
POPULATION DENSITIES, ACTIVITY, MICROHABITATS, AND THERMAL BIOLOGY OF A UNIQUE CREVICE- AND LITTER-DWELLING ASSEMBLAGE OF REPTILES ON UNION ISLAND, ST. VINCENT AND THE GRENADINES

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Abstract.—The slopes above Chatham Bay on Union Island, St. Vincent and the Grenadines, support one of the last mature secondary forests in the Grenadines. The characteristics of the forest allow it to support a unique herpetofauna that includes four small crevice- and litter-dwelling reptilian species (*Gonatodes daudini*, *Bachia heteropa*, *Sphaerodactylus kirbyi*, and *Typhlops tasymicris*). We examined population sizes and densities, activity periods, microhabitat use, thermal biology, and water loss rates of these four presumably syntopic species to better understand these poorly known species and the unique ecological system of the forest floor on which they depend. Our findings show that *G. daudini*, *S. kirbyi*, and *B. heteropa* are present in the ~37-ha area of forest above Chatham Bay at a ratio of approximately 2:1:12, respectively, and tentatively estimated total population sizes are about 6,600 *G. daudini*, 3,200 *S. kirbyi*, and 39,000 *B. heteropa*. Each of the four species was found to exploit separate microhabitats based on specific needs for cover, moisture, and thermal environments. The conditions necessary for these species to thrive apparently are available only in relatively mature forest situated to receive and hold moisture. This unique assemblage and the forest that supports it are under severe and imminent threat from exotic mammals and development, and the preservation of the area above Chatham Bay should be a high conservation priority of regional governmental agencies and non-governmental organizations.

Key Words.—*Bachia heteropa*; *Gonatodes daudini*; Grenadines; habitat associations; population densities; *Sphaerodactylus kirbyi*; thermal environment; *Typhlops tasymicris*.

INTRODUCTION

The islands of the West Indies are geographically isolated and have a relatively mild and stable climate. Consequently, they support a number of unique island ecosystems, with diverse natural floral and faunal communities (e.g., Whittaker and Fernandez-Palacios 2007). Because many island ecosystems are small, they are more vulnerable to human mediated changes than those on the mainland (Vitousek 1988). With the arrival of humans, the natural resources of these islands have been heavily exploited (Newsom and Wing 2004), and many of the natural ecosystems have been replaced by human-dominated landscapes. Only about 10% of the original vegetation still exists on these islands (Hedges 2006). The few remaining largely natural areas in the West Indies are invaluable resources of special

biological interest that are becoming increasingly rare and are deserving of study and conservation efforts.

Union Island, St. Vincent and the Grenadines (SVG), is a relatively small (8.4 km²) West Indian island in the Grenadine Archipelago located between the larger islands of St. Vincent and Grenada (12°36'N, 061°26'W). Union Island is dry, with an annual average rainfall of only 1,000 mm (Daudin and de Silva 2007). The peak of Mt. Taboi, the highest point on the island, has a maximum elevation of 330 m. It is characterized by seasonal dry forest habitat (Fiard 2003) that has seen dramatic transformations in the past (Wilson et al. 2006). Amerindian tribes are thought to have settled on Union around 5,000 BC and were present until the mid-18th century when the first Europeans arrived (Newsom and Wing 2004). Over the next 150–200 years, nearly all of Union's forests were clear-cut for extensive monocultures (e.g., cotton; Howard 1952). Due to the



FIGURE 1. Critical habitat provided by the old secondary forests in the area above Chatham Bay, St. Vincent and the Grenadines, on the northwestern slope of Mt. Taboi. Clearings for agricultural or residential purposes are evident near the far (northern) end of the area and a resort, currently servicing the yachts that anchor in the bay, can be seen expanding up the slope. (Photographed by Mel J. Rivera Rodríguez).

combination of low rainfall and a long history of human disturbance, much of Union's remaining woodlands are classified as dry, secondary forest (Fiard 2003).

The area located above Chatham Bay, on the northwestern slope of Mt. Taboi, holds one of the few relatively intact stands of old secondary forest remaining in the Grenadines (Fiard 2003). Canopy height frequently exceeds 20 m and canopy cover is > 80% except in the immediate vicinity of a trail bisecting the area; principal trees include *Citharexylum spinosum*, *Ceiba pentandra*, *Mangifera indica*, *Bursera simaruba*, *Annona squamosa*, *Capparis hastata*, *Spondias mombin*, *Tabebuia pallida*, *Hippomane mancinella*, *Albizia caribaea*, *Acacia farnesiana*, and *Pisonia fragrans* (McTaggart et al. in press). Despite the area's small size (~37 ha), it supports a surprisingly diverse herpetofauna. All but one of the 15 reptilian species recorded from the island have been found there (Quinn et al. 2010). These include a lizard (*Gonatodes daudini*) discovered in 2005 (Powell and Henderson 2005), and to date known only from Union Island; a snake (*Typhlops tasymicris*) until recently known only from two specimens collected on Grenada in 1968 (Yorks et al. 2003; Rivera Rodríguez et al. in press-b); and a non-native snake (*Tantilla melanocephala*) presumably introduced from South America with sand or gravel used on road construction (Henderson and Powell 2006).

Our research focused primarily on four cryptic reptilian species that are known to occur together only in the area above Chatham Bay. *Gonatodes daudini* is the only West Indian endemic in the genus (Powell and Henderson 2005). *Sphaerodactylus kirbyi*, a dwarf

gecko until recently known only from the more northerly Grenadines (Daudin and de Silva 2007), was found on Union Island for the first time in 2010. *Bachia heteropa alleni*, a Grenada Bank endemic, is a semi-fossorial worm lizard found under cover objects on the forest floor (e.g., Henderson and Powell 2009). *Typhlops tasymicris* was discovered in the Grenadines in the course of this study (Rivera Rodríguez et al. in press-b). We examined population sizes and densities, activity periods, microhabitat use, thermal biology, and water loss rates of these four sympatric and presumably syntopic species in order to better understand their natural history in the unique ecological system on the forest floor of this biologically important site.

MATERIALS AND METHODS

From 4–22 June 2010, we conducted surveys of the forest floor on the north- and west-facing hillsides above Chatham Bay at elevations of 31–234 m (12°35.800 N, 61°26.700 W) on the northwestern slope of Mt. Taboi (Fig. 1). We employed 19 transects in leaf litter and 10 consisting mostly of large rocks. Locations of transects were dictated by topography; we placed those in litter where relatively straight lines could be surveyed in contiguous habitats, whereas we situated those associated with rocks in conjunction with overhanging rock outcrops. Prior to laying out transects, we spent three days surveying the focal area and adjacent areas to make sure that sites where transects were established reflected available habitats. We conducted initial surveys and litter transects at all times of day, with

approximately equal effort employed from before dawn (0430) to well after dark (2100). Because initial surveys revealed that *G. daudini* was most active (presumably foraging) at 0500–0800, we conducted most rock transects at those times to enhance the likelihood of encountering geckos active in crevices. We used a Fluke 51 digital thermometer with type-K thermocouples (Fluke Corp., Everett, Washington, USA) to record field temperatures and a Garmin E-Trex Venture HC handheld GPS device accurate to approximately 15 m (Garmin International, Inc., Olathe, Kansas, USA) for locations and elevations.

Although proving a negative is impossible, to confirm the assumption that the focal species are essentially restricted to the forested slopes above Chatham Bay, we queried Jacque Daudin and Mark de Silva, who have conducted numerous surveys of Union. In addition, we spoke with Jon Boone, who had visited Union Island in 2005. None were aware of any of the four species in habitats other than above Chatham Bay. Furthermore, two of us (RWH and RP) had conducted surveys during previous trips to Union (e.g., Henderson and Powell 2006) and, concurrent with this study, several investigations were implemented in various habitats across the island (e.g., Hedman et al. 2010; Quinn et al. 2010; Rivera Rodríguez et al., in press-a), one of which (McTaggart et al., in press) involved a rapid assessment of varying habitats and employed both visual and litter transects by day and night. Finally, during the final days of this study, we repeated our surveys of habitats adjacent to the focal area and found only one *S. kirbyi* very near the crest (and immediately adjacent to our study area) on the much drier southern face of Mt. Taboi in a moist area under a termite mound.

Litter transects included an area within 1 m on either side of a transect. Transects were straight (within limitations imposed by topography) and ranged in length from 4.0–30.0 m and covered a total area of 459.8 m². Lengths of transects varied according to terrain, often ending at rock faces or near the edges of steep cliffs. We recorded date, start time, end time, litter depth, and a short description of habitat (e.g., type of litter, presence of rocks/logs, type of foliage) for each transect. We measured ambient air and substrate temperatures at the beginning of each transect. Two researchers surveyed each transect by marking the start location and then sifting through the litter and lifting all cover (e.g., rocks, logs, deadfall) along the length of the transect at an average rate of 1.6 min/m². A third person recorded data and watched the edges of transects for escaping animals. When at an endpoint, we measured the transect using a 60 m tape. We measured transects after completion to avoid entering them before they had been surveyed. When we encountered animals, we recorded time, type and approximate size of cover (taken as a rectangle

formed by the greatest length and width), ambient air temperature, substrate temperature, and, when possible, cloacal temperature.

We measured rock transects as rectangular areas containing rock outcrops with widths of 5.6–12.0 m and lengths of 6.4–19.6 m, covering a total area of 1,056.7 m². We recorded ambient air temperatures immediately before three researchers simultaneously surveyed each transect. To improve our ability to visually locate geckos, we began surveys at the lowest point and moved up the slope as we progressed. We used flashlights to illuminate spaces under and between rocks and visually counted the total number of geckos. When a transect was completed, we measured its length and width and recorded the total number of animals sighted. In each location where an individual was found, we recorded ambient temperature at the rock surface and under the rock on which the animal was sighted.

To estimate the total area of habitat apparently suitable for use by the four focal species, we analyzed digitized maps using Adobe Illustrator CS 11.0.0 (Adobe Systems, Inc., San Jose, California) and ImageJ 1.43u (National Institutes of Health, Bethesda, Maryland; <http://rsbweb.nih.gov/ij/index.html>). Because suitable habitat did not occur elsewhere on the island, we used population densities calculated from our transects extrapolated to the total area of suitable habitat in the area above Chatham Bay to estimate total island population sizes.

We collected 21 *G. daudini*, 10 *S. kirbyi*, 17 *B. heteropa*, and four *T. tasymicris* to gather information on thermal biology and water loss rates. To determine thermal preferences, we used methods of Bauwens et al. (1995), modified to accommodate smaller animals from relatively stable thermal environments. We created a thermal gradient by using a plastic food storage container (40 x 26 x 8 cm) with a substrate composed of 3 cm of sand (to provide drainage) covered by a 1 cm layer of soil sprayed with water to prevent desiccation of animals. A lid was placed on the container to maintain a constant high humidity and to prevent excess movement of air. A Fluke 52II dual input digital thermometer with type-K thermocouples was used to monitor temperature extremes at either end of the gradient. The container was placed in a cool (20° C) room with a 75 W light bulb beneath one end adjusted to create a gradient of approximately 20–35° C. We allowed the gradient to equilibrate until temperatures did not fluctuate more than 2° C for 30 min. We introduced animals to the gradient and recorded cloacal temperatures each hour for 3 h.

To determine size-specific water-loss rates, we used methods of Turk et al. (2010). We held individuals under natural ambient conditions without food on moist paper towels in 1¼ cup containers with screened lids for 18–26 h before being subjected to desiccation. Mean

TABLE 1. Numbers of animals encountered in transects and extrapolated population density estimates for four species of reptiles from the slopes above Chatham Bay, Union Island.

Species	No. Individuals		Estimated Individuals/m ²		Individuals/ha		Total Population
	Litter (459.8 m ²)	Rock (1,056.7 m ²)	Litter	Rocks	Litter	Rocks	
<i>Bachia heteropa</i>	34	0	0.0739	0	739	0	38620
<i>Gonatodes daudini</i>	6	23	0.0087	0.02180	87	218	6562
<i>Sphaerodactylus kirbyi</i>	9	1	0.0196	0.00095	196	9	3170
<i>Typhlops tasymicris</i>	2	0	--	--	--	--	--

temperature (\pm S.D.) and relative humidity at the beginning of the sampling period were $29.1 \pm 0.17^\circ\text{C}$ and $78.1 \pm 0.91\%$, respectively. Because Dunson and Bramham (1981) indicated that rates of water loss leveled off after approximately 4 h, we placed lizards in dry containers and recorded body masses initially and every hour for a period of 4 h to the nearest 0.001 g using a Denver Instrument Company[®] Model S-110 electronic scale (Denver, Colorado). We excluded from analyses data from individuals that shed or defecated during the study. Animals used for studies of desiccation or thermal preferences were rehydrated and released at original sites of capture.

We placed nine iButton thermochrons (model DS1921G, Maxim Integrated Products, Inc., Sunnyvale, California, USA) in areas representing specific microhabitats found on the forest floor: Under large boulders ($n = 2$), on top of large boulders ($n = 2$), under a small rock in leaf litter ($n = 1$), under the leaf litter on the forest floor ($n = 2$), under a log ($n = 1$), and under a termite mound ($n = 1$). Each logger recorded temperature data every 30 min from 1530 h on 10 June to 1700 h on 20 June.

We used JMP 7.0.2 (SAS Institute, Cary, North Carolina, USA) for statistical analyses. All means are presented \pm one SD (except as indicated). We used a paired t-test to compare body and substrate temperatures for *B. heteropa* in the field, an unpaired t-test to compare body temperatures of *G. daudini* and *S. kirbyi* in the temperature gradient, and ANOVA to analyze desiccation rates for all four species. We \log_{10} -transformed temperature and water-loss data and tested the transformed values to assure normality. For all statistical tests, $\alpha = 0.05$.

RESULTS

Population densities and total population sizes.—We found six *G. daudini*, nine *S. kirbyi*, 34 *B. heteropa*, and two *T. tasymicris* in leaf-litter transects and 23 *G. daudini* and one *S. kirbyi* in rock transects (Table 1). Map analysis of the area (Fig. 2) showed the total area of suitable litter habitat above Chatham Bay to be approximately 36.8 ha and the total area of habitat containing moist litter and rock outcroppings to be

approximately 15.5 ha. We extrapolated our observed population densities to areas of suitable habitat. For *G. daudini*, those corresponded to the areas indicated by dark green in Fig. 2, whereas for *B. heteropa* and *S. kirbyi*, we found animals everywhere in the shaded areas (both dark and light green) where cover existed. Estimates of total population sizes were 6,562 *G. daudini*, 3,170 *S. kirbyi*, and 38,620 *B. heteropa*. We did not calculate population density or size for *T. tasymicris* because of the very low number of sightings.

Activity periods.—We found 18 of 23 active (exposed) *G. daudini* presumably foraging in crevices or on rocks during daylight hours when temperatures under cover

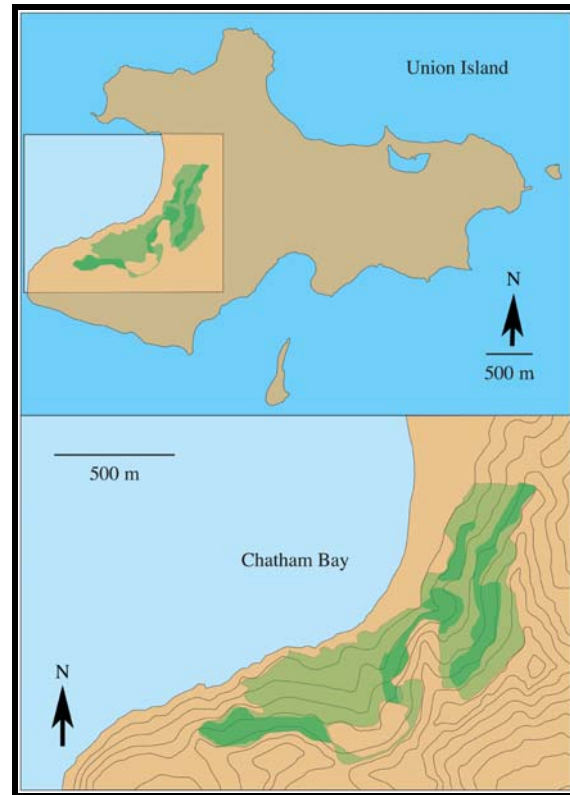


FIGURE 2. Area of critical habitat above Chatham Bay (green), Union Island, St. Vincent and the Grenadines, and areas within that habitat with moist litter associated with rocky outcroppings (dark green). The proposed road would bisect the critical habitat between the escarpments to the north. Contour interval = 30.5 m (100 ft).



FIGURE 3. Typical microhabitat and position of active *Gonatodes daudini* in a rock crevice. (Photographed by Mel J. Rivera Rodríguez)

(e.g., large boulders, termite mounds, or fallen logs) were higher than ambient temperatures. In sharp contrast, we found all eight inactive animals (under cover objects) when ambient temperatures were higher than temperatures under the cover where these geckos were found. Geckos generally were active between daybreak and 0800, or when weather conditions caused ambient temperatures to fall. Encounters with active *S. kirbyi* were relatively consistent throughout daylight hours, and no active individuals were found more than 1 h before sunrise or after dark. Daily fluctuations in temperature had no apparent effect on the activity of these lizards. We found *B. heteropa* at all times of day and in all environmental conditions in which we conducted surveys, but only under cover (e.g., rocks, termite mounds). Consequently, determining their state of activity or rest was not possible.

Microhabitat use.—The areas in which we found the highest densities of *G. daudini* were rock outcroppings of large boulders with small crevices at their base. We saw 27 of 33 active geckos hanging upside down on the upper edges of crevices (Fig. 3, Table 2). Generally, only one gecko occupied each crevice; in only one instance did we find two geckos (one a gravid female) < 5 cm apart in a single crevice. Individuals found outside rocky outcrops were generally associated with insulating cover.

We found nine of 10 active *S. kirbyi* in leaf litter (Table 2). Six inactive geckos were under rocks and termite mounds. One individual was in the moist area under the same termite mound on the dry southern face of Mt. Taboi (12°35.693N 061°26.695W) where we

found multiple eggs of three distinct sizes that appeared to be those of *Thecadactylus rapicauda*, *Hemidactylus mabouia*, and *S. kirbyi*.

We found 43 *B. heteropa*, of which 36 were under relatively small rocks resting on the surface (Table 2). We found no exposed individuals. One *B. heteropa* egg was found under a rock with two adults. We found five *Typhlops tasymicris* over the course of our study, but only two during surveys (Table 2). Two were in litter, two under rocks, and one individual was under a termite mound < 5 cm from a *B. heteropa*.

Thermal biology.—Cloacal temperatures of *B. heteropa* taken in the field ($28.9 \pm 1.3^\circ\text{C}$, $26.0\text{--}30.9^\circ\text{C}$; $N = 22$) were significantly higher than corresponding substrate temperatures ($26.6 \pm 0.9^\circ\text{C}$, $24.8\text{--}28.2^\circ\text{C}$; $df = 21$, $t = -10.57$, $P < 0.001$), with differences of $0.5\text{--}4.5^\circ\text{C}$ ($2.3 \pm 1.0^\circ\text{C}$). *Bachia heteropa* and *T. tasymicris* tended to burrow into the soil instead of moving within the gradient, so we determined thermal preferences in the gradient only for the geckos. Mean snout-vent length (SVL) and mass of the *G. daudini* ($N = 3$) exposed to the gradient were 27.2 ± 2.5 mm ($25\text{--}30$ mm) and 0.58 ± 0.12 g ($0.44\text{--}0.65$ g), respectively. Mean SVL and mass of the *S. kirbyi* ($N = 3$) were 20.3 ± 1.2 mm ($19\text{--}21$ mm) and 0.26 ± 0.01 g ($0.26\text{--}0.27$ g), respectively. Mean cloacal temperatures of *G. daudini* in the thermal gradient was $23.1 \pm 2.2^\circ\text{C}$ ($19.9\text{--}26.8^\circ\text{C}$), whereas those of *S. kirbyi* ($25.3 \pm 1.7^\circ\text{C}$, $24.0\text{--}28.1^\circ\text{C}$) were significantly higher ($df = 16$, $t = -2.37$, $P = 0.03$) and varied less. The natural thermal environment under boulders where *G. daudini* was most frequently encountered was remarkably stable (fluctuating < 1°C in

TABLE 2. Environmental conditions and microhabitats for *Gonatodes daudini* (Gd), *Sphaerodactylus kirbyi* (Sk), *Bachia heteropa* (Bh), and *Typhlops tasymicris* (Tt). Elevations are presented as ranges and substrate temperatures as means (\pm one SD) where animals were found. Ambient temperatures are means and ranges recorded by iButton thermochrons (see text). Surface area of cover objects is the mean surface area in contact with the substrate. All substrates were moist.

Species	Elevation (m)	Mean Substrate Temperature ($^{\circ}$ C)	Ambient Temperature ($^{\circ}$ C)	Mean Size of Cover Objects (cm^2)	Total	Number of Individuals						
						Rocks and Crevices	In Litter	Under Logs	Under Rocks	Termite Mounds	Tree trunks	Exposed Roots
Gd	32–199	27.3 \pm 0.82	26.6 \pm 0.47 25.5–28.5	3,644 \pm 1,862	55	33	1	10	8	2	1	0
Sk	31–234	26.4 \pm 0.63	26.1 \pm 1.30 23.5–37.0	1,184 \pm 226	16	1	9	0	4	2	0	0
Bh	88–234	26.8 \pm 0.85	26.4 \pm 0.54 25.5–28.0	527 \pm 304	43	0	1	3	36	2	0	1
Tt	159–179	28.1 \pm 0.20	26.2 \pm 0.91 23.5–37.0	—	5	0	2	0	2	1	0	0

24 h), whereas the temperature in leaf litter where *S. kirbyi* was commonly found fluctuated more (Table 2).

Desiccation rates.—Mean SVL and mass of animals used for desiccation studies were 27.8 \pm 2.4 mm (23–31 mm) and 0.47 \pm 0.15 g (0.16–0.65 g) for *G. daudini* (N = 19), 22.8 \pm 3.3 mm (19–29 mm) and 0.26 \pm 0.01 g (0.17–0.37 g) for *S. kirbyi* (N = 10), 38.5 \pm 3.5 mm (36–41 mm) and 0.97 \pm 0.24 g (0.52–1.34 g) for *B. heteropa* (N = 16), and 227 \pm 32 mm (190–264 mm) and 3.85 \pm 1.90 g (1.97–5.93 g) for *T. tasymicris* (N = 4). Mass-specific water-loss rates ranged from 2.32 \pm 1.23 mg/g/h (*T. tasymicris*) to 15.99 \pm 6.30 mg/g/h (*B. heteropa*; Table 3). For all species, the greatest water loss occurred during the first hour (32.3 \pm 10.5% for *T. tasymicris* to 55.7 \pm 25.2% for *G. daudini*) and decreased thereafter (Fig. 4). Log₁₀-transformed water-loss rates (Fig. 5) differed significantly by species (ANOVA, df = 3, F = 7.69, P < 0.001). Those of the three lizard species did not differ significantly from one another, although the difference between *B. heteropa*

and *G. daudini* approached significance (Fisher’s PLSD, P = 0.06), whereas that between *S. kirbyi* and the other two species did not (P \geq 0.41). However, all lizard rates differed significantly from that of *T. tasymicris* (all P < 0.001).

DISCUSSION

Due to the size and secretive nature of the species included in the study, we undoubtedly missed animals during surveys. Consequently, our estimates of population densities are conservative. When those numbers are extrapolated to the estimated area of suitable habitat, the resulting figures present only a rough estimate of total population sizes. Although approximations, they almost certainly provide an accurate representation of relative numbers, showing an approximate ratio of 2:1:12 for *G. daudini*, *S. kirbyi*, and *B. heteropa*, respectively.

No population density estimates are available for West Indian populations of *Bachia* or *Gonatodes* (Henderson

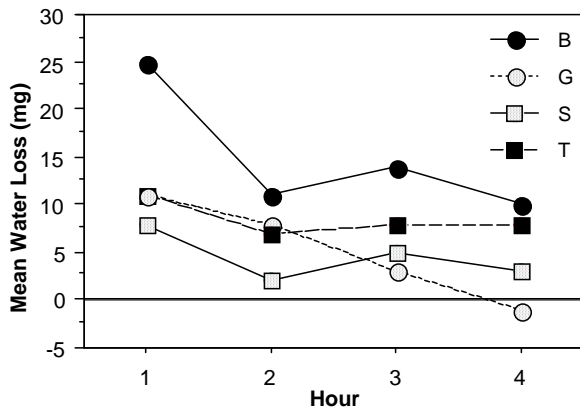


FIGURE 4. Rates of water loss (%) per hour in *Bachia heteropa* (B), *Gonatodes daudini* (G), *Sphaerodactylus kirbyi* (S), and *Typhlops tasymicris* (T).

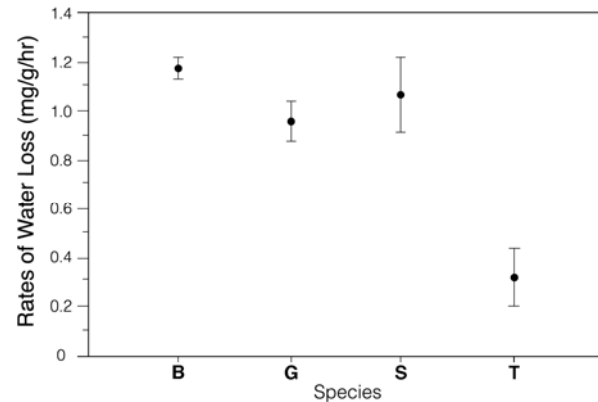


FIGURE 5. Mean log₁₀-transformed mass-specific water-loss rates (mg/g/h) for *Bachia heteropa* (B), *Gonatodes daudini* (G), *Sphaerodactylus kirbyi* (S), and *Typhlops tasymicris* (T) from Union Island. Error bars indicate one standard error (SE).

TABLE 3. Rates of mass-specific water loss (mg/g/h) and the percentage of water loss during the first hour that *Gonatodes daudini*, *Sphaerodactylus kirbyi*, *Bachia heteropa*, and *Typhlops tasymicris* were subjected to desiccation.

Species	N	Mean Mass (g)	Mass-specific Water Loss (mg/g/hr)	Total Mean Water Loss (mg)	Water Lost in First Hour (%)
<i>G. daudini</i>	19	0.47	11.83 ± 10.23	21.53 ± 17.76	55.7 ± 25.2
<i>S. kirbyi</i>	10	0.29	15.09 ± 13.87	15.80 ± 13.88	49.4 ± 23.1
<i>B. heteropa</i>	16	0.97	15.99 ± 6.30	60.33 ± 22.45	43.8 ± 11.9
<i>T. tasymicris</i>	4	3.85	2.32 ± 1.23	33.25 ± 16.07	32.3 ± 10.5

and Powell 2009). Colli et al. (1998) suggested that *Bachia* spp. might not be as “rare” as generally perceived, but their discussion focused on mainland species in sandy soils collected by following plows. Similarly, published population estimates for *Gonatodes* spp. (e.g., Oda 2008) deal almost exclusively with arboreal geckos, rendering comparisons with litter- and outcrop-dwelling *G. daudini* meaningless. However, our estimates for *S. kirbyi* are very low when compared to those of most other West Indian *Sphaerodactylus*. For example, Turk et al. (2010) recorded a high of 7,650 *S. fantasticus fuga*/ha on Dominica (mean 1,210.0 ± 823.0/ha for 10 transects in coastal forest), Steinberg et al. (2007) recorded mean densities of 2,562.5 ± 632.5 *S. vincenti*/ha (maximum 5,625/ha) on St. Vincent at sites where at least one lizard was found, Breuil (2002) recorded 10,000 *S. fantasticus kerukera*/ha on Grand Terre (Guadeloupe) and 7,900 *S. phyzacinus*/ha on Grand Îlet (Îles des Saintes), Nava et al. (2001) recorded ecological densities (under rocks) to 52,000 *S. parvus*/ha on Anguilla, and Thomas and Kessler (1996) recorded a density of 10,000 *S. klauberi*/ha on Puerto Rico. Our estimates also were substantially lower than the maxima recorded for other West Indian congeners in Henderson and Powell (2009), which ranged as high as 67,600/ha for *S. macrolepis* in continuous Seagrass (*Coccoloba uvifera*) habitats on Guana Island in the British Virgin Islands (Rodda et al. 2001). Our estimates, however, are comparable to those recorded by Hensley et al. (2004) for at least one species in some habitats on St. Eustatius. Although they recorded 1,427, 1,757, and 727 *S. sabanus*/ha at high, mid, and low elevations on the Quill, densities at the same sites were only 159, 195, and 72/ha for *S. sputator*. Also on St. Eustatius, they recorded densities of 801 *S. sputator*/ha and 188 *S. sabanus*/ha in dead agaves. We are unable to discern whether the relatively low densities recorded for *S. kirbyi* on Union reflect local conditions, a relatively recent colonization of the island, or possible competitive interactions with *G. daudini*.

Microhabitat use differed greatly between the geckos (*G. daudini* and *S. kirbyi*) and the semi-fossorial to fossorial species (*B. heteropa* and *T. tasymicris*). Geckos consistently exposed themselves when active,

exploiting rocks and crevices or the upper layers of leaf litter, and used cover objects only while inactive. In contrast, *B. heteropa* and *T. tasymicris* appeared to remain under cover at all times. *Typhlops tasymicris* apparently used a wider range of microhabitats than *B. heteropa*, but the low number of encounters precluded definitive conclusions. One *T. tasymicris*, however, was found in a termite mound with a *B. heteropa*, suggesting that the two species can and do coexist.

Gonatodes daudini generally foraged in close association with rock outcrops, but had a very short activity period coinciding with the cool early morning hours, presumably to prevent desiccation on the relatively dry rock surfaces. *Sphaerodactylus kirbyi* apparently must also limit its exposure to desiccating environments while foraging throughout the day, but accomplished this by remaining in moist leaf litter. The one *S. kirbyi* found on the much drier southern face of Mt. Taboi was in a moist area under a termite mound, with eggs of its own species commingled with those from two other species. Although anecdotal, such communal nesting suggests that geckos will risk competition with or predation by larger species for access to moist microhabitats in dry environments.

Data on water-loss rates are not available for *Bachia* spp. or *Gonatodes* spp., but our data for *S. kirbyi* are somewhat higher than those reported for other species of *Sphaerodactylus*. Turk et al. (2010) recorded a mean water loss rate for *S. fantasticus fuga* on Dominica of 10.4 mg/g/h. Steinberg et al. (2007) recorded rates of 13.55 ± 0.79 and 7.63 ± 0.95 mg/g/h for *S. v. vincenti* in two different habitats on St. Vincent and summarized data for other congeners. These ranged from a low of 3.2 ± 0.23 mg/g/h for *S. beattyi* on St. Croix (Snyder 1979) to 103.96 ± 4.88 mg/g/h for *S. gageae* at Humacao, Puerto Rico (Nava 2004). However, Nava’s (2004) data for three species at different locales were invariably much higher than those recorded for other species, with the difference almost certainly attributable to varying techniques. In addition to those for *S. beattyi*, comparable data include 7.00 and 3.58 mg/g/h for *S. cinereus* and 7.38 and 3.13 mg/g/h for *S. notatus* in the Florida Keys (Dunson and Bramham 1981), 3.44 ± 0.44, 3.55 ± 0.34, 4.95 ± 0.54, and 3.84 ± 0.60 mg/g/h for *S.*

macrolepis and 6.48 ± 1.49 mg/g/h for *S. parthenopion* in the British Virgin Islands (Maclean 1985), 5.5 ± 0.31 mg/g/h for *S. macrolepis* on St. Croix (Synder 1975), and 7.68 mg/g/h for *S. vincenti psammius* on Martinique (Leclair 1978). The relatively higher rate for *S. kirbyi* on Union might explain why it is generally restricted to the most mesic habitat on a dry island.

Although the three lizards are more vulnerable to desiccation than the proportionately larger *T. tasymicris*, they employed different strategies to deal with the threat of water loss. *Gonatodes daudini* appeared to limit exposure by curtailing activity and avoiding high temperatures while essentially conforming to ambient temperatures, whereas *S. kirbyi* appeared to regulate body temperature more effectively while foraging in a natural thermal gradient in moisture-retaining litter. In contrast, *B. heteropa* and *T. tasymicris* restricted their activity to thermally stable environments under rocks and in deep litter, respectively.

A note on conservation.—This assemblage of small and secretive crevice- and litter-dwelling reptiles is dependent on conditions available only in relatively mature forest situated to receive and hold moisture on an otherwise dry island. That environment, equally important for the ten other reptilian species known to occur there as well as for the entire biota, occurs only in the area above Chatham Bay. Although these species and the forest that sustains them have withstood a previous disruption when the island was cleared for agriculture during the colonial period (Howard 1952), this unique assemblage of reptiles and the forest on which they depend are again under severe and imminent threat, specifically by exotic mammals and development. Uncontrolled browsing by feral goats is destroying the vegetative understory (e.g., Powell et al. 2005; Tolson et al. 2007; Henderson and Powell 2009), and feral cats, which are proficient predators of small reptiles (e.g., Grant 1940; Iverson 1978; García et al. 2001; Daudin and de Silva 2007; Henderson and Powell 2009), are encountered frequently. Both groups of animals need to be controlled.

Protected from human activity for many years by its relative inaccessibility, a road constructed on the island in 2005 now provides ready access into the study area, and plans are in place to extend the road through the heart of the site. Roads can effectively fragment populations (e.g., Andrews et al. 2008), which in this case are already small. Direct mortality attributable to road kills (e.g., Andrews and Gibbons 2008) are unlikely to affect the focal species, which presumably do not move far, but could have a severe and negative impact on other reptiles (e.g., *Mastigodryas bruesi*) known to occur at the site (Quinn et al. 2010) and known to be vulnerable to road kills on Union (RP, pers. obs.).

Spatial effects are likely to be severe, beginning with construction and progressing through daily use (e.g., Andrews et al. 2008). In particular, the road as planned would traverse the area at a level that would destroy much of the critical habitat immediately below the escarpments that provide cover for *G. daudini* and are the source of the smaller rocks interspersed with litter that are used by all four species. In addition, development along the beach, a regional problem (e.g., Powell and Henderson 2008; Henderson and Powell 2009), is progressing rapidly, despite the current economic downturn. A resort, presently focused on servicing yachts that anchor in the bay, is expanding up the slope (Fig. 1), with much of the new construction involving cabins for housing land-based tourists. At the very least, expansion of the resort should be restricted to the immediate vicinity of the beach and the planned road extension should be diverted to a lower elevation that would provide access to the resort without destroying critical habitat higher on the slopes.

Unfortunately, even recommendations from the SVG Department of Forestry, which is supportive of conservation efforts, carry little weight when balanced against revenue-enhancing developmental interests. Further complications arise because the area contains both public and private lands that are imprecisely surveyed, rendering ownership of specific parcels uncertain. However, because this biotic community is unique in the Grenadines and the watershed is the most important on Union Island, its preservation is of the utmost concern. That should be and is a high priority for regional non-governmental organizations such as the SVG National Trust (<http://svgnationaltrust.org/>), Sustainable Grenadines Inc. (susgren@vincysurf.com), and the Union Island Environmental Attackers (<http://environmentalattackers.org/>). All hope to marshal international support to conserve the slopes above Chatham Bay in much the same way that the Mayreau Environmental Development Organization effectively mobilized regional and international pressure to facilitate the implementation of the Tobago Cays Marine Park Management Plan (http://en.wikipedia.org/wiki/Tobago_Cays).

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LITERATURE CITED

- Andrews, K.M., and J.W. Gibbons. 2008. Roads as catalysts of urbanization: Snakes on roads face differential impacts due to inter- and intraspecific ecological attributes. Pp. 145–153 *In* Urban Herpetology. Herpetological Conservation, volume 3. Mitchell, J.C., R.E. Jung Brown, and B. Bartholomew (Eds.). Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.
- Andrews, K.M., J.W. Gibbons, and D.M. Jochimsen. 2008. Ecological effects of roads on amphibians and reptiles: a literature review. Pp. 121–143 *In* Urban Herpetology. Herpetological Conservation, volume 3. Mitchell, J.C., R.E. Jung Brown, and B. Bartholomew (Eds.). Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.
- Bauwens, D., T. Garland, Jr., A.M. Castilla, R. Van Damme. 1995. Evolution of sprint speeds in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49:848–863.
- Breuil, M. 2002. Histoire naturelle des amphibiens et reptiles terrestres de l'Archipel Guadeloupéen. Guadeloupe, Saint-Martin, Saint-Barthélemy. Patrimoines Naturels, Paris 54:1–339.
- Colli, G.R., M.G. Zatz, and H.J. da Cunha. 1998. Notes on the ecology and geographical distribution of the rare gymnophthalmid lizard *Bachia bresslaui*. *Herpetologica* 54:169–174.
- Daudin, J., and M. de Silva. 2007. An annotated checklist of the amphibians and terrestrial reptiles of the Grenadines with notes on their local natural history and conservation. *Applied Herpetology* 4:163–175.
- Dunson, W.A., and C.R. Bramham. 1981. Evaporative water loss and oxygen consumption of three small lizards from the Florida Keys: *Sphaerodactylus cinereus*, *S. notatus*, and *Anolis sagrei*. *Physiological Zoology* 54:253–259.
- Fiard, J.-P. 2003. The phytosociologic and dynamic outline of the main forestry groups of Union Island. Pp. 47–53 *In* A Natural History Monograph of Union Island. Daudin, J. (Ed.). Désormeaux, Martinique, French West Indies.
- García, M.A., C.E. Diez, and A.O. Alvarez. 2001. The impact of feral cats on Mona Island wildlife and recommendations for their control. *Caribbean Journal of Science* 37:107–108.
- Grant, C. 1940. The herpetology of Jamaica. II. The reptiles. *Bulletin of the Institute of Jamaica, Science Series* 1:61–148.
- Hedges, S.B. 2006. An overview of the evolution and conservation of West Indian amphibians and reptiles. *Applied Herpetology* 3:281–292.
- Hedman, H.D., D.N. Muñiz Pagan, and R. Powell. 2010. *Chelonoidis carbonaria* (Red-footed Tortoise). Size and thermal biology. *Herpetological Review* 41:484–485.
- Henderson, R.W., and R. Powell. 2006. Geographic distribution: *Tantilla melanocephala* (NCN). *Herpetological Review* 37:501.
- Henderson, R.W., and R. Powell. 2009. Natural History of West Indian Reptiles and Amphibians. University Press of Florida, Gainesville, Florida, USA.
- Hensley, R.L., S.M. Wissmann, R. Powell, and J.S. Parmerlee, Jr. 2004. Habitat preferences and abundance of dwarf geckos (*Sphaerodactylus*) on St. Eustatius, Netherlands Antilles. *Caribbean Journal of Science* 40:427–429.
- Howard, R.A. 1952. The vegetation of The Grenadines, Windward Islands, British West Indies. *Contributions from the Gray Herbarium of Harvard University* 174:1–129.
- Iverson, J.B. 1978. The impact of feral cats and dogs on populations of the West Indian Rock Iguana, *Cyclura carinata*. *Biological Conservation* 14:63–73.
- Leclair, R., Jr. 1978. Water loss and microhabitats in three sympatric species of lizards (Reptilia, Lacertilia) from Martinique, West Indies. *Journal of Herpetology* 12:177–182.
- MacLean, W.P. 1985. Water loss rates of *Sphaerodactylus parthenopion* (Reptilia: Gekkonidae), the smallest amniote vertebrate. *Comparative Biochemistry and Physiology* 82A:759–761.
- McTaggart, A.L., D.P. Quinn, J.S. Parmerlee, Jr., R.W. Henderson, and R. Powell. *In press*. A rapid assessment of reptilian diversity on Union Island, St. Vincent and the Grenadines. *South American Journal of Herpetology*.
- Nava, S.S. 2004. Microhabitat selection, resource partitioning, and evaporative water loss by dwarf geckos (*Sphaerodactylus*), on Puerto Rico. M.S. Thesis. University of Texas, El Paso, USA. x + 48 p.
- Nava, S.S., C.R. Lindsay, R.W. Henderson, and R. Powell. 2001. Microhabitat, activity, and density of a dwarf gecko (*Sphaerodactylus parvus*) on Anguilla, West Indies. *Amphibia-Reptilia* 22:455–464.
- Newsom, L.A., and E.S. Wing. 2004. On Land and Sea: Native American Uses of Biological Resources in the West Indies. University of Alabama Press, Tuscaloosa, Alabama, USA.
- Oda, W.Y. 2008. Microhabitat utilization and population density of the lizard *Gonatodes humeralis* (Guichenot, 1855) (Reptilia: Squamata: Gekkonidae) in forest areas in Manaus, Amazon, Brazil. *Boletim do Museu*

Herpetological Conservation and Biology

- Paraense Emílio Goeldi Ciências Naturais 3:165–177.
- Powell, R., and R.W. Henderson. 2005. A new species of *Gonatodes* (Squamata: Gekkonidae) from the West Indies. *Caribbean Journal of Science* 41:709–715.
- Powell, R., and R.W. Henderson. 2008. Urban herpetology in the West Indies. Pp. 389–404 *In* Urban Herpetology. Herpetological Conservation, volume 3. Mitchell, J.C., R.E. Jung Brown, and B. Bartholomew (Eds.). Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.
- Powell, R., R.W. Henderson, and J.S. Parmerlee, Jr. 2005. Reptiles and Amphibians of the Dutch Caribbean: St. Eustatius, Saba, and St. Maarten. St. Eustatius National Parks Foundation, Gallows Bay, St. Eustatius, Netherlands Antilles.
- Quinn, D.P., A.L. McTaggart, T.A. Bellah, E.J. Bentz, L.G. Chambers, H.D. Hedman, R.R. John, D.N. Muñiz Pagan, and M.J. Rivera Rodríguez. 2010. An annotated checklist of the reptiles of Union Island, St. Vincent and the Grenadines. *Reptiles and Amphibians* 17:222–233.
- Rivera Rodríguez, M.J., E.J. Bentz, R.R. John, R.W. Henderson, and R. Powell. *In press-a*. *Mastigodryas bruesi* (Windward Tree Racer, White Snake). Miscellaneous behaviors. *Herpetological Review*.
- Rivera Rodríguez, M.J., E.J. Bentz, D.P. Scantlebury, R.R. John, D.P. Quinn, J.S. Parmerlee, Jr., R.W. Henderson, and R. Powell. *In press-b*. Rediscovery of the Grenada Bank endemic, *Typhlops tasymicris* (Squamata: Typhlopidae). *Journal of Herpetology*.
- Rodda, G.H., G. Perry, R. Rondeau, and J. Lazell. 2001. The densest terrestrial vertebrate. *Journal of Tropical Ecology* 17:331–338.
- Snyder, G.K. 1975. Respiratory metabolism and evaporative water loss in a small tropical lizard. *Journal of Comparative Physiology* 104:13–18.
- Snyder, G.K. 1979. Water loss and oxygen consumption in tropical *Sphaerodactylus*. *Oecologia* 38:107–110.
- Steinberg, D.S., S.D. Powell, R. Powell, J.S. Parmerlee, Jr., and R.W. Henderson. 2007. Population densities, water-loss rates, and diets of *Sphaerodactylus vincenti* on St. Vincent, West Indies. *Journal of Herpetology* 41:330–336.
- Thomas, R., and A.G. Kessler. 1996. Nonanoline reptiles. Pp. 347–362 *In* The Food Web of a Tropical Rain Forest. Reagan, D.P., and R.B. Waide (Eds.). University of Chicago Press, Chicago, Illinois, USA.
- Tolson, P.J., M.A. García, and C.L. Ellsworth. 2007. Habitat use by the Mona Boa (*Epicrates monensis monensis*) on Isla Mona, West Indies. Pp. 118–126 *In* Biology of the Boas and Pythons. Henderson, R.W., and R. Powell (Eds.). Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- Turk, P.A., N.N. Wyszynski, R. Powell, and R.W. Henderson. 2010. Population densities and water-loss rates of *Gymnophthalmus pleii*, *Gymnophthalmus underwoodi*, and *Sphaerodactylus fantasticus fuga* on Dominica, West Indies. *Salamandra* 46:125–130.
- Vitousek, P.M. 1988. Diversity and biological invasions of oceanic islands. Pp. 181–189 *In* Biodiversity. Wilson, E.O., and F.M. Peter (Eds.). National Academy Press, Washington, D.C., USA.
- Whittaker, R.J., and J.M. Fernandez-Palacios. 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press Inc., New York, New York, USA.
- Wilson, B.S., J.A. Horrocks, and A. Hailey. 2006. Conservation of insular herpetofaunas in the West Indies. *Applied Herpetology* 3:181–195.
- Yorks, D.T., R.W. Henderson, and R. Powell. 2003. *Typhlops tasymicris*. *Catalogue of American Amphibians and Reptiles* 780:1–2.

Bentz et al.—A Unique Crevice- and Litter-dwelling Assemblage of Reptiles



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