BREVIORA

Museum of Comparative Zoology

US ISSN 0006-9698

CAMBRIDGE, MASS. 20 APRIL 2000 NUMBER 508

NEW RECORDS AND DISTRIBUTIONAL AND ECOLOGICAL NOTES OF LEPTODACTYLID FROGS, *LEPTODACTYLUS* AND *ELEUTHERODACTYLUS*, FROM THE BRITISH VIRGIN ISLANDS

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ABSTRACT. Information on distribution and habitat use of frogs in the British Virgin Islands is needed for assessing population trends and status and for elucidating biogeographic patterns. We discovered 10 new populations of the four known species of Leptodactylidae on five of the 17 islands visited: *Eleutherodactylus antillensis* on Great Camanoe, Great Thatch, Jost Van Dyke, and Beef Island; *E. schwartzi* on Beef Island, Frenchmans Cay, and Jost Van Dyke; *E. cochranae* on Great Thatch and Jost Van Dyke; and *Leptodactylus albilabris* on Beef Island. We confirmed all but three previous island records: *E. cochranae* and *L. albilabris* on Virgin Gorda and an unidentified *Eleutherodactylus*, known only from the stomach of a snake, on Peter Island. The earlier *E. cochranae* record is probably in error, but *L. albilabris* and *Eleutherodactylus* seem to have disappeared from Virgin Gorda and Peter Island, respectively. The mean body size of adult males of *E. antillensis* and *E. schwartzi* was smaller on Virgin Gorda than on Tortola, and males of *E. schwartzi* were relatively large on the tiny (33 ha) island of Great Dog. On all islands except Tortola, *E. schwartzi* was almost exclusively associated with bromeliads. Island elevation and area explained 61% of the variation in the number of species when all 17 islands were included in the

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model. Elevation was the most important factor (partial $r^2 = 0.35$), whereas area explained little of the observed variation (partial $r^2 = 0.02$). The availability of specific habitat features, such as aquatic breeding sites for *L. albilabris* and retreat and nesting sites for *Eleutherodactylus,* are critical for populations on small islands. The distribution patterns in the British Virgin Islands do not indicate widespread extirpations or declines of frogs comparable to those observed in Puerto Rico and other parts of the world.

> *. . . there is an urgent need to document the distribution and abundance of amphibians.*
>
> *Leonard (1997)*

INTRODUCTION

Precipitous declines in a number of anuran populations within the past few decades have led to local extirpations and even species extinctions (Mittermeier *et al.,* 1992; Pechmann and Wilbur, 1994; Phillips, 1994; Blaustein and Wake, 1995). In Puerto Rico alone, three species of frogs (genus *Eleutherodactylus,* family Leptodactylidae) have disappeared within the past 20 years, and an additional seven show serious declines (Rivero, 1991; Joglar and Burrowes, 1996). Efforts to document and understand changes in anuran population and distribution characteristics are severely constrained by the paucity of baseline data, making it difficult to distinguish between natural population fluctuations and those caused by human activities. Furthermore, in many cases, we simply do not know where populations occurred or still occur. Knowledge of habitat requirements and factors that limit the growth of populations is also incomplete for most species of frogs in neotropical areas.

The British Virgin Islands (BVI), located on the easternmost portion of the Puerto Rico Bank in the Caribbean Sea, consist of about 50 islands, some of which are mere rocks or sand bars. During the last glacial maximum, the entire bank was united as a single land mass, which subsequently fragmented into numerous islands with the rising of sea levels (Heatwole *et al.,* 1981). Most of the islands have been isolated from each other and the rest of the bank for approximately 4,000–10,000 years (reviewed by Lazell, 1983).

Four species of leptodactylid frogs occur in the BVI: *Leptodactylus albilabris, Eleutherodactylus antillensis, E. schwartzi,* and *E. cochranae* (MacLean, 1982). All but *E. schwartzi*, which is endemic to the BVI, are widespread on the islands of the Puerto Rico Bank and also occur in Puerto Rico itself (Rivero, 1978; MacLean, 1982; Schwartz and Henderson, 1991).

Leptodactylus albilabris has a biphasic life cycle with aquatic larvae, whereas *Eleutherodactylus* species are completely terrestrial and have direct development. The distribution and habitat use patterns of all four species on the islands are poorly known, although other components of the herpetofauna of the BVI have received intensive attention over the past two decades (Mayer and Lazell, 1988; Lazell, 1983, 1991, 1995; Dmi'el *et al.,* 1996). Lazell (1983) was aware of seven populations of leptodactylid frogs on four islands of the BVI. Mayer and Lazell (1988) added two new island records, including one for an islet of only 24 ha (Frenchmans Cay). Lazell (1991) reported a previously overlooked record for the 33-ha Great Dog Island (Heatwole *et al.,* 1981), bringing the total number of known populations to 11 on seven different islands. Ten additional islands that are larger than Frenchmans Cay had not been surveyed for frogs before our study. In many cases, the survey coverage of those islands known to support frogs was incomplete.

Every October from 1993 to 1997, we investigated the distribution and ecology of leptodactylid frogs in the BVI. Based on surveys of 17 islands, we report on the distribution of *Leptodactylus* and *Eleutherodactylus* species, including new island records for 10 populations. Our objectives were to (a) compile baseline data on the distribution, habitat use, and natural history of the frogs on different islands; (b) compare present distributions to historical records; and (c) examine the pattern of distribution in relation to predictions from island biogeography (MacArthur and Wilson, 1967; Lazell, 1983).

METHODS

Survey Methods

Our operations were based on Guana Island, located ca. 0.5 km north of the east end of Tortola, BVI. The survey periods were 7–30 October 1993, 2–21 October 1994, 3–19 October 1995, 8–28 October 1996, and 8–28 October 1997. During these periods, we also visited the following islands one or more times: Tortola (14–16 October 1993; 4–6, 13–15 October 1994; 6–8, 14–15 October 1995; 11–12, 15–16, 19–20 October 1997), Beef Island (3–5 October 1995, 23 October 1996), Frenchmans Cay (7 October 1995), Virgin Gorda (26–28 October 1993, 9–11 October 1994, 17–18 October 1996), Jost Van Dyke (11–12 October 1995), Great Dog (10–11, 16 October 1996; 21 October 1997), Great Camanoe (12 October 1996), Scrub (13 October 1996), Mosquito (16–17 October 1996), Anegada (20–21 October 1996), Cooper (22–23 October 1996), Peter (24–25 October 1996, 25–26 October 1997), Great Thatch (26–27 October 1996), and Great Tobago (17–18 October 1997). We also present data for Necker and Little Thatch, where residents have been listening for frogs for several years and one of us (JL) spent several rainy nights (three nights in October 1993 on Necker and one night in October 1996 on Little Thatch).

We used visual encounter surveys, auditory transect surveys, and night driving methods to locate frogs (Heyer *et al.,* 1994). We walked along trails in likely habitats after sunset listening for calls of males, and we scanned the ground and vegetation with headlamps for frogs. In 1996, we also played recorded advertisement calls of *E. antillensis* and *E. schwartzi* to induce frogs to call. In 1995 and 1996, the use of a car allowed us to cover longer distances on larger islands (Tortola, Beef Island, Anegada, Virgin Gorda); we stopped every few minutes to listen for frog calls. For each new island record, we collected at least one voucher specimen, which was deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ).

In 1993, we systematically recorded information on each *Eleutherodactylus* heard or seen during those surveys carried out on foot and noted the following for each frog captured: species, sex, calling or not (for males), gravid or not (for females), snout–vent length (SVL), weight, microhabitat (ground, tree or bush, bromeliad, agave, herbaceous vegetation), and perch height. In 1994 and 1995, we obtained comparable information only for frogs included in a separate study on vocal behavior. In 1996, we measured the body size of *E. schwartzi* on Great Dog and Virgin Gorda to examine the hypothesis suggested by initial observations that the frogs on Great Dog were relatively large. We also measured the body size of a sample of *E. antillensis* on Guana in 1996.

To obtain additional information on habitat use and dispersion of *Eleutherodactylus,* we set up auditory transects in October 1994 on three islands (Guana, Tortola, and Virgin Gorda) and in October 1996 on Guana. In 1994, there were two transects on Guana, two on Sage Mountain, Tortola, and one on Gorda Peak, Virgin Gorda. On Guana, Transect 1 was in the north of the island along a ridge where *E. antillensis* appeared to be abundant, and Transect 2 was near the southwest tip of the island where an isolated patch of the species occurred.

The transects followed the course of relatively straight sections of existing trails or paths, which marked the middle of the transect. In 1994, each transect was 150 m long and 6 m wide. In 1996 on Guana, Transect 1 was 815 m long and Transect 2 was 300 m long. We increased their width from 6 m to 10 m, because previous observations indicated that we could accurately record all calling frogs within 5 m from the center of the transect. We placed a flag every 5 m in the center of the transect to divide it into sections of 3 × 5 m (in 1994) or 5 × 5 m (in 1996) on each side of the transect.

In 1994, we recorded the presence/absence of arboreal and terrestrial bromeliads with a crown diameter >10 cm in every 5-m × 3-m section of the transect. In 1996 on Guana, we measured habitat variables only for Transect 1. The variables measured for each 5-m × 5-m section were: (a) sum of crown diameters of bromeliads (none, not present; low, <30 cm; moderate, 30–100 cm; high, >100 cm), (b) percentage of ground covered by leaf litter, (c) depth of leaf litter/humus (measured for 152 or 47% of the 5-m × 5-m sections), and percent vegetation cover at heights of (d) <1 m, (e) 1–2 m, and (f) >2 m. The depth of the leaf litter and humus in each section was the average of three randomly located measurements obtained by poking a pencil in the leaf litter and measuring the depth of penetration. We estimated the percentage of ground covered by vegetation at different vertical layers and by leaf litter visually.

To survey frogs, two observers walked along the midline of the transect after sunset and recorded the number and species of calling males in each section of the transect. We traced the exact location of frogs only when this was required to verify their presence within the transect boundaries. In 1994, we surveyed the transects for frogs on Guana on four consecutive nights (17–18, 18–19, 19–20, and 20–21 October). Transect 1 was surveyed twice each night on two nights and three times on one night to obtain information on the consistency of the number of calling frogs within nights. Transect 2 was surveyed once on 18 October. In 1996, we surveyed Transect 1 once each on 18 and 25 October and twice on 28 October. Transect 2 was surveyed once (on 18 October). We surveyed both transects on Tortola twice on 13 October 1994 and the transect on Virgin Gorda once on 10 October 1994. We checked transects only on nights when rain had fallen during the 24-hour period prior to the search, and conditions were favorable for calling.

Data Analysis

We used a multiple regression analysis to examine the effects of island size and elevation on the number of species present. We also applied multiple regression to a reduced data set that excluded both islands that contained the full complement of four species (Tortola and Jost Van Dyke) to include the distance from potential source populations in the analysis. The source for island size and elevation was Lazell (1983). The distance to the nearest potential source population was measured as the shortest distance between an island and either Tortola, Jost Van Dyke, or Virgin Gorda, whichever distance was shortest.

We used one-way ANOVA to examine differences in body size of adult male *E. antillensis* and *E. schwartzi* among years. We also used ANOVA to compare SVL of *E. antillensis* and *E. schwartzi* among years and islands.

We calculated the variance/mean ratio as an index of dispersion of calling males of *E. antillensis* in 5-m and 50-m sections of Transect 1 on Guana in 1996 and used the χ^2 test to determine whether the pattern was significantly different from random (Krebs, 1989). We performed a multiple regression analysis to examine the effects of habitat variables, measured in each 5-m × 5-m section of the transect, on the number of calling frogs on Guana on 28 October 1996, when the number of frogs was the greatest. We also performed the same analysis using the number of 5-m × 5-m sections with frogs (1) and without frogs (0) as the dependent variable. The value for each section of the transect in the second case was determined based on whether calling frogs were found within a transect section during any of the four surveys in 1996.

DISTRIBUTION

Species Diversity

The number of species per island varied from zero to four (Table 1). Only two islands, Tortola and Jost Van Dyke, contained the full complement of four species. One island had three species, three had two, and four had one. We found no frogs on the remaining seven islands.

Area and elevation explained 60.7% of the variance in the number of species among islands (multiple regression: $F_{2,14} = 10.8$, $P = 0.002$). Elevation explained most of this variance (simple $r = 0.76$, partial $r^2 = 0.35$), whereas island area contributed very little to the model (simple $r = 0.51$, partial $r^2 = 0.02$). When the two islands with the full complement of species were deleted from the analysis and the distance to nearest potential source population was added as an independent variable, the model was marginally significant ($r^2 = 0.51$, $F_{3,11} = 3.79$, $P = 0.04$). In this model, island area (simple $r = 0.22$, partial $r^2 = 0.25$) and distance to a potential source population (simple $r = -0.007$, partial $r^2 = 0.21$) explained most of the variance, whereas the contribution of elevation was small (simple $r = 0.50$, partial $r^2 = 0.001$).

Leptodactylus albilabris

We found *L. albilabris* on four of the 17 islands: Beef, Tortola, Jost Van Dyke, and Anegada (Table 2). This species had not been previously documented from Beef (372 ha), separated from Tor-

TABLE 1. NUMBER OF SPECIES OF FROGS IN RELATION TO ISLAND AREA, ELEVATION, AND DISTANCE FROM A POTENTIAL SOURCE POPULATION. ISLAND AREA AND ELEVATION ARE FROM LAZELL (1983). DISTANCES FOR EACH ISLAND WERE MEASURED EITHER FROM TORTOLA, JOST VAN DYKE, OR VIRGIN GORDA (WHICHEVER DISTANCE WAS SHORTEST).

Island	No. of Species	Area (km^2)	Elevation (m)	Distance to Potential Source Population (km)
Tortola	4	5,444	521	NA
Anegada	1	3,872	8.5	32.5 (Tortola)
Virgin Gorda	2	2,130	414	11.7 (Tortola)
Jost Van Dyke	4	840	398	NA
Peter	0	429	177	5.5 (Tortola)
Beef	3	372	244	0.1 (Tortola)
Great Camanoe	1	337	187	2.1 (Tortola)
Guana	1	297	266	0.5 (Tortola)
Cooper	0	138	155	6.8 (Tortola)
Great Thatch	2	123	187	0.7 (Tortola)
Scrub	0	97	141	3.7 (Tortola)
Great Tobago	0	87	147	4.0 (Jost Van Dyke)
Mosquito	0	50	95	17.7 (Virgin Gorda)
Great Dog	1	33	89	11.1 (Virgin Gorda)
Necker	0	30	32	22.0 (Virgin Gorda)
Frenchmans Cay	2	24	131	0.1 (Tortola)
Little Thatch	0	24	100	0.5 (Tortola)

tola by a ca. 100-m wide channel. Our attention was first called to the presence of *L. albilabris* on this island by Dr. Gregory Mayer, who reported hearing calls and locating tadpoles, which were inspected by one of us (JL), in temporary pools among rocks in scrub vegetation several years ago. We did not locate this site but found *L. albilabris* in muddy ditches around the airport (MCZ 124777–81, 125954). In 1995, we located several males calling from inside tufts of grass and from small cavities in the mud banks close to the water's edge, as well as many metamorphosed juveniles. We did not hear calls of *L. albilabris* east of the airport.

On Tortola, we heard calls of *L. albilabris* from roadside ditches throughout the island and from small pools on Sage Mountain (MCZ 107339, 110992–5, 117677). On Jost Van Dyke, we heard

L. albilabris in a riverbed by Old Hill west of White Bay and in a marshy site in the town of Great Harbour (MCZ 110990–1).

On Anegada, we found several concentrations of *L. albilabris* in an area called the Slob, ca. 1.5 km northwest of the airport (MCZ 125953). The frogs were in wet areas under dense shrubs on coral-limestone substrate covered by leaf litter and humus. Several males were calling from land crab holes, and we also saw many metamorphosed juveniles.

We did not find *L. albilabris* on any of the other islands, including Virgin Gorda, which we visited in three different years. In 1993 and 1994, our surveys were confined to Gorda Peak, but in 1996, we spent many hours driving around the island after sunset during and after rain. Extensive pools were present on Gorda Peak in 1993, but these were dry in 1994 and contained little water in 1996. Roadside ditches, where these frogs commonly occurred on Tortola, contained water, but we detected no frogs. Small, temporary freshwater puddles were present on Great Camanoe.

Eleutherodactylus antillensis

We found *E. antillensis* on eight of the 17 islands visited: Virgin Gorda, Great Camanoe, Guana, Beef, Tortola, Frenchmans Cay, Great Thatch, and Jost van Dyke (Table 2). The species has not been previously reported from Great Camanoe, Great Thatch, or Beef (MCZ 132823). In addition, we have found no previous records of *E. antillensis* from Jost Van Dyke, although MacLean (1982) reported the distribution of the species to encompass "all major islands" of the Virgin Islands. On Jost Van Dyke, calling males of *E. antillensis* were patchily distributed in areas west of White Bay toward Old Hill and east to Great Harbour, including the town site (MCZ 124786). On Great Camanoe, we located frogs in the hills on the southwest portion of the island (MCZ 125949). On Great Thatch, we found *E. antillensis* throughout the densely vegetated south slope of the island (MCZ 125950).

Eleutherodactylus schwartzi

We located *E. schwartzi* on six of the 17 islands visited: Virgin Gorda, Great Dog, Beef, Frenchmans Cay, Tortola, and Jost Van

TABLE 2. RECONFIRMED, UNCONFIRMED, AND NEW ISLAND RECORDS FOR LEPTODACTYLID FROGS IN THE BRITISH VIRGIN ISLANDS.[a]

Island	Survey Dates	Species			Source of Previous Records
		New Record	Previous Record Confirmed	Previous Record Not Confirmed	
Anegada	20–21 Oct. 1996	—	La	—	MacLean, 1982
Virgin Gorda	26–28 Oct. 1993 9–11 Oct. 1994 17–18 Oct. 1996	—	Ea, Es	Ec, La	MacLean, 1982 (all 4 spp.); Schwartz and Henderson, 1985 (Es)
Great Dog	10–11, 15 Oct. 1996 21 Oct. 1997	—	Es	—	Heatwole *et al.*, 1981
Great Camanoe	12 Oct. 1996	Ea	—	—	—
Guana	7–30 Oct. 1993 2–21 Oct. 1994 9–19 Oct. 1995 8–18 Oct. 1996 8–28 Oct. 1997	—	Ea	—	Mayer and Lazell, 1988; Lazell, 1991
Beef Island	3–5 Oct. 1995 23 Oct. 1996	Es, La, Ea	—	—	
Tortola	14–16 Oct. 1993 4–6, 13–15 Oct. 1994 6–8, 14–15 Oct. 1995 11–12, 15–16, 19–20 Oct. 1997	—	Ea, Es, Ec, La	—	MacLean, 1982 (all 4 spp.); Schwartz and Henderson, 1985 (Es)

TABLE 2. CONTINUED.

Island	Survey Dates	Species: New Record	Species: Previous Record Confirmed	Species: Previous Record Not Confirmed	Source of Previous Records
Peter Island	24–25 Oct. 1996 25–26 Oct. 1996	—	—	E. sp.	Henderson and Sadjak, 1996 (*Eleutherodactylus* in stomach of snake)
Frenchmans Cay	7 Oct. 1995	Es	Ea	—	Mayer and Lazell, 1988 (Ea)
Great Thatch	26 Oct. 1996	Ea, Ec	—	—	—
Jost Van Dyke	11-12 Oct. 1995	Ea, Es, Ec	La	—	Schwartz and Thomas, 1975 (La); MacLean, 1982 (La)

[a] Ea, *Eleutherodactylus antillensis*; Ec, *E. cochranae*; Es, *E. schwartzi*; La, *Leptodactylus albilabris*; E. sp, unidentified species of *Eleutherodactylus*.

Dyke (Table 2). The presence of this species on Beef, Frenchmans Cay, and Jost Van Dyke was previously undocumented. On Beef, we found *E. schwartzi* along the road that transects the island and in a patch of terrestrial bromeliads (*Bromelia pinguin*) along a path that diverges from the main road near its northern end (MCZ 124782).

On Frenchmans Cay, we heard calls of *E. schwartzi* from gardens along the road east from the bridge to Tortola (MCZ 124783). On Jost Van Dyke, we heard calls of scattered *E. schwartzi* from gardens, pastures, and gullies in and around Great Harbour (MCZ 124785).

In 1996, we confirmed the presence of *E. schwartzi* on Great Dog Island (MCZ 125946–8), an islet of 33 ha, first reported by Heatwole *et al.* (1981). Numerous frogs were present in a ca. 13-m × 16-m patch of bromeliads, *Hohenbergia antillana,* located near the peak of the ridge that extends along the length of the island. In addition, on the night of 10–11 October 1996, we heard a single male calling near the beach in dense vegetation on the south side of the island ca. 500 m from this patch. We located five egg clutches of *E. schwartzi* on 10 October within bromeliads (Ovaska *et al.,* 1998).

We observed numerous *E. schwartzi* on Sage Mountain, Tortola, and on Gorda Peak, Virgin Gorda, and we also heard calls and observed frogs in other areas of these two islands (MCZ 107340–1, 115830–8, 117567–9, 117688–92, 119247–51, 116273, 124784, and U.S. National Museum of Natural History 329482–91).

Eleutherodactylus cochranae

We located *E. cochranae* on three of the 17 islands visited: Tortola, Jost Van Dyke, and Great Thatch (Table 2). The species has not previously been reported from Jost Van Dyke or Great Thatch. Based on advertisement calls by males, *E. cochranae* was the most widely distributed and abundant frog species in the areas surveyed on Jost Van Dyke (MCZ 124787–8). These included areas west from White Bay toward Old Hill and east to Great Harbour. Calling males were perched on cacti, trees, and arboreal and terrestrial bromeliads.

On Great Thatch, we surveyed the southern slope of the densly vegetated island and captured *E. cochranae* (MCZ 125951). On Tortola, we captured *E. cochranae* on Sage Mountain (MCZ 116269–71) and also heard advertisement calls from other forested locations, including sites near sea level. We did not hear calls of *E. cochranae* on Frenchmans Cay, a 24-ha islet separated from Tortola by a channel <10 m wide, although males were calling in adjacent areas on Tortola on the same night.

We also did not find *E. cochranae* on Virgin Gorda, although we searched for it several times in 3 years (1993, 1994, and 1996). MacLean (1982) lists this species from Virgin Gorda, but we have been unable to locate a voucher specimen or any other report of its occurrence there.

BODY SIZE OF *ELEUTHERODACTYLUS*

The SVL of calling males of *E. antillensis* did not show significant differences among years on any of the islands examined, although males tended to be smaller on Tortola in 1994 than in 1993 and 1995 (Guana: $F_{3,48} = 1.67$, $P = 0.19$; Tortola: $F_{2,49} = 3.07$, $P = 0.06$; Virgin Gorda: $F_{1,57} = 0.18$, $P = 0.67$). Similarly, there were no significant differences in SVL of *E. schwartzi* among years (Tortola: $F_{1,16} = 0.01$, $P = 0.90$; Virgin Gorda: $F_{2,36} = 0.38$, $P = 0.68$). The data for all years were therefore combined for analyses of interisland differences.

The average SVL of adult male *E. antillensis* varied among Guana, Tortola, and Virgin Gorda ($F_{2,141} = 24.9$, $P < 0.001$; Fig. 2). Males on Virgin Gorda were smaller ($\bar{x} = 27.2$ mm) than those on Guana ($\bar{x} = 29.3$ mm) and Tortola ($\bar{x} = 29.2$ mm). The average SVL of calling males of *E. schwartzi* also differed among islands ($F_{2,71} = 29.4$, $P < 0.001$; Fig. 1). Males were the smallest on Virgin Gorda ($\bar{x} = 22.3$ mm), largest on Great Dog Island ($\bar{x} = 25.6$ mm), and intermediate on Tortola ($\bar{x} = 23.8$ mm).

The average weight of calling males of *E. antillensis* was 1.7 g (SD = 0.1, $n = 51$; 1993–96 combined) on Guana, 1.3 g on Virgin Gorda (SD = 0.2 g, $n = 58$; 1993–94 combined), and 1.7 g on Tortola (SD = 0.3, $n = 52$; 1993–95 combined). The average weight of calling males of *E. schwartzi* was 0.9 g (SD = 0.2 g, $n = 16$; 1993 and 1994 combined) on Tortola, 0.8 g (SD = 0.1

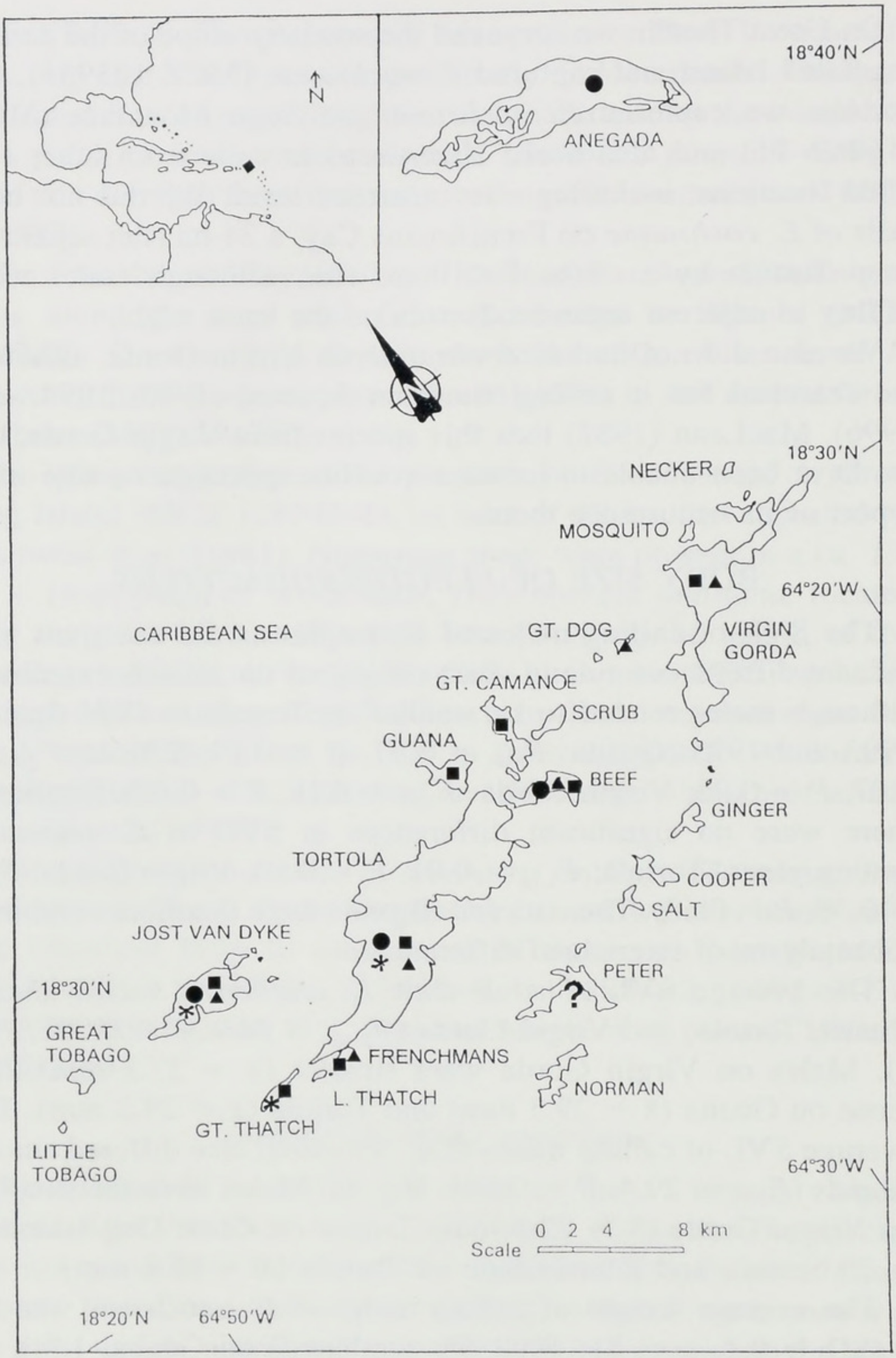

Figure 1. Map of the British Virgin Islands indicating major islands and those mentioned in the text. Insert shows the position of the these islands in the Caribbean. ● *L. albilabris,* ■ *E. antillensis,* ▲ *E. schwartzi,* ✻ *E. cochranae.*

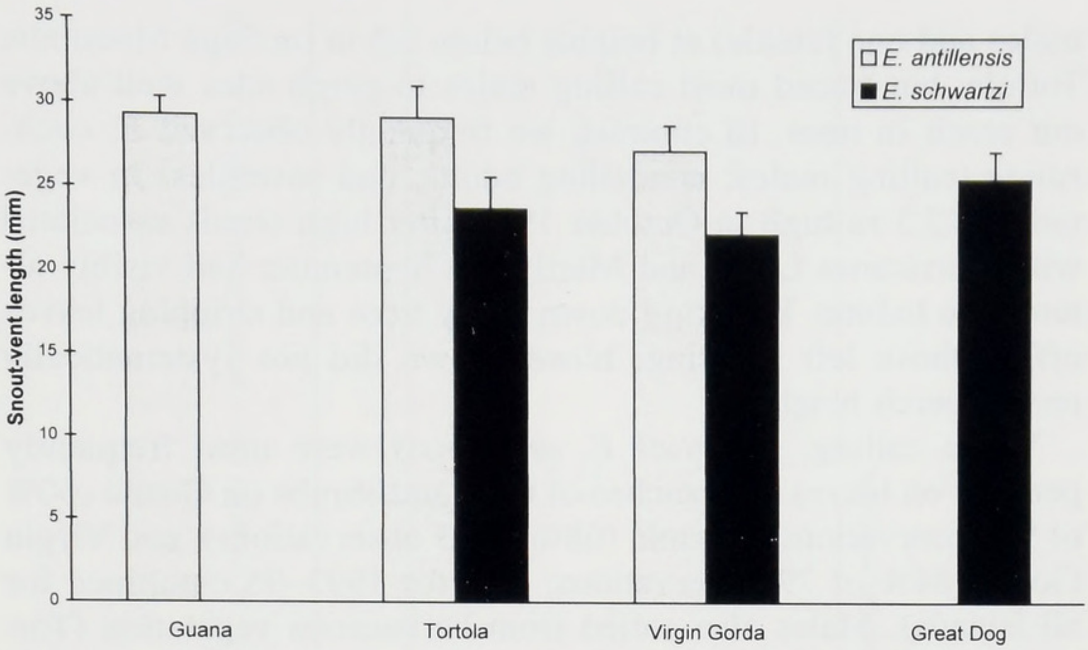

Figure 2. Snout–vent length (SVL) of calling males of *Eleutherodactylus antillensis* and *E. schwartzi* from Guana, Tortola, Virgin Gorda, and Great Dog. Mean, top of bars; 1 SD, vertical lines.

g, *n* = 39; 1993, 1994, and 1996 combined) on Virgin Gorda, and 1.2 g (SD = 0.2 g, *n* = 17; 1996) on Great Dog.

Both species were sexually dimorphic with respect to body size, females being larger than males. The SVL of 14 female *E. antillensis* measured in 1993 was 33.8 mm (SD = 4.6 mm, range = 28.0–43.2) and their weight was 2.7 g (SD = 1.2 mm, range = 1.2–4.8 g; all islands combined). Ten female *E. schwartzi* were 31.2 mm in SVL (SD = 3.0 mm, range = 25.5–35.5 mm) and weighed 1.9 g (SD = 0.4 g, range = 1.2–2.7 g).

HABITAT USE BY *ELEUTHERODACTYLUS*

Eighty-nine percent of all male *E. schwartzi* (*n* = 45) and 74% of male *E. antillensis* (*n* = 171) located in October 1993 were perched in vegetation <2.5 m high while calling (data for Tortola, Virgin Gorda, and Guana combined). The remaining 11% of calling *E. schwartzi* and 26% of *E. antillensis* were perched higher than 2.5 m and thus were out of our reach. We did not capture *E. cochranae* in 1993, although we audiotaped calls of this species on Tortola. In 1994, we captured nine *E. cochranae* (eight males and one female) at heights below 2.5 m on Sage Mountain, Tortola, but traced most calling males to perch sites well above our reach in trees. In contrast, we frequently observed *E. cochranae* (calling males, noncalling adults, and juveniles) in vegetation <2.5 m high in October 1995 after high winds associated with Hurricanes Louis and Marilyn in September had visibly altered the habitat, knocking down many trees and stripping leaves off of those left standing; however, we did not systematically record perch heights.

While calling, males of *E. antillensis* were most frequently perched on leaves or branches of trees and shrubs on Guana (60% of 94 observations), Tortola (68% of 53 observations), and Virgin Gorda (84% of 79 observations; data for 1993–95 combined for all islands). Males also called from herbaceous vegetation (Tortola: 28%; Virgin Gorda: 4%), terrestrial and arboreal bromeliads (Guana: 14%; Virgin Gorda: 4%), and agave plants (Guana: 24%). On Tortola, calling *E. schwartzi* were perched on trees or shrubs (75% of 16 recordings) and herbaceous vegetation (25%). In contrast, the majority of observations of calling *E. schwartzi* on Virgin Gorda were from bromeliads (84% of 45 recordings), followed by trees and shrubs (13%) and herbaceous vegetation (2%).

When examined in relation to the availability of bromeliads along auditory transects in 1994, the distribution of calling males of *E. antillensis* and *E. schwartzi* differed significantly from random on Virgin Gorda but not on Tortola (Table 3). On Virgin Gorda, males of *E. schwartzi* were restricted to sections of the transect that contained bromeliads. In contrast, male *E. antillensis* were not associated with bromeliads either on Virgin Gorda or Tortola (Table 3). On Guana, male *E. antillensis* were found exclusively in sections of Transect 2 containing bromeliads, but the relationship was not statistically significant based on habitat availability, due to the small sample size (Table 3). The frogs were most abundant on Transect 1, where bromeliads were present in every section, thus precluding a similar analysis.

On Guana in 1996, calling males of *E. antillensis* were aggregated among 5-m × 10-m sections of the transect during all but one check (Table 4). On a larger scale, when the transect was

TABLE 3. NUMBER OF CALLING MALES OF *ELEUTHERODACTYLUS ANTILLENSIS* AND *E. SCHWARTZI* ON VIRGIN GORDA, TORTOLA, AND GUANA IN OCTOBER 1994.[a]

Island (Transect No.)	Bromeliads Present	Bromeliads Absent	Total	X^2	*P*
Virgin Gorda (1)				23.1	<0.01
No. of *E. antillensis*	12	22	34		
No. of *E. schwartzi*	18	0	18		
No. of Sections	24	36	60		
Tortola (1 + 2)				5.2	$<0.1, >0.05$
No. of *E. antillensis*	11	18	29		
No. of *E. schwartzi*	19	11	30		
No. of Sections	50	70	120		
Guana (2)				3.5	$<0.1, >0.05$
No. of *E. antillensis*	10	0	10		
No. of Sections	44	16	60		

[a] Counted in 3- × 5-m sections of auditory transects in relation to the presence of bromeliads.

TABLE 4. DISPERSION OF CALLING MALE *E. ANTILLENSIS* ALONG A 10 × 815-M TRANSECT (TRANSECT 1 IN TEXT) ON GUANA ISLAND IN OCTOBER 1996.

Date	Transect Divided into 5 × 10-m Sections (no. sections = 163)			Transect Divided into 10× 50-m Sections (no. sections = 16)[1]		
	Variance/Mean Ratio	X^2	*P*	Variance/Mean Ratio	X^2	*P*
18 Oct.	1.2	196.4	<0.05	2.6	39.5	<0.001
25 Oct.	1.3	208.4	<0.05	2.8	42.3	<0.001
28 Oct. (Check 1)	1.7	281.2	<0.05	6.2	92.9	<0.001
28 Oct. (Check 2)	1.2	192.1	>0.05	3.1	47.0	<0.001

[1] The last 15 m was omitted from the analysis to achieve equal division of the transect.

divided into 50-m × 10-m sections, calling males were highly aggregated during each check. The habitat attributes measured explained little of this dispersion. The number of calling males was significantly correlated with the habitat variables both when only data for the night with the most calling frogs (74 frogs on first transect check on October 28; $F_{6,143} = 2.95$, $P < 0.01$) were included and when each section of the transect was scored based on whether or not it was used by frogs during any of the checks ($F_{6,143} = 5.67$, $P < 0.001$). In both cases, the correlations were weak ($r^2 = 0.11$ and 0.19 for the two models, respectively).The partial r^2 for the habitat variables in the better, second model ranged from 0.007 to 0.054 and were the highest for the sum of crown diameters of bromeliads (0.045) and percent substrate covered by leaf litter (0.054).

DISCUSSION

We found 10 previously unreported populations of leptodactylid frogs on five islands (Great Camanoe, Beef, Frenchmans Cay, Great Thatch, and Jost Van Dyke) and confirmed all but three of previous records from the BVI. Demonstrating the absence of a species is always problematic, and these small frogs are inconspicuous when not calling and could be missed easily. The month of October, however, is generally favorable for locating frogs, because, together with November, it has the highest average rainfall per month (6.44 and 6.57 inches of rain in October and November, respectively, based on weather records from 1960 to 1984 obtained from Water and Sewage Department and Planning Division, Road Town, Tortola, and compiled by A. Swain). Rainfall is probably the most important factor affecting activity by *Eleutherodactylus* species in the BVI, although activity is also likely to take place on humid, rainless nights. It was not always possible, however, to time our visits to the different islands during or immediately after rain. Our confidence that we located all species is greatest for small islands that we visited repeatedly, such as Guana. We are also highly confident that there are no native frogs on either Necker or Little Thatch, because no frogs have ever been seen or heard there either by us or by residents. The only amphibian ever found on Necker was the introduced *Hyla (Osteopilus) septentrionalis,* which was collected there on 19 October 1993 from a crack in a recently imported wooden beam (MCZ 119258).

Two of the three previous records that we failed to confirm were from Virgin Gorda (*E. cochranae* and *L. albilabris*; MacLean, 1982), and the remaining record was from Peter Island: an unidentified *Eleutherodactylus* found in the stomach of a snake, *Liophis* (*Alsophis*) *portoricensis* (Henderson and Sadjak, 1996). This snake (MCZ 37303) was collected by Chapman Grant on 14 August 1932. The frog, uncataloged, was sent to the late Albert Schwartz for identification, but R. W. Henderson (personal communication) subsequently was unable to locate it in Schwartz's materials.

On Peter Island in 1996, we walked throughout the inhabited, eastern part of the island at night, and in 1997 we spent a rainy night on the south side of the western part of the island investigating a verdant gully, which to us appeared the best site for locating frogs. *Eleutherodactylus* seems to have disappeared from Peter Island at some time since 1932. On Virgin Gorda, we covered much of the island at night in the rain in three different years, including likely habitats on Gorda Peak (but excluding the roadless, easternmost portion of the island). We have found no records other than MacLean (1982) of either *E. cochranae* or *L. albilabris,* nor have we been able to locate voucher specimens. Furthermore, MacLean *et al.* (1977) do not report *E. cochranae* or *L. albilabris* from Virgin Gorda, raising suspicions about the 1982 listings. We conclude that the record for *E. cochranae* on Virgin Gorda is in error and that there is no evidence that the range of this species extends east of Tortola. We cannot, however, conclusively dismiss the possible former presence of *L. albilabris* on the island based on accounts of residents, who remember "ditch frogs" in and around Spanish Town many years ago before the extensive ponds were drained for the construction of a marina and a hotel.

When all 17 islands visited were considered, elevation and area explained much of the variation (61%) in the number of species among islands, with elevation being the most significant factor. The importance of elevation in biogeographical patterns of small islands was emphasized by Lazell (1983), and our data support this hypothesis. Our data also show that even very small islands, such as Frenchmans Cay, a mere 24 ha, can support at least two species of frogs. Frenchmans Cay is relatively high, 131 m, which might allow it to support more species than expected based on area alone. Both Frenchmans Cay and Beef, however, are separated from Tortola by narrow, bridged channels. Frogs dispersing in the rain can easily cross such bridges (JL, unpublished data from New England and China). Therefore, the number of species on these islands may reflect repeated colonizations from Tortola rather than permanent populations. The reconfirmation of *E. schwartzi* from Great Dog Island, an islet of only 33 ha located at least 3 km from the nearest potential colonization source (Virgin Gorda), shows that this species can persist on very small islands, provided suitable moist microhabitats, such as bromeliads, are present.

Leptodactylus albilabris, which has an aquatic larval stage, can be expected to be absent from islands that do not have suitable water bodies for breeding. Apart from temporary pools on Gorda Peak, drainage ditches (mostly paved) in Spanish Town on Virgin Gorda, and small freshwater puddles on Great Camanoe, we did not observe potential aquatic breeding habitats on the islands where we failed to locate this species.

Stewart and Pough (1983) showed experimentally that the availability of retreat and nest sites can limit population growth of *E. coqui* in Puerto Rico. Terrestrial and arboreal bromeliads, plants that hold moisture in their leaf axils, may provide such sites for terrestrially breeding forest frogs. Of the three species of *Eleutherodactylus* that we studied, *E. schwartzi* was most closely associated with bromeliads, an association also pointed out by Schwartz and Henderson (1991). On all islands except Tortola, we found *E. schwartzi* almost exclusively in terrestrial and arboreal bromeliads. Broader habitat use on Sage Mountain, Tortola, can be explained by the relatively high rainfall and dew that this highest point in the Virgin Islands receives. On Great Dog, we found *E. schwartzi* nests with egg clutches only in a small patch of terrestrial bromeliads, which most likely facilitated the persistence of the population.

Eleutherodactylus antillensis and *E. cochranae* used a variety of microhabitats in addition to bromeliads. Most male *E. antillensis* called from perch heights <2.5 m in vegetation. Previously, Rivero (1978) and Henderson and Schwartz (1991) also noted that males often called from low vegetation. We observed *E. cochranae* using cavities in tree trunks and branches for calling, retreat, and nest sites (Ovaska and Caldbeck, 1997, and unpublished data). Most calling male *E. cochranae* were high in the trees, thus limiting our access to this species. Schwartz and Henderson (1991) stated that males call from 1 m (3 ft) above ground to high in the trees. According to Schwartz and Henderson, the species occurs primarily in xeric forests. On Tortola, however, we found *E. cochranae* together with *E. schwartzi* and *E. antillensis* in mesic forest on Sage Mountain. The habitat on Great Thatch was also mesic, and only Jost Van Dyke could be characterized as mainly xeric.

Eleutherodactylus antillensis was the most widespread of the three species. Although not associated with bromeliads on the relatively wet islands of Tortola and Virgin Gorda, the presence of bromeliads appeared to become more important with increasing aridity. On the relatively dry island of Guana, the frogs were associated with sites that contained bromeliads and abundant leaf litter, although these factors explained only a little of the spatial dispersion of frogs along transects. Abundant leaf litter might be important for breeding, as all nests of this species that we have found have been under leaf litter (Ovaska and Caldbeck, 1997, and unpublished data).

The mean body size of adult males of both *E. antillensis* and *E. schwartzi* differed among islands. Woolbright (1989) found that the growth of male *E. coqui* in the field ceased after reproductive maturity was attained. Furthermore, the period of growth could be extended in the laboratory under conditions that were unfavorable for breeding, thus resulting in greater maximum body size. Therefore, frogs that live under social or environmental conditions that favor the early attainment of reproductive maturity can be expected to be relatively small. The selective pressures responsible for the observed patterns in body size among islands cannot be resolved from our data, and studies that specifically address this question are desirable. The differences were consistent among years, indicating that the operational factors are persistent over time.

There are six islands larger than Frenchmans Cay in the BVI that have not been surveyed for frogs (Prickly Pear, Ginger, Salt, Norman, and Little Jost Van Dyke). All, however, are relatively dry and might not be suitable for frogs. Additional populations that were undetected by us may also continue to be discovered on the islands that we surveyed. Nevertheless, our study provides baseline data that may become increasingly important because of regional and global changes in climate patterns.

ACKNOWLEDGMENTS

Arnold Grobman generously shared his knowledge of frogs of the BVI and together with his wife opened his home to us, facilitating fieldwork on Virgin Gorda. We are grateful for able assistance and company provided by Gad Perry and Kate LeVering, who spent many a rainy night helping us to locate frogs under less than ideal conditions. Wenhua Lu accompanied us on several occasions, and many volunteers helped with the surveys over the years. Gregory Mayer pointed us to possible sites with *L. albilabris* on Beef Island. Our work was financed personally and by The Conservation Agency, through grants from the Falconwood Foundation.

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