* is thus 12.6 mm, while the upper limit for *flavogaster* is 13.0 mm. Therefore this character allows separation with slightly less than 90 per cent con-

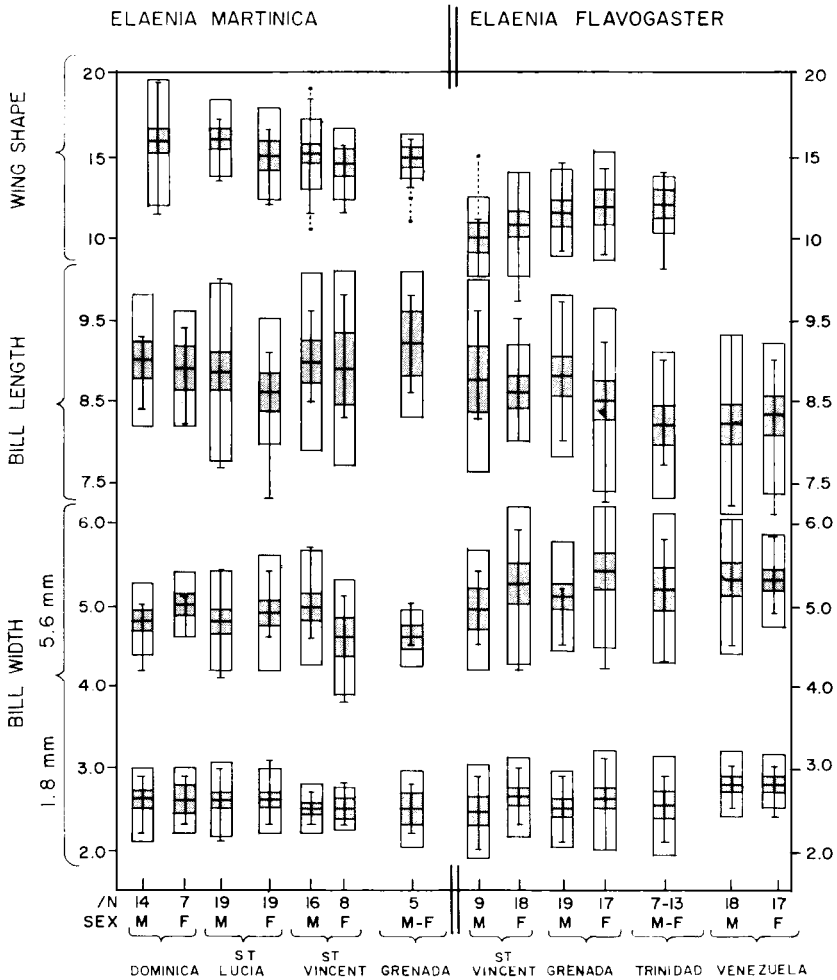


Figure 8. Morphological variation in two species of *Elaenia* in the Caribbean. Given are range, mean, ± 2 S.D. (open blocks), and ± 2 S.E. (dark blocks) for characters as described in text. Dotted lines indicate wing shape of specimens omitted because of apparent mislabeling.

fidence, and in conjunction with differences in coloration proves useful in separating unlabeled or questionable specimens. Of 14 such specimens from St. Vincent, 11 were assigned to one or the other species.

Bill length was measured both from the base of the culmen and from the proximal rim of the nostril. The former, which showed a smaller coefficient of variation, was taken with dividers and a ruler reading to 0.5 mm; the latter was made with a vernier caliper reading to 0.1 mm.

TABLE 2
MEAN (\bar{X}) AND VARIANCE (S^2) FOR SEVERAL CHARACTERS (SEE TEXT) IN *E. martinica*
AND *E. flavogaster*

Species-island	Sex	N	Wing length		Bill length ¹		Bill length ²		Bill width ³		Bill width ⁴	
			\bar{X}	S^2	\bar{X}	S^2	\bar{X}	S^2	\bar{X}	S^2	\bar{X}	S^2
<i>E. martinica</i>												
Martinique	♂	9	80.8	1.11	15.8	.36	8.8	.73	2.5	.08	4.7	.21
Dominica	♂	14	80.77	15.01	14.9	.67	9.0	.18	2.6	.04	4.8	.06
	♀	7	79.07	12.92	14.5	1.29	8.9	.12	2.6	.04	5.0	.22
St. Lucia	♂	19	80.4	4.56	15.3	.47	8.8	.30	2.6	.05	4.8	.09
	♀	19	76.47	3.62	14.5	.89	8.6	.21	2.6	.04	4.9	.13
St. Vincent	♂	16	79.00	6.58	15.1	.34	9.0	.29	2.5	.02	4.9	.12
	♀	8	75.64	13.67	14.7	.50	8.9	.37	2.5	.03	4.6	.13
Grenada	♂ - ♀	5	79.5	3.38	14.6	.36	9.2	.21	2.5	.05	4.6	.03
<i>E. flavogaster</i>												
St. Vincent	♂	9	78.70	7.78	14.8	.35	8.9	.15	2.5	.08	4.9	.14
	♀	17	76.25	6.60	14.5	.47	8.6	.18	2.6	.06	5.2	.23
Grenada	♂	19	80.4	8.30	15.1	.28	8.8	.28	2.5	.05	5.1	.11
	♀	17	78.63	3.80	14.6	.64	8.5	.31	2.6	.09	5.4	.21
Trinidad	♂ - ♀	7-13	78.3	14.2	14.4	.81	8.2	.20	2.5	.10	5.2	.24
Venezuela	♂	18	80.2	.24	13.9	.54	8.2	.29	2.8	.05	5.3	.19
	♀	17	77.2	.26	14.0	.48	8.3	.21	2.8	.04	5.3	.08

¹ From base of culmen.

² From proximal rim of nostril.

³ 1.8 mm from tip.

⁴ 5.6 mm from tip.

Bill width was measured with the caliper at 5.6 and 1.8 mm from the tip. Differences in means between species were evaluated using analysis of variance with nested classification for sexes, and differences between sexes were compared with the t-test.

It is seen in Figure 8 that *E. martinica* has a longer and more pointed bill. Allopatric populations of the two species differed significantly in bill length and width at 5.6 mm ($P < .001$), but not in bill width at 1.8 mm ($P > .10$). Bill lengths of *flavogaster* in Brazil are at least 1 mm shorter than those in Venezuela (Schoener, 1965 and pers. comm.). The two species also show highly significant differences in bill length and width at 5.6 mm on Grenada. Here, the bill of *martinica* is longer and narrower than in other populations. This suggests character displacement, although the sample size is small and differences from allopatric *martinica* are not significant.

On St. Vincent bill dimensions of *flavogaster* converge towards those of *martinica*, and differences between the two species are not significant. Thus bill size was of no use in identifying doubtful specimens from St.

Vincent. If the sexes in the two species are taken separately, interspecific differences in bill length and width are greater, although still not significant ($P > .10$). Apparently although there is no true character displacement in *flavogaster*, females on both Grenada and St. Vincent have retained the shorter, wider bills of allopatric populations. Similarly, the female *martinica* on St. Vincent has the narrowest bill of the population examined. Bossert (1963) predicts that in the evolution of character displacement frequency distributions should be skewed away from each other, and changes should be more pronounced in the less abundant species. Neither of these expectations is met in the two elaenias.

Graphical analysis of paired characters (bill length vs. bill width and wing length, and bill width vs. wing length and wing shape) added no information to univariate analysis. Average coefficients of variation for all bill characters was compared for allopatric and sympatric populations of each species. These and the significance of their differences (t-test) were $.071 \pm .012$ and $.059 \pm .010$ ($P < .01$) for *martinica*; and for *flavogaster*, $.074 \pm .015$ and $.064 \pm .013$ ($P < .10$). This suggests that greater selective pressure resulting from interspecific competition has reduced variability on St. Vincent and Grenada.

DISCUSSION

Comparison of the densities of *E. martinica* and *E. flavogaster* in areas of sympatry and allopatry indicates competition between the two species. On Grenada *flavogaster* appears to exclude *martinica* from habitats occupied elsewhere by both species. On St. Vincent densities of *martinica* are depressed in these habitats, as compared with those on St. Lucia. Densities of *flavogaster* on St. Vincent do not differ from those exhibited in allopatric situations, and it never inhabits mesic forest. The situation, then, is of a species with a narrower niche, *flavogaster*, excluding a species with a broader niche from habitats potentially occupied by both. Thus *martinica* is not necessarily more abundant in its preferred habitats, but in those that lie outside the niche of *flavogaster*. Miller (1967) introduces this "included niche" concept as a common phenomenon.

Figure 5 shows that relative numbers of *flavogaster* increase from mesic to xeric habitat on St. Vincent. Why is this species unable to inhabit mesic forest, while *martinica* does? This question cannot be answered fully (cf. Lanyon, 1956). Proximate reasons must include behavioral if not physiological factors, while the ultimate determinants may lie in competitive relations in the larger mainland fauna.

The geographic distribution of the two species implies that *flavogaster* has recently invaded the Lesser Antilles from the mainland. Bond (1948) distinguishes two major elements in the West Indian avifauna—a tropical

North American contingent spreading via the Greater Antilles, and a more recent South American element dispersing both from the west, mainly via Jamaica, and from the south by the Trinidad-Grenada route. The latter element, which includes the Tyrannidae, consists of only the most aggressive South American species. The geographic source of *E. martinica* is not clear, but Bond (1963) feels that it may have come from the west rather than from the south. If this is so, then the species may never have been well established on Grenada.

Robertson (1962), on the other hand, concludes that *martinica* has spread from the south. In the northern West Indies it is the Lesser Antillean forms, including *E. martinica*, that are expanding their ranges rather than those of northern origin, and according to Robertson it would appear that this represents the conclusion of earlier invasions by South American species. This is substantiated by present changes in the southern Lesser Antilles. Robertson (1962) lists seven species, including *E. flavogaster*, that are extending their ranges there.

Thus *E. flavogaster*, if not *E. martinica*, represents an invasion of the West Indian fauna by an aggressive South American element. In addition, such evidence as exists suggests that *flavogaster* has only recently become widespread on St. Vincent. Clark (1905) records *flavogaster* only in coastal Kingston Valley. Similarly, Thayer (1923) wrote that *flavogaster* was "Common coastwise in St. Vincent. . . Not found in mountains"; while *martinica* was "Very common, especially in mountains." I. A. E. Kirby (pers. comm.) feels that *flavogaster* is now more widespread than during his youth. Of course some of this change may be due to alteration of habitat by man.

Difficult to explain is the interesting difference between the status of the two species on Grenada and St. Vincent. Several alternatives may be considered. First, equilibrium on St. Vincent may not yet have been achieved. Second, evolution of behavioral and/or morphological differences or some critical difference in the physical or biotic environments on the two islands may increase the competitive advantage of *martinica* on St. Vincent.

What evidence is there of continued competition on St. Vincent? While zoogeographic evidence suggests recent invasion of St. Vincent by *flavogaster*, it is unlikely that competitive displacement should require more than a few generations. However the possibility exists that *martinica* populations in xeric habitats constitute an unstable equilibrium maintained by emigration from mesic habitats.

In vertebrates, conventional competition for space may augment or replace direct competition for resources. Such interference behavior may be especially prevalent in temporary situations caused by sibling species re-

uniting before they have had time for ecological divergence. Miller (1967) cites evidence that often the species with the narrower niche is the larger and more aggressive, and is perhaps more efficient in its exploitation of the habitat. In the elaeenias, observations on aggressive relations were equivocal, although *flavogaster* is slightly larger. A related observation may be relevant: I noted that *flavogaster* was active all day in arid habitats, while *martinica* sang only at dawn and then retired, seemingly to avoid the heat of the day. Thus *flavogaster* may be both physiologically and behaviorally better adapted to establishing territories in these habitats.

Study of feeding behavior suggests competition for food. While significant differences occurred in feeding method and height, there was a considerable overlap between the two species. Although this overlap may not result in competitive exclusion, any sharing of resources should limit population size. Such competition need not occur throughout the year, but only in some critical period such as the dry season or breeding season. This study was made at the end of the former and beginning of the latter. Perhaps more frequent hawking for insects by *flavogaster*, possibly enhanced by its wider bill, gives it an advantage in the dry season. Alternation of wet and dry seasons acting on differences in feeding behavior might produce a shifting competitive advantage permitting coexistence.

If competition for food exists, it is not clear why greater character displacement has not occurred. Perhaps habitat displacement occurred too rapidly on Grenada, while on St. Vincent insufficient time has elapsed for divergence. Schoener (1965) found that for most congeneric species on islands character ratios are at least 1.24, but for small species eating abundant and varied foods they are often less. Character ratios for bill length and bill width are 1.00–1.04 (mean 1.02) on St. Vincent, and 1.02–1.06 on Grenada. These values are at the lower end of the range Schoener found for small omnivorous species; and show that divergence in the two species is minimal. MacArthur and Wilson (1967) hypothesize that in generalized species exploiting abundant resources selection may actually favor convergence. Therefore, competition need not necessarily produce displacement.

Grant (1965) suggests that release from competition in larger mainland faunas allows insular populations to evolve larger bills, permitting utilization of a greater range of food particles. But while bill length in *flavogaster* increases somewhat on the islands, bill width decreases, suggesting that it responds to different selective pressures. Similarly, Van Valen (1965) found increased variance of bill size on islands and attributed it to reduced competition. However, coefficients of variation of bill size in *flavogaster* on Grenada and St. Vincent are no greater than in Venezuela. Therefore, intrageneric competition of the two elaeenias appears to over-

ride the effects discussed by Grant and Van Valen, and *flavogaster* does not exploit a broader niche on the islands.

On islands, where total numbers are limited by area, it may be necessary for similar species to occupy a wide range of habitats, partitioning food between themselves. For example, Lack (1944) found 21 pairs of species separated by habitat or locality and 9 showing differences in feeding habits on Great Britain, while on smaller islands, 5 occupied different habitats and 6 showed differences in feeding. On Grenada, where *flavogaster* restricts it to mountain forest, *martinica* can maintain only a limited population and is subject to catastrophe; whereas on St. Vincent the two species share most habitats and greater total *Elaenia* populations attained. However, Schoener (1965) and MacArthur and Pianka (1966) argue that if additional species are to succeed they must partition space rather than restrict food. That is, small species exploiting abundant food resources can more efficiently utilize a smaller range of habitats, excluding congeneric competitors from them. Moreover, I suggest that because feeding behavior depends on neuromuscular patterns, it may be considerably more rigid than habitat selection. Thus differences in habitat preferences may evolve more readily than feeding behavior.

Wilson (1965) suggests that species utilizing disturbed habitats are "pre-adapted" for colonization. *Flavogaster* may demonstrate such a role in the Windward Islands by invading lowland habitats and displacing *martinica* to more stable internal habitats. On Grenada greater numbers of *martinica* were presumably replaced by the newly-established but more aggressive *flavogaster*. Differences in feeding behavior were not sufficient for coexistence, and *martinica* was restricted to the mountains.

It is not apparent whether the partial coexistence on St. Vincent is permitted by actual divergence of feeding behavior or if differences in the physical environment, available food sources, or extrageneric competitors alter the relative fitness of the two species there. As was emphasized earlier, the islands are remarkably similar ecologically. Passerine and prepasserine species number 36 and 35 on St. Vincent and Grenada respectively (Bond, 1963), and no other small tyrannids appear to affect the success of *flavogaster* in mesic habitats on St. Vincent, or of *martinica* in xeric habitats on Grenada.

SUMMARY

The ranges of *Elaenia flavogaster* and *E. martinica* overlap in the southern Lesser Antilles. Where allopatric, *martinica* is found in all habitats, while *flavogaster* prefers open habitats and is never found in mesic forest. Zoogeographic evidence indicates the *flavogaster* has recently invaded from Trinidad, while *martinica* represents a much earlier invasion

of undetermined origin. On Grenada the two occupy different habitat niches, with *martinica* being found only in mountain forest. On St. Vincent the two species occupy overlapping niches. *Flavogaster* is more abundant in open, xeric habitats, while *martinica* is commoner in mesic habitats, and is again found alone in mountain forest. Thus *flavogaster*, a species with narrower habitat preferences, depresses populations of *martinica* when the two are sympatric.

Considerable overlap occurs in both method and height of feeding, but significant differences exist. While both species feed predominantly on fruits and berries, *flavogaster* more frequently takes insects in flight. The bill of *flavogaster* tends to be shorter and wider than that of *martinica*. Allopatric populations of the two species differ significantly in these respects, and on Grenada these differences may be slightly increased by character displacement in *martinica*. On St. Vincent the two species are more similar than elsewhere, and do not differ significantly, although interspecific differences in bill size and shape tend to be preserved in females. Bill width at the nostril is more responsive than bill length in all cases. Variance in bill size does not increase in insular populations of *flavogaster*, and decreases in *martinica* where sympatric with *flavogaster*.

It is not clear why exclusion on St. Vincent has been incomplete. Obscure environmental differences between Grenada and St. Vincent may have altered competitive relationships on the latter, and it is hoped that this study will provide a basis of comparison for future observations.

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