

Distributional Patterns in St. Croix *Sphaerodactylus* Lizards: the Taxon Cycle in Action

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ABSTRACT

Two species of small gekkonid lizards, genus *Sphaerodactylus*, occur on St. Croix. *S. macrolepis* occupies most of the island, and *S. beattyi* is restricted to three disjunct areas in the eastern part of St. Croix. There is little or no overlap of the two species' ranges. At several points the two are very sharply parapatric. We compare the current distributions with records from the late 1930's and from 1965. Borders between the two species appear to have oscillated back and forth during the last 40 years. This distributional pattern is probably due to the competitive exclusion of *beattyi* by *macrolepis* from the more mesic portions of the island, which appears to be the most favorable habitat for both species. Evaporative water loss is significantly lower for *beattyi*, supporting this interpretation. We discuss a model of interspecific competition along an environmental gradient which could explain these observations.

CURRENT INTERPRETATIONS OF PATTERNS in island biogeography depend on the belief that regularities are to be found in the extinction and colonization of species on islands. A 'distant' view of insular biotas (discussed by Williams 1969) tries to explain the number of species as a balance between colonization and extinction rates, which are considered functions of variables such as area and distance from the source of colonists (e.g., Gilpin and Diamond 1972). Complementing this line of investigation is the close view of islands, in which one pays close attention to the biological details of a small group of species in order to understand the ways an island community can react to invasion, and tries to delineate the essential features of a good colonist (Williams 1969, Lack 1976). One problem facing the latter approach to island studies is that certain transient stages in the colonization process are rarely found. In particular, the initial contact between ecologically similar species is a seldom-observed stage in island colonization, because the colonizing species suffers rapid extinction, drives the resident species to extinction, or—presumably the least likely possibility—both species evolve niche differences that allow coexistence.

Two species of the lizard genus *Sphaerodactylus* on the island of St. Croix (U.S. Virgin Islands), *S. macrolepis* and *S. beattyi*, appear to be at this critical stage of faunal build-up. In this paper we discuss the distribution of these species on St. Croix. Our data indicate that *macrolepis* is a fairly recent invader of St. Croix and that it has excluded the endemic *beattyi*

from most of the island. In addition, our data, together with previous distributional surveys, show that the edges of the two species' ranges have fluctuated back and forth during the last 40 years, perhaps in response to short-term climatic fluctuations.

SUBJECTS, SETTINGS AND METHODS

Sphaerodactylus is a small gekkonid lizard which is diverse and widespread in the West Indies (56 species according to Schwartz and Thomas 1975). The two St. Croix species are strictly terrestrial, rarely ascending more than a few inches onto the vegetation. Both species are abundant in situations where leaf litter accumulates, such as on forest floors, along walls, and in gullies, and eat small arthropods. In such places these lizards may be found by turning over rocks and logs or by shuffling through the litter. In dry forest with rocky soil and little litter they are uncommon, and they are essentially absent from fields and other dry, open habitats.

During early September 1975 and January 1976 we spent two weeks surveying the distributions of the two species on St. Croix. One of us (WPM) returned in April 1976. Using the distributional data of Thomas and Schwartz (1966, see fig. 3) we began our survey at the points of contact between the two species as previously known, searching until we found the current contacts between the ranges. We sought the lizards in all accessible areas with suitable microhabitat. At all but the most barren sites, we searched until we found several animals. We also hunted for *beattyi* in the eastern two-thirds of St. Croix, although our mapping efforts there were less

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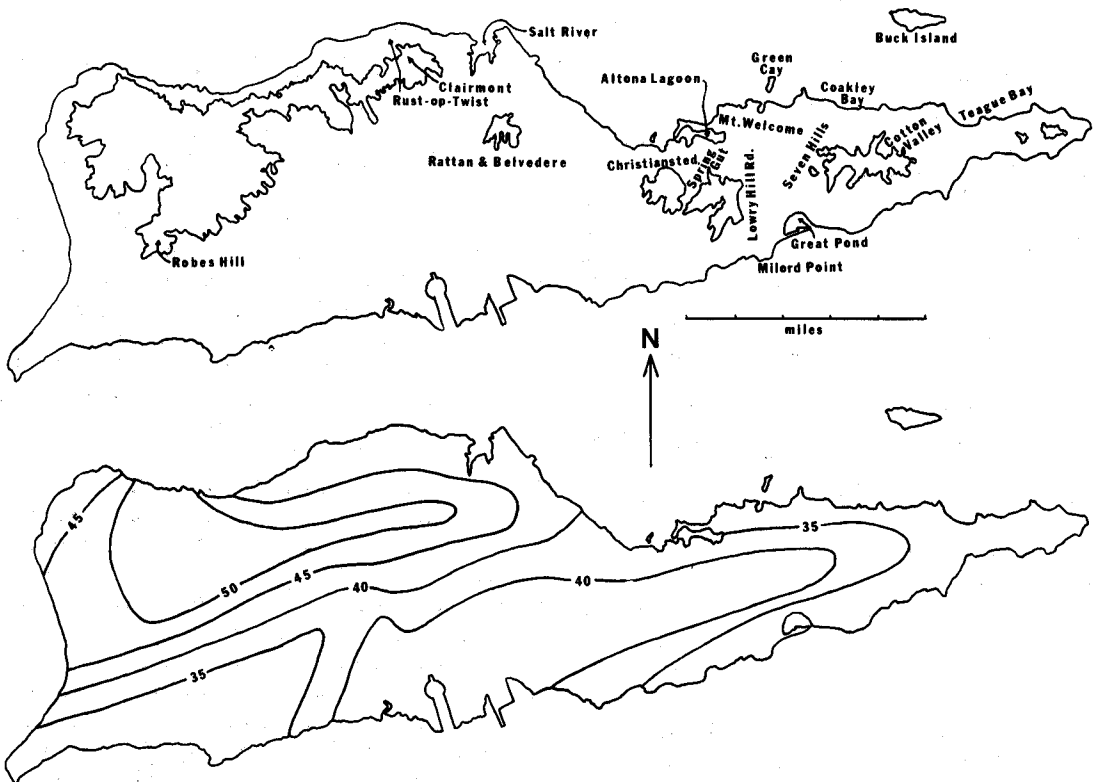
intense than near contact zones. The two species are readily and unequivocally identifiable in the field.

St. Croix's area is 230 km², and its highest elevation is 355 m. Rainfall is highly seasonal and variable from year to year (by about a factor of 2). Figure 1 shows the 400 ft (121 m) contours and the localities to which we refer. Figure 2 depicts isohets of mean annual rainfall. Where undisturbed, the northwestern range is cloaked with moist forest and the rest of the island with dry forest, grading to cactus scrub at the eastern and southwestern peninsular projections. Most of St. Croix's vegetation has been disturbed by man at one time or another.

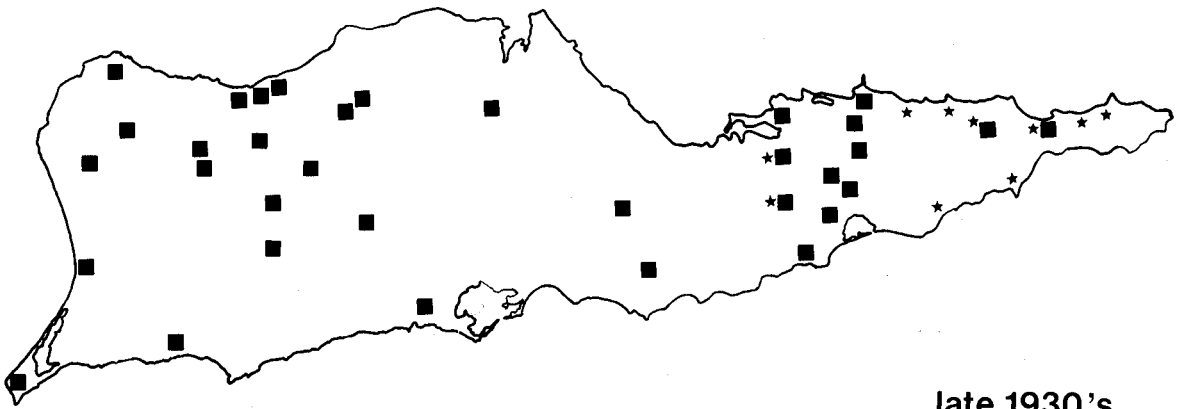
RESULTS

The present distribution of *S. beattyi* comprises three disjunct areas, two of which are surrounded by the range of *S. macrolepis*. Figure 3 summarizes the distributional data discussed below. We describe each area and compare the current ranges to those found by Beatty in the 1930's (Grant and Beatty 1944) and by Thomas and Schwartz (1966). These data show that at least one and possibly all three areas have varied considerably in extent during the last 40 years.

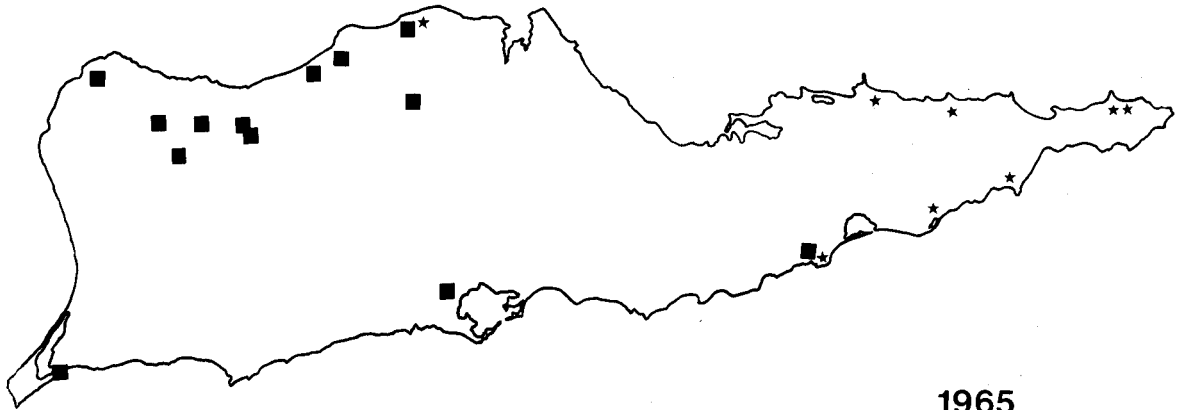
AREA 1, EASTERN ST. CROIX.—Only *S. beattyi* now occurs to the east of a line connecting Coakley Bay and the east end of Great Pond. The beach at Coakley Bay is approximately 370 m long; only *macrolepis* occurs at the west end, and only *beattyi* at the east end. The intervening area is salt pond and manchineel thicker; no lizards were found there, or elsewhere near this very poisonous tree. Along Seven Hills Road, *macrolepis* was alone in the lower, level area and only *beattyi* was found above 500 ft. elevation. In between was a new housing development, where neither species was found. The most intriguing spot we found in this area was immediately east of Great Pond, where we have observed changes in the distribution of both species during the period of our work. Approximately one hectare of thick, low thorn scrub is dissected by a gully. In September 1975 the gully was filled with dead leaves and debris, *macrolepis* was very abundant but no *beattyi* was seen. We returned in January 1976 to find *beattyi* in large numbers, but no *macrolepis*. The surrounding brush had a low density of lizards. Only *macrolepis* was found to the west (none found within 35 m) and only *beattyi* to the east (10 m). In April 1976, the amount of litter in the gully was greatly reduced, and both



FIGURES 1 and 2. Figure 1 (above). St. Croix with place names used in text and 400-foot contours. Figure 2 (below). Distribution, in inches, of mean annual rainfall for years 1918-1967 (Jordan 1975).

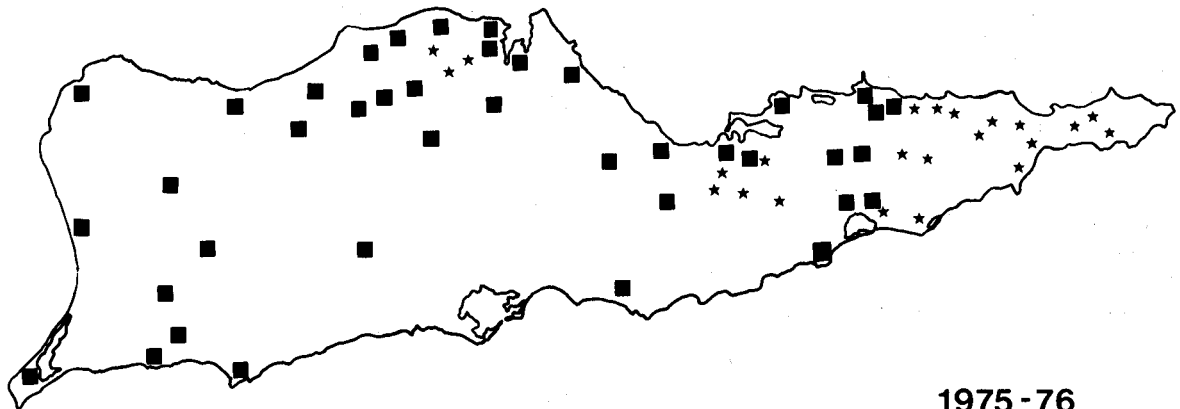


late 1930's



1965

— miles —



1975-76

FIGURE 3. Distribution records for *Sphaerodactylus macrolepis* (squares) and *S. beattyi* (stars). See text for details.

species were present, though not abundant.

In 1966, Thomas and Schwartz found *beattyi* at Milord Point to the west of Great Pond, about 1.2 miles from the present contact between the two species. In 1976, only *macrolepis* occurred at Milord Point, as well as between there and the eastern edge of Great Pond. Thus, during the past decade there has been a reduction in the range of *beattyi* along the south coast and a corresponding expansion in the range of *macrolepis*. The available data do not allow us to make such statements about the species distributions on the north coast, although the locality indicated for *beattyi* near Coakley Bay by Thomas and Schwartz is now occupied by *macrolepis*. The data of Beatty suggest that in the late 1930's *beattyi* had much the same range it occupies today. Grant and Beatty report *macrolepis* in Cotton Valley, two miles east of the easternmost extent of *macrolepis* today, and at Teague Bay. After intensive search, we are certain that these enclaves do not exist today. *S. beattyi* is alone on Green Cay and Buck Island.

Three quarters of *beattyi*'s range is included in our Area 1 (about 20 km²). Within Area 1, *beattyi* is found in a wide range of habitats. It reaches its greatest densities in moist, shaded, deep litter. The western edge of Area 1 has the highest densities of *beattyi*.

AREA 2, HILLS SOUTH OF CHRISTIANSTED.—*S. beattyi* occupies a set of steeply sloping hills south of Christiansted that rise to 751 feet and are covered with dry forest. Much of the southern slope of the hills is open habitat where we were unable to find any *Sphaerodactylus*. The surrounding lowlands are occupied by *macrolepis*. Near the northern end of Spring Gut Road, at about 100 ft. elevation, we found the two species in abundance and in close contact, but with very little range overlap. The area is a heterogeneous mixture of houses, open fields, and woods in a flat valley. The two species meet along a creek which is bordered on both sides by woods. Both are abundant and seem to occupy mutually exclusive areas. The transition between the two species is dramatic and is not associated with a sharp change in habitat. An attempt was made to map the vicinity, but was abandoned due to regular and intensive human disturbance. We hope to be able to locate another contact zone where distributions can be followed on a long-term basis.

Unfortunately, Thomas and Schwartz (1966) did not make observations within Area 2. Grant and Beatty (1944) record two localities for *beattyi* in the vicinity of Christiansted. One was Spring Gut, in the center of Area 2 at 400 ft elevation, and the other

was Mt. Welcome, a small hill on the coast, about 1 km north of the present edge of *beattyi*'s range. Only *macrolepis* occurs on Mt. Welcome at this time. In addition, Grant and Beatty give a series of seven localities along Lowry Hill Road for *macrolepis*, suggesting that Areas 1 and 2 were disjunct then, as they are now. Area 2 occupies at least 5 km².

AREA 3, WEST OF SALT RIVER.—The easternmost portion of the western range has an isolated pocket of *beattyi*, no more than a few square kilometers in size. The vegetation there is dry forest, similar to that found in Areas 1 and 2. Along the ridgecrest the population density is very low, making exact location of range boundaries impossible. At Clairmont (about 500 ft elevation) *beattyi* was moderately common. The steep slopes precluded more extensive mapping, especially below Clairmont. Thomas and Schwartz (1966) found *beattyi* on the coast at Rust-op-Twist, below Clairmont. This record appears to represent a temporary expansion of Area 3. We searched extensively along the north shore and on the lower hill sides above Rust-op-Twist and found only *macrolepis*.

THE RANGE OF *macrolepis*.—Almost 90 percent of St. Croix is occupied by *S. macrolepis*. Since the three *beattyi* areas included large amounts of dry forest, we searched for this species wherever this habitat was found. The Rattan and Belvedere Hills south of Salt River and Robes Hill at the southwestern end of the western range have only *macrolepis*, even though both seem suitable for *beattyi*. The most xeric portion of the range of *macrolepis* is southwest St. Croix, which has an annual rainfall similar to that of Area 1 (fig. 2) in *beattyi*'s range. *Macrolepis* occupies all of St. Croix's moist forest.

DISCUSSION

Any interpretation of the pattern of distribution of these two species must account for two points: the ranges of the two species are mutually exclusive and the borders are often sharply defined; and, each species occupies a broad range of habitats. We are aware of some of the problems that can arise when one attempts to determine the distributional limits of species. If in a patch of suitable habitat one species is common relative to another, there is some chance that the rarer species would be missed in a survey such as ours. Thus, it is possible that the overlap between the two species is somewhat broader and more diffuse than we have pictured here, particularly in areas where both species are rare. If exhaustive sampling showed that this was indeed the case, the assertions we make about sharp limits to each species' range

would have to be changed to statements about abrupt changes in the abundance of the two species.

The most likely mechanism leading to a sharply defined boundary in a homogeneous habitat is interspecific competition. There has been little work done on the biology of these lizards, so we can only speculate about the exact nature of the competitive interaction. Certain facts, however, suggest that the competition between the two species may be quite intense. They are similar in size and behavior, are active during the same periods of the day, are the only small ground lizards over most of their ranges, and are generalized in their diets (WPM unpublished data). In many groups of lizards, sympatric congeners differ greatly in size or in habitus or both (e.g., West Indian *Anolis* Schoener 1969). From the size data of King (1962) and Thomas and Schwartz (1966), it appears that broadly sympatric pairs of *Sphaerodactylus* species also differ greatly in size. The two St. Croix species are of very similar size (maximum S-V about 30 mm for both). We are planning manipulative experiments to elucidate further the mechanisms generating the sharp borders we have observed.

The overall distribution of the two species accords well with what is known about their physiology. Dr. Gregory Snyder has kindly allowed us to cite his data on oxygen consumption and evaporative water loss in *macrolepis* and *beattyi*. As can be seen in table 1, *beattyi* has a considerably lower rate of water loss

as measured by percent of body weight lost per day. The species less resistant to water loss, *macrolepis*, occupies the wettest portion of the island. *Beattyi* is restricted to the dry eastern end of the island, and to limestone hills exposed to the trade winds, areas which should be expected to dry quickly after rain. However, details from the distributions show that the two species are not merely dividing the island according to their physiological requirements. The arid southwest corner of St. Croix is occupied by *macrolepis*; within the range of *beattyi*, the greatest densities are in moist sites, such as near the edge of Area 2 at Spring Gut. The sharp partitioning of the island is likely the result of interspecific competitive interactions acted out against a backdrop of intrinsic physiological differences. On islands where *macrolepis* is the only sphaerodactyl, it occurs over the entire island, including habitats comparable to those occupied by *beattyi* on St. Croix. Thus, in the absence of *beattyi*, *macrolepis* would probably occupy the entirety of St. Croix. Since *beattyi* reaches its greatest density in pockets of moist habitat within its range, particularly near its western edge, it appears that it is absent from many areas which it could occupy successfully.

We have not yet considered the possible historical origins of this situation. *Sphaerodactylus beattyi* is endemic to St. Croix. Thomas and Schwartz (1966) consider this to be the most distinctive species of the genus in the Greater Puerto Rican region. Presumably, *beattyi* has been evolving on St. Croix for a long time. A distinctive subspecies has been described from the south of Area 1, and we have noticed a distinctive tail pattern in the Area 3 population. In contrast, *macrolepis* shows no geographical differentiation on St. Croix, is the most widespread member of the genus on the Puerto Rico bank, and is the only one of these species to colonize other banks (St. Croix and Anguilla). Thomas and Schwartz consider the St. Croix populations to be the same subspecies as *macrolepis* from the other Virgin Islands. Most of the other reptile and amphibian species are clearly distinct at the species level. Thus, *macrolepis* appears to be a relatively recent invader of St. Croix. Gunther described *macrolepis* in 1859, giving St. Croix as type locality, while *beattyi* was not described by Grant until 1937, suggesting that *macrolepis* has been widespread there for at least 120 years. Man may have unwittingly assisted in its invasion, either by actually transporting propagules or by clearing large tracts of land for cultivation of sugar cane, and in the process exterminating *beattyi* from the wetter portions of the island. Presumably, *beattyi* once occupied much more of St. Croix than it does today.

TABLE 1. Oxygen consumption and evaporative water loss in *Sphaerodactylus macrolepis* and *S. beattyi* at 30°C.

Body weight (g)	Oxygen consumption (ml O ₂ g ⁻¹ h ⁻¹)	Evaporative water loss (% body wt day ⁻¹)
<i>Sphaerodactylus macrolepis</i> (data from Snyder 1975)		
0.40	0.22	14
0.42	0.23	18
0.47	0.32	8
0.48	0.17	15
0.47	0.27	11
0.48	0.24	14
mean	0.45	13.3
S.E.	0.01	1.40
<i>Sphaerodactylus beattyi</i> (Snyder, new data)		
0.40	0.31	5
0.26	0.29	9
0.33	0.30	10
0.41	0.22	7
0.37	0.19	6
0.47	0.19	7
0.38	0.20	7
0.34	0.23	10
mean	0.37*	7.6**
S.E.	0.02	0.70

*significantly different at the 98% level.

**significantly different at the 99% level.

Models of interspecific competition that can be used to depict patterns of mutually exclusive species ranges are readily devised. The simplest method is to allow the parameters of the Lotka-Volterra model to be functions of position along an environmental gradient (such as moisture) and to assume that dispersal occurs over distances that are short compared with the spatial scale of the gradient (Pielou 1974). If the competition coefficients are very close to one (if the negative effect of an individual of Species 1 on the per-capita growth rate of Species 2 is nearly the same as the effects of that individual upon its own species per-capita growth rate) then the superior competitor at any point on the environmental gradient will be the species with the highest carrying capacity. Stable parapatry occurs when $K_1(x)$ and $K_2(x)$ cross once. Figure 4 shows the case in which Species 1 is a gen-

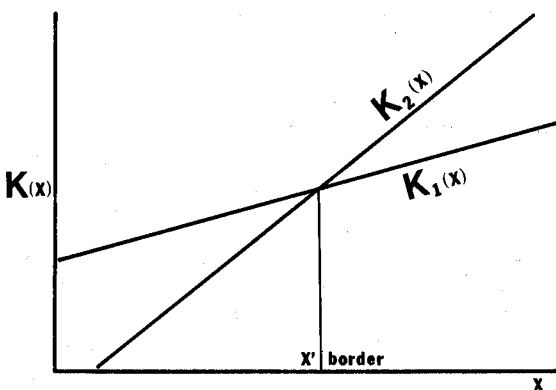


FIGURE 4. Carrying capacities of two species as a function of an environmental gradient. Intense competition results in the border at x' .

eralist able to live in moderate abundance all along the gradient, while Species 2 is specialized to one end of this gradient. If the tolerance to water loss of *beattyi* represents one part of an adaptive compromise (i.e., food-gathering efficiency might be reduced as a consequence), then the relative carrying capacities of the two species of *Sphaerodactylus* along a gradient of surface moisture might agree with this model. Fluctuations in rainfall would then lead to movement of the boundary between the species. We plan to follow this situation for several years to see if climate

and distributions are correlated as we expect. Regardless of the proximal cause for these fluctuations, their existence demonstrates that the parapatric distribution of these two species does not merely reflect a habitat discontinuity. Moreover, in the model Species 1 reaches its greatest abundance at the contact zone, whereas Species 2 reaches its greatest density away from it. This prediction matches our observations.

The sharp distributional transition between *macrolepis* and *beattyi* is reminiscent of those described by Jaeger (1971), Brown (1971), Miller (1964, 1967), and others on continental areas; like these, the distributional pattern seems to arise from competition acting on a shifting background of physical factors.

CONCLUSION

The problem of what controls the distributional limits of species is a central one in ecology and biogeography. Competitive exclusion seems to be the controlling factor of the distributional patterns described in this paper. The evidence for this conclusion may be categorized as follows: (a) the two species are similar in size and habitats; (b) the distributions are parapatric, both now and in the past; (c) both the overall ranges and the physiological data indicate that *beattyi* is better adapted to xeric conditions than is *macrolepis*, which is apparently why one has not excluded the other on St. Croix; and (d) there is reason to believe that, in the absence of either species, the other would be more widely distributed than at present. Sharp parapatry is rarely observed on small islands, although two introduced species of ants on Bermuda show it (Haskins and Haskins 1965, Crowell 1968). Such intense competition is seldom observed among island vertebrates, presumably because it is an unstable situation which soon leads to extinction or to evolutionary accommodation. It must, however, occur frequently during the build-up of insular faunas.

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