CONTACT ZONES AND HYBRIDIZATION IN THE JAMAICAN HUMMINGBIRD, *TROCHILUS POLYTMUS* (L.)

FRANK B. GILL, F. J. STOKES, AND C. STOKES

Academy of Natural Sciences
Philadelphia, Pennsylvania 19103

Jamaica (4411 square miles) in the West Indies is the smallest island in the Western Hemisphere on which a bird species is known to have differentiated into taxonomically distinct populations (Bond 1956:95). One race *T. p. scitulus* of the endemic Jamaican Hummingbird *Trochilus polytmus* (L.) is confined to the extreme eastern end of the island, while the other, *T. p. polytmus*, occurs widely over the rest of the island. Here, we examine the geographical relationships of these two forms with particular emphasis on the zones of contact. Our study is based on the examination of museum specimens in the collections of the Museum of Comparative Zoology (MCZ), American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), U.S. National Museum (USNM), the Institute of Jamaica in Kingston (JI), and on the results of field studies in eastern Jamaica in January 1971.

GENERAL BIOLOGY OF *TROCHILUS POLYTMUS*

Trochilus polytmus, often called Doctor Bird or Streamer-tail, is one of the most widespread and abundant bird species on the island of Jamaica (Bond 1936). It is common at all elevations and in nearly all habitats, including gardens. It feeds at various flowers including many cultivated or escaped exotics. At the time of our visit in January 1971, the flowers of the Tahiti apple (*Syzygium malaccensis*, Myrtaceae) were the most frequented nectar source in eastern Jamaica. African flame trees (*Spathodia campanulata*, Bignoniaceae), the endemic mahoe (*Hibiscus elatus*, Malvaceae), and to a lesser extent *Thunbergia alata* (Acanthaceae) and *Gliricidia sepium* (Leguminosae) were also used, but such flowers as *Cajanus cajan* (Leguminosae) and *Hibiscus rosasinensis* (Malvaceae), which are known to be favorites of *Trochilus*, were rarely visited.

Except for the general nesting observations of Gosse (1847), the breeding biology of *T. polytmus* has not been studied. Nests have been found in almost every month of the year, but January and June appear to be the months of greatest nesting activity (Gosse 1847:102). Presumably, *T. polytmus* is polygamous like most known sexually dimorphic hummingbirds. We observed courtship once in a grove of mahoe trees, where an adult male *scitulus* (one of nine) displayed with spread gorget and tail in front of a perched female by swinging in a short pendulum-like arc accompanied by rhythmic chirping.

Plumage color of *Trochilus polytmus* has been described in detail by Ridgway (1911) and Bond (1936). Timing and patterns of molts have not been studied in this species, but the usual sequence of male plumages appears to be as follows:

1. *Immature* males leave the nest with a metallic green gorget and back but dull brownish-black belly feathers. The rectrices have light brownish-green tips. The nape and pileum are a mixture of blackish and green feathers, none of which are elongated as in the adult male. There is no dull immature plumage that resembles the typical female plumage, although Gosse (1847) records an aberrant female-plumaged individual with paired testes.
2. *Subadult* males acquire the body plumage coloration of adult males, including the full black crown with elongated nape feathers and the bright metallic green covering the entire underparts. The flight feathers are not replaced with this change of body plumage.
3. *Adult* male plumage is attained through replacement of the flight feathers. Adult rectrices lack the light tips of younger birds and include the greatly elongated next-to-outermost pair of tail feathers so characteristic of this species. Wing feathers are apparently replaced at the same time; the wings of adult males average about 3 mm longer than the wings of young and subadult males. The ninth primary (next to outermost) elongates relative to the outermost primary during this molt and becomes the longest remex, an unusual hummingbird condition shared only with the genus *Goldmania* (Ridgway 1911).

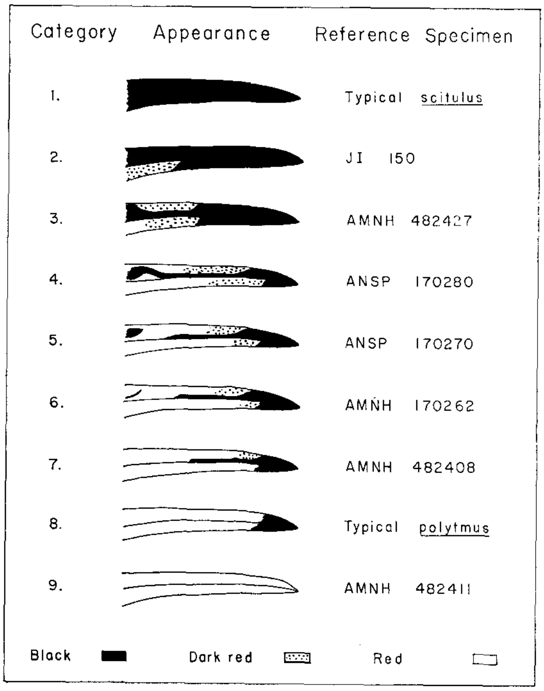

FIGURE 1. Categories of bill coloration of *Trochilus polytmus.*

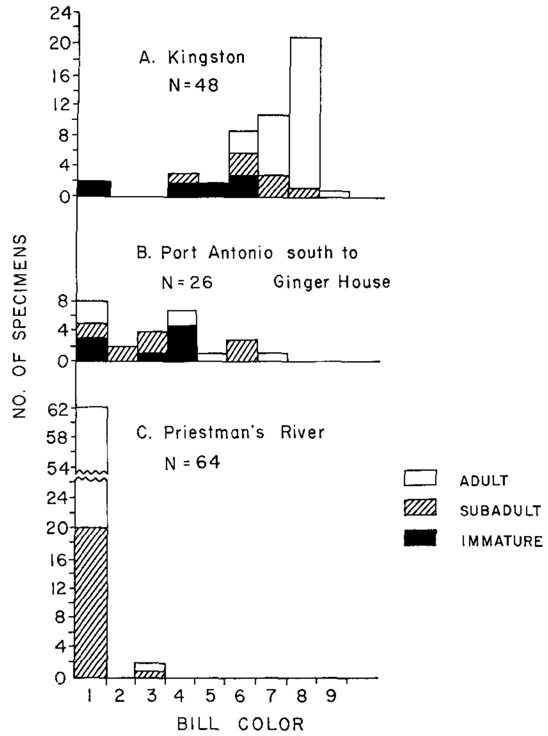

FIGURE 2. Distribution of specimens over range of bill color categories illustrated in figure 1. Localities include: (A) Kingston, a typical *T. p. polytmus* locality; (B) the hybrid zone between *T. p. polytmus* and *T. p. scitulus* on the north side of Jamaica; (C) Priestman's River, the type locality of *T. p. scitulus.* The sample of "subadult" specimens from Priestman's River also includes "immature" specimens.

COMPARISON OF *T. P. POLYTMUS* AND *T. P. SCITULUS*

T. p. polytmus and *T. p. scitulus* are best characterized by adult male bill color, which is typically red with a black tip in *polytmus* and completely black in *scitulus.* The base of the lower mandible of female *polytmus* is reddish as compared to black in female *scitulus,* but because these differences are not nearly as pronounced as in the males, females are not analyzed in this study.

Bill color of male *T. polytmus* is here evaluated in terms of nine character states, ranging from pure red to pure black (fig. 1). The majority of adult male specimens from Kingston, a typical *polytmus* locality, has bright red bills with limited black tips (Categories 7 and 8). A few adult specimens have more pronounced black on the bill, including a dark nostril edge (Category 6). Immature and subadult male *T. p. polytmus* have darker bills than adult males (fig. 2). Relatively little variation in bill color is evident in the large sample of specimens from Priestman's River, the type locality of *T. p. scitulus.*

Plumage color differences between *T. p. polytmus* and *T. p. scitulus* involve mainly the shade of green which is a slightly darker, less yellow-green in *scitulus* (Brewster and Bangs 1901; Bond 1936).

T. p. scitulus averages smaller in wing-length, tail length, and bill length than *T. p. polytmus* (Brewster and Bangs 1901; Ridgway 1911; Bond 1936; table 1). Conspicuous in live birds and fresh specimens is the broad, flared base of the upper mandible of *polytmus,* but narrower base in *scitulus* (Brewster and Bangs 1901:48). In both races, the wings of females average about 13% shorter in length than the wings of (adult) males. Bills of females average slightly longer than those of males.

There are no known differences in behavior or vocalizations between *T. p. polytmus* and *T. p. scitulus.*

T. p. polytmus is found throughout Jamaica except in the extreme east where it is replaced by *T. p. scitulus* (fig. 3). *T. p. polytmus* occurs along the northern coast as far east as Port Antonio, in the Blue Mountains to Sugar Loaf Peak (just east of Blue Mt. Peak), perhaps farther, and along the southern coast to extreme western St. Thomas Parish (Bond 1956). *T. p. scitulus* is found east of Port Antonio on the northern coast, in the John Crow mountain region east of the Rio Grande

TABLE 1. Size characteristics[a] of three populations of *Trochilus polytmus*.

	Winglength				Bill length[b]				Bill width[a]			
	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range	N	$\bar{X}$	SE	Range
Kingston												
Adult Male	31	65.0	0.225	63.0–67.5	46	20.1	0.128	17.6–21.9	15	3.70	0.257	3.3–4.4
Immature Male	16	61.9	0.197	60.5–64.0								
Hybrid Zone (Port Antonio and vicinity)												
Adult Male	6	64.5	0.645	62.5–66.5	16	20.0	0.220	18.5–21.2	15	3.60	0.104	2.9–4.1
Immature Male	9	61.5	0.380	60.0–63.0								
Priestman's River												
Adult Male	10	63.5	0.240	62.0–64.5	17	18.7	0.063	17.0–20.5	12	2.94	0.092	2.4–3.4
Immature Male	6	60.3	0.653	59.0–62.5								

[a] In millimeters.
[b] Age classes combined.

Valley, and east of the Morant River Valley in the southern lowlands. So far as is known, there is no altitudinal replacement of *polytmus* by *scitulus* in the Blue Mountains; typical *polytmus* abound at the top of Blue Mountain Peak (Bond, pers. comm.). Ridgway (1911: 340) records *polytmus* as being accidental at Priestman's River, probably referring to the two intermediate specimens (MCZ 37496, AMNH 482427) from that locality with red bill bases (Category 3, see fig. 2), and also mentions (p. 342) that *scitulus* is accidental in the vicinity of Kingston, probably referring to a black-billed immature male specimen

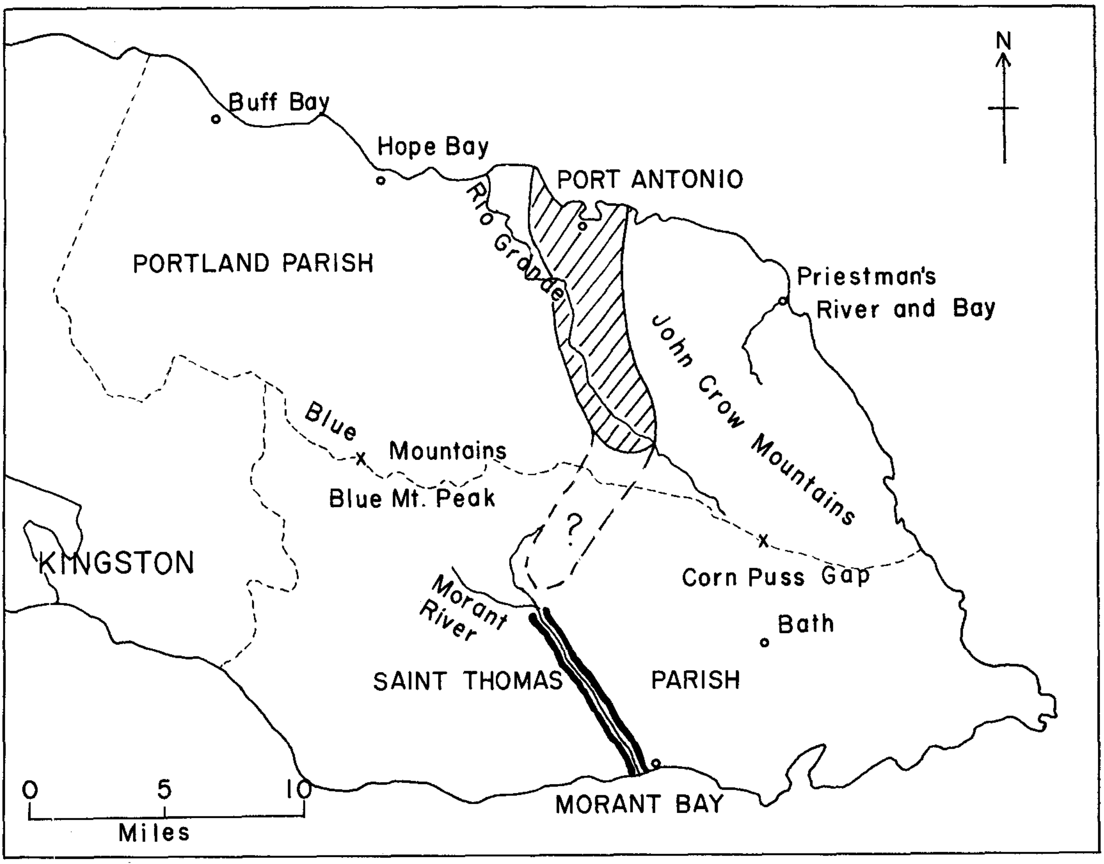

FIGURE 3. Map of eastern Jamaica showing location of hybrid zone (slanted lines) between *T. p. polytmus* and *T. p. scitulus* on the north side of the island, and the zone of contact and isolation at the Morant River Valley (heavy black) on the south side of the island. *T. p. polytmus* occurs west of these zones, while *T. p. scitulus* occurs to the east.

(MCZ 37452) from that locality. Additional evidence of occasional wandering by *scitulus* is provided by a recent record of an adult male *scitulus* netted at Hardwar Gap, a well-known *T. p. polytmus* locality in the Blue Mountains north of Kingston (Bond, pers. comm.).

CONTACT ZONES BETWEEN *T. P. POLYTMUS* AND *T. P. SCITULUS*

In January 1951, Bond (1956; pers. comm.) collected sample specimens at a series of localities along the north coast of Jamaica and discovered an intermediate population in the vicinity of Port Antonio, the area of contact between *T. p. scitulus* and *T. p. polytmus*. Jeffrey-Smith (1956) noted some mingling of the two forms at Bath.

Delimitation of the zones of contact between *T. p. scitulus* and *T. p. polytmus* was the primary objective of our field work. We spent 9 days in January 1971 in the vicinity of Port Antonio to extend the observations of Bond (1956), and 4 days at Bath and the adjacent Morant River Valley to establish the location of the contact zone on the southern coast of the island. In the time available, we censused roadsides and adjacent footpaths by stopping whenever the distinctive notes of *Trochilus* were heard, suitable flowers spotted, or birds actually seen. The bill colors and plumage (long tail vs. short tail) of all males encountered in this way (225 total) were recorded.

Some specimens were taken and at two localities (Ginger House and Cambridge) live *Trochilus* were netted for inspection and then released. But because it was not possible to collect large numbers of *Trochilus* specimens during our stay in Jamaica, visual counts and observations of the different bill-color forms were an essential source of data. The need for careful and critical observations of bill color was clearly recognized because red bills can appear black in poor light or if inspection is casual. Consequently, we recorded only those males which were studied at close range in such a way as to eliminate any doubt in our own minds that the correct bill color had been seen; this may have introduced a slight bias toward increased frequency of forms with red bills, which are easier to discern. Of course, we were not able to distinguish among all of the categories delimited in figure 1. Rather, we noted whether the bill was "red" (Categories 7–9), "black" (Category 1), "black intermediate" (Categories 2–3), or "red intermediate" (Categories 4–6). We tended to allocate individuals to the extreme "red" or "black" categories unless a sustained close look allowing more specific allocation was obtained. The value to our studies of short-tailed males with "red intermediate bills" is uncertain because of the variation in bill color due to age evident in the Kingston population. Adult males with bills in Categories 2–5 probably reflect hybridization as do young males with bills in Categories 2 and 3. For purposes of analysis, we consider these collectively as intermediate and conservatively treat short-tailed males with red intermediate bills as typical *polytmus*. These data provide an accurate picture of the location and approximate width of the contact zones and to some extent the degree of interbreeding between the two forms, but larger samples of specimens are needed to establish the extent of hybridization and introgression away from these zones.

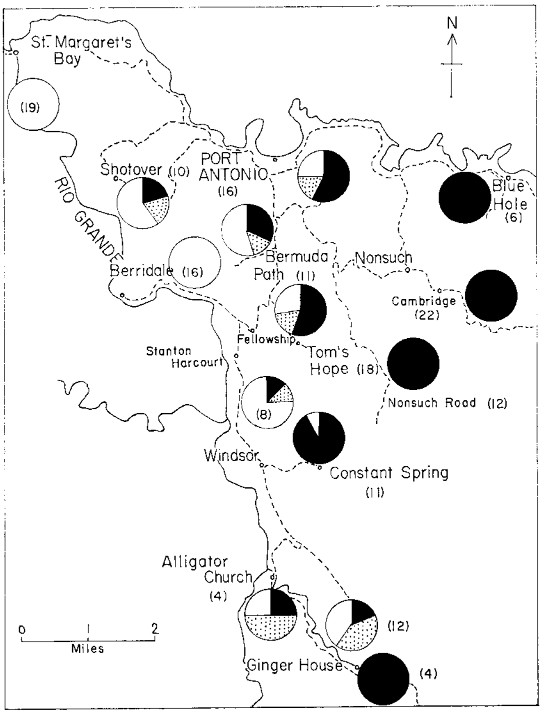

FIGURE 4. Bill-color compositions of *Trochilus* populations in the contact zone on the north side of Jamaica. In each circle graph, black indicates per cent *scitulus*, white indicates per cent *polytmus*, and stippling indicates per cent intermediates (see p. 173). Sample size is indicated in parentheses after each locality.

Our field work on the north side of Jamaica revealed that the zone of contact between *T. p. polytmus* and *T. p. scitulus* extends 8 miles S from Port Antonio to Ginger House, and is as little as 3 miles wide at its northern end (figs. 3 and 4). Only typical *polytmus*

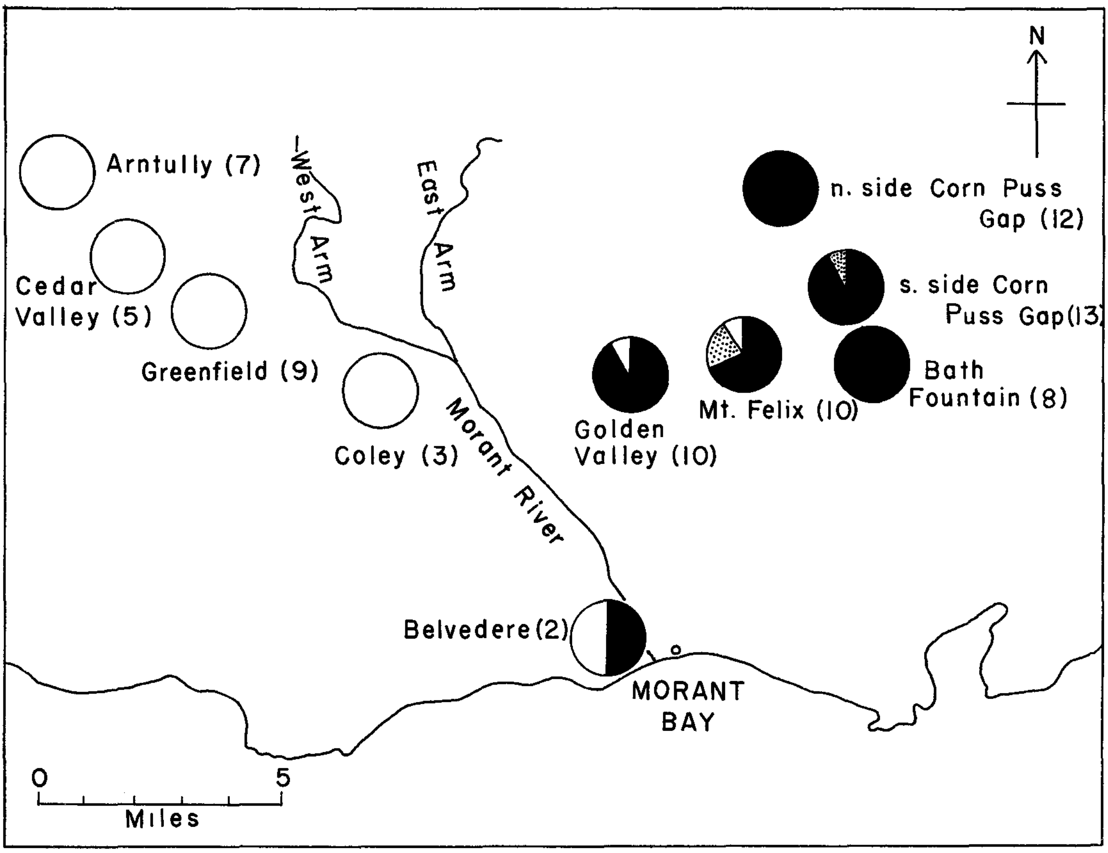

FIGURE 5. Bill-color compositions of *Trochilus polytmus* populations on the south side of Jamaica. See figure 4 for explanation.

were found in the vicinity of Hope Bay (6 total) and in the vicinity of St. Margaret Bay at the north end of the Rio Grande (19 total), localities which are respectively located 8 miles and 4 miles W of Port Antonio. Some *scitulus* (2 out of 10) and intermediates were found near Spring Bank and Shotover, 2.5 miles W of Port Antonio. About 55% of the individuals (16 total) within a one-mile radius of Port Antonio were typical *scitulus*, the rest were *polytmus* and intermediates. All males (22 total including 10 that were netted and examined in the hand at Cambridge) that we found 3.5 miles W of Port Antonio were typical *scitulus*. (Two intermediate males have been taken further east in the large samples of specimens from Priestman's River, 7.5 miles SE of Port Antonio.) The linear distance between apparently typical *polytmus* populations near St. Margaret's Bay and apparently typical *scitulus* populations near Cambridge is about 8 miles.

A second east-west transect across the contact zone about 2 miles inland was also censused (fig. 4). Only adult male *polytmus* and red-billed young males were found along the road between Berridale and Fellowship. Proportions of *scitulus*, *polytmus*, and intermediates similar to those found at Port Antonio were present along the road to Toms Hope, 0.7 miles E of Fellowship. Only typical *scitulus* (12 total) were found along the north-south dirt road from Nonsuch to Constant Spring, 1.2 miles E of Tom's Hope. The linear distance between Berridale and this road is 3 miles.

Both *scitulus* and *polytmus* as well as intermediates occur along the main road that follows the valley of the Rio Grande south from Port Antonio to Ginger House (fig. 4). Two localities that we sampled along this road have already been mentioned, namely, Port Antonio and Tom's Hope. A census along the trail to Bermuda, which starts from the main road 1.5 miles S of Port Antonio, yielded about 35% *scitulus*, somewhat less than at the adjacent localities. The proportions of *scitulus* are rather low (about 10%) S of Fellowship, suggesting an eastward bending of the contact zone. However, the population at Constant Spring, one mile to the east of the main road, included only 9% (1 of 11 males) *polytmus*, indicating an abrupt change of the phenotypes. A similar abrupt change of *scitulus* phenotypes appears to take place just south of Ginger House, but only a few males were observed there. The mountain forests at the end of the valley, NW of Corn Puss Gap, are inhabited by *scitulus*.

The presence of intermediate bill-color phenotypes in the zone of contact is indicative of successful interbreeding between *scitulus* and *polytmus* (fig. 2), but adequate samples of adult male specimens from this zone are needed to evaluate the possibility of partial reproductive isolation.

Size characteristics of the hybrid population are more similar to *T. p. polytmus* than to *T. p. scitulus* (table 1). However, detailed analysis of mensural variation in and adjacent to the contact zone must await acquisition of large specimen samples. Particular caution is needed in the analysis of bill width, a character easily distorted by tying of the specimens' bills.

The contact zone on the south side of the Blue Mountains lies further west than that on the north side and appears to coincide with the valley of the Morant River (figs. 3 and 5). Occasional *polytmus* or intermediates occur in the *scitulus* populations on the southeastern slopes of the Blue Mountains, e.g., south of Corn Puss Gap, Mt. Felix, and Golden Valley. *T. polytmus* is rare, in January at least, in the coastal lowlands of the District of Morant E of the Morant River. The few individuals found in this area were *scitulus*. The only two (adult) males seen on the west bank of the lower Morant River (one mile N of Belvedere) included one typical *T. p. polytmus* and one typical *T. p. scitulus*. The vegetation along the banks and in the dry bed of the Morant River itself supports few *T. polytmus*; in fact, there appears to be a hiatus in the range of this species that coincides with the valley. *Trochilus* reappears as a familiar garden bird in the foothills of the Blue Mountains on the west side of Blue Mountain Valley in the District of Upper St. David; all birds observed in this area were typical *T. p. polytmus*. Thus the ranges of *T. p. polytmus* and *T. p. scitulus* are separated by the Morant River Valley on the south side of the island. Presumably, the two forms come into full contact in the mountains near the northern end of the Morant River Valley. Further field work in the extreme eastern Blue Mountains may reveal a connection between this area and the hybrid zone on the north side of the island as illustrated by the dashed line in figure 3.

DISCUSSION

Present evidence indicates that *T. p. polytmus* and *T. p. scitulus* may have been geographically isolated in the lowlands by the humid valley of the Rio Grande on the north side of Jamaica and by the Morant River Valley on the south side. Whether the species inhabited the tropical rain forests that were originally in the Rio Grande Valley (Asprey and Robbins 1953) is not known, but there can be little doubt that this hummingbird has benefitted greatly from man-made changes in habitat and flower availability. It seems likely, therefore, that expansion of the two hummingbird populations into the Rio Grande Valley, followed by interbreeding, has resulted from the cutting of the primeval rain forests and the introduction of exotic flowers. That the contact between the two forms in this area may be a rather recent event is also suggested by the following statements of Jeffrey-Smith (1956:24): "From 1903 I knew of the existence of a black-billed streamer tail in Portland and the adjoining Parish of St. Thomas. Indeed the red-billed doctor bird is unknown at Port Antonio I was told."

It seems, therefore, that classical processes of geographic isolation followed by secondary contact are at least partly responsible for the presently observed situation in *Trochilus polytmus*. Although further collecting is needed to establish the actual extent of introgression, it appears from this study that the zone of secondary contact and hybridization in the valley of the Rio Grande is less than 10 miles wide at its widest point and is perhaps as little as 3 miles across in some places. Few avian hybrid zones are this narrow; most are between 35 and 200 miles wide (Hubbard 1969). Only two other comparably narrow hybrid zones have been described: (1) conspicuous hybridization between *Campylorhynchus rufinucha humilus* and *C. r. nigricaudatus* is restricted to a 6.5-mile-wide zone or less (Selander 1965); (2) hybridization between gray-headed and brown-headed brown morphs of *Zosterops borbonica* on Reunion Island takes place in a zone about 5 miles wide in continuous populations in the highlands and about one mile wide at certain lowland river beds (Gill 1973). There is no evidence of selection against hybridization in *Campylorhynchus* but there is a suggestion of this in *Zosterops*.

Counterselection is usually considered an important determinant of hybrid zone widths (Mayr 1963; Bigelow 1965; Hubbard 1969), and very likely limits penetration of *polytmus* characters into *scitulus* populations, which inhabit an area of geological, botanical, and climatological distinction. The high rainfall characteristic of this eastern tip of Jamaica once supported rain forests unlike those found elsewhere on the island (Asprey and Robbins 1953). Also, the John Crow Mountains are limestone formations whereas the Blue Mountains consist primarily of metamorphic rocks. These two formations are separated by exposed shale beds in the valley of the Rio Grande and the indigenous vegetation changes accordingly (G. Proctor, pers. comm.). Possibly also the difference in bill widths between *polytmus* and *scitulus* reflect particular flower preferences or differences in insect-catching abilities.

Geographic differentiation in natural populations is determined in large part by the interaction of natural selection, which promotes divergence through adaptation to different environments, and gene flow, which opposes divergence by increasing genetic homogeneity of adjacent populations as well as by favoring homeostatic gene combinations which may become resistant to evolutionary change (Mayr 1963). Mobile organisms such as birds rarely differentiate into distinct local populations without conspicuous isolation (Mayr 1963) and, in particular, the rarity of avian subspeciation within the confines of small oceanic islands suggests that island size imposes some constraints on the process of geographic differentiation. Yet distinct bird populations can diverge on a small island, as the situations in *Zosterops borbonica* (Gill 1973) and *Trochilus polytmus* demonstrate.

The situation in *Trochilus polytmus* resembles that in *Zosterops* on Reunion Island in that it seems to have involved at least some geographic isolation, followed by secondary contact and interbreeding. Both situations involve narrow but conspicuous geographic isolation in some areas, but hybridization in a zone of contact between continuous populations in other areas. Classical forms of geographic isolation thus seem important, which might explain the rarity of such cases because few small oceanic islands have major geographic barriers within their confines. Yet the barriers involved are not particularly impressive as regards their size or apparent severity; minor features such as small lava flows and river valleys are effective barriers even for such mobile birds as hummingbirds. As a possible explanation, we suggest that some island populations may become highly susceptible to interpopulation divergence because of decreased genetic homeostasis.

Genetic homeostasis increases resistance to evolutionary change, but should decrease under conditions of reduced genetic variability, such as in small isolated populations (Mayr 1963:534). Usually this facilitates divergence between island populations, examples of which have provided the raw material for current theories regarding the importance of isolation and interruption of gene flow. In certain cases, as in *Zosterops* and *Trochilus*, the same process may facilitate divergence of partially isolated populations within the confines of one small island. It should be recalled that the present abundance and distribution of both these birds is a recent phenomenon resulting from man-made changes in the available habitats; previously their populations were much smaller.

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