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Population densities and water-loss rates of *Gymnophthalmus pleii*, *Gymnophthalmus underwoodi* (Gymnophthalmidae), and *Sphaerodactylus fantasticus fuga* (Sphaerodactylidae) on Dominica, West Indies

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Abstract. *Gymnophthalmus pleii* and *G. underwoodi* (Gymnophthalmidae) occupy xeric woodlands along the western coast of Dominica, whereas *Sphaerodactylus fantasticus fuga* (Sphaerodactylidae) is a dwarf gecko found in more mesic microhabitats in the same general area. We studied population densities and desiccation rates of all three species in order to determine relationships between lizard sizes, rates of water loss, and habitat associations at two different sites. Populations of all three species appear to be allopatric. Mean population density estimates were 1,338.0 ± 385.1 *G. pleii*/ha (0–3,440/ha) at Cabrits National Park and 127.0 ± 127.0 *G. underwoodi*/ha (0–1,270/ha) and 1,210.0 ± 823.0 *S. fantasticus fuga*/ha (0–7,650/ha) at Batali Beach. The desiccation rate for *G. pleii*, which occupies the most xeric habitats, was significantly lower than those for both other species. The rates for *G. underwoodi*, of which only juveniles were examined, and *S. fantasticus fuga* did not differ significantly, and both occurred in similar habitats. As predicted, smaller lizards in all three species lost water faster than larger lizards.

Key words. Desiccation rates, habitat associations, Lesser Antilles, litter-dwelling, population densities.

Introduction

Three species of small diurnal lizards (Fig. 1) are associated with leaf litter in dry forests along the western (leeward) coast of Dominica, Lesser Antilles. *Gymnophthalmus pleii* (maximum SVL 48 mm; Schwartz & Henderson 1991) and *G. underwoodi* (maximum SVL 43 mm; Hardy et al. 1989) (Gymnophthalmidae) are the only two species in the genus known to occur in the West Indies, and both species occur sympatrically on Guadeloupe and Martinique (Schwartz & Henderson 1991, Henderson & Powell 2009). The presence of *G. pleii* on Dominica was documented by Schwartz & Henderson (1991) and Malhotra & Thorpe (1999). However, based on observations of lizards with varying scale counts, Malhotra & Thorpe (1999) and Malhotra et al. (2007) suggested that *G. underwoodi* also might be present. Breuil (2002) showed that both species occurred on Dominica, Williamson & Powell (2004) listed Dominica in the range of *G. underwoodi*, and Daniells et al. (2008) included both species in an annotated checklist. *Sphaerodactylus fantasticus* (maximum SVL 29 mm; Schwartz & Henderson 1991) (Sphaerodactylidae) is found on Montserrat, Guadeloupe and its satellites, Marie-Galante, La Désirade, and Dominica (Thorpe et al. 2008, Daniells et al. 2010). On Dominica, the distribution of *S. fantasticus fuga* is limited to the western coast (Malhotra & Thorpe 1999). These dwarf geckos have recently been found to be genetically similar to a population on western Basse Terre, Guadeloupe (*S. f. fantasticus*), suggesting that they are relatively recent (but pre-human) colonizers of Dominica (Malhotra & Thorpe 1999, Thorpe et al. 2008, Daniells et al. 2010).

Little is known about the natural history of these three species of small, litter-dwelling lizards (Henderson & Powell 2009). Their secretive nature, cryptic lifestyles, and an ability to quickly disappear from sight render observations difficult (e.g., Nava et al. 2001, Steinberg et al. 2007). All three species are diurnal and associated with xeric woodlands (Schwartz & Henderson 1991), suggesting that water loss rates should be equally high as a result of xeric conditions or equally low as a consequence of adaptations to the dry climate. Leclair (1978) documented a desiccation rate for *G. pleii* of 1.79 mg/g/h on Martinique.

On Dominica, we evaluated population densities, habitat associations, and water loss rates to test the following predictions: (1) Because of apparently similar niches, Gause's exclusion principle (e.g., Allaby 1998) would apply, and populations of the three species will be allopatric; (2) because of lower ratios of surface area to body mass, larger individuals will exhibit lower desiccation rates; and (3) because species of *Gymnophthalmus* are generally associated with drier microhabitats than many species of

Figure 1. Three small diurnal, litter-dwelling lizards from the western (leeward) coast of Dominica, West Indies: A. *Gymnophthalmus pleii* (Gymnophthalmidae) from Cabrits National Park; B. *Gymnophthalmus underwoodi* from Batali Beach; and C. male *Sphaerodactylus fantasticus fuga* (Sphaerodactylidae) from Batali Beach. Photographs by Robert Powell.

Sphaerodactylus (e.g., Treglia 2006, Henderson & Powell 2009), water loss rates of *G. pleii* and *G. underwoodi* will be lower than those of *S. fantasticus fuga*.

Materials and methods

We conducted our study from 5 through 25 June 2008, which is the beginning of the rainy season on Dominica (Malhotra et al. 2007), at Cabrits National Park (15°35'10" N, 61°28'20" W) and Batali Beach (15°27'08" N, 61°26'47" W). Prior to the onset of the study, we conducted surveys throughout the day at both sites to evaluate activity periods. Because all three species were active from mid-morning through mid-afternoon (ca. 1000–1400 h) on sunny days, we conducted population surveys during those times and under those conditions. Plot sampling (e.g., Steinberg et al. 2007, for *Sphaerodactylus vincenti* on St. Vincent) proved ineffective, because some lizards were observed escaping from plots before all litter could be removed and inspected. Instead, we used the methods of Hensley et al. (2004), walking 20 transects ranging in length from 12.0 to 54.5 m in leaf litter at sites in Cabrits National Park and at Batali Beach. Transects varied in length because the extent of litter-covered areas was variable. No transect began or terminated <2 m from the edge of a suitable habitat patch. For all transects, we counted all animals flushed from an area within 50 cm on either side of the transect and recorded the percentage of litter cover (combining visual estimates by the same two observers), litter depth (by averaging measurements of depth using a ruler at 5-m intervals along the transect), litter type (by collection and identification of leaves), extent of insolation (by estimating the portion of the area exposed to full or filtered sunlight), soil moisture (categorized as either dry, moist, all sand, or all rock by filtering handfuls of substrate material through our hands), substrate composition (i.e., content of rocks, gravel, etc.), and miscellaneous observations (e.g., distance from coast, presence of fallen fruits).

We collected 19 *G. pleii* from Cabrits National Park and 4 *G. underwoodi* and 24 *S. fantasticus fuga* from Batali Beach to determine and compare desiccation rates. We also determined the desiccation rate for a single *G. underwoodi* taken in open secondary forest along the trail to Kachibona Lake at an elevation of >300 m. Based on dissections of museum specimens, we considered *Gymnophthalmus* spp. to be adults if SVL ≥ 30 mm and *S. fantasticus fuga* adults if SVL ≥ 20 mm. Following the methods of Steinberg et al. (2007), we measured SVL to the nearest 0.1 mm using a Mitutoyo© Absolute Digimatic Caliper (CD–6" CSX; Mitutoyo America Corp., Elk Grove Village, Illinois, USA) before placing lizards individually in 1¾-cup Ziplock© Snap 'n Seal containers (SC Johnson, Racine, Wisconsin, USA) with screened lids, with moist paper towels for water but without food for 18–20 h before being subjected to desiccation during midday peak activity periods. Containers were placed together at a shaded location exposed to ambient fluctuations of temperature and humidity. Mean temperature and relative humidity on days when animals were subjected to desiccation were 30.9 ± 0.2ºC and 63.8 ± 0.6%, respectively. Because Dunson & Bramham (1981) indicated that rates of water loss essentially leveled off after about 4 h, each animal was weighed to the nearest 0.001 g initially and then every hour for 5 h on a Denver Instrument Company© Model S–110 (Denver, Colorado, USA) scale in a closed room at ambient temperature and humidity. Data for one *S. fantasticus fuga* that defecated during the 5-h period were excluded from analyses. All lizards were subsequently rehydrated and released at their original sites of capture.

We used StatView 5.0 (SAS Institute, Cary, North Carolina, USA) for statistical analyses. Data were $\log_{10}$-transformed to assure normality. The individual *G. underwoodi* from an elevation of >300 m was excluded from comparisons between species. Means are presented ± one SE. For all tests, α = 0.05.

Results

Based on surveys conducted throughout the day, both *Gymnophthalmus underwoodi* and *G. pleii* were active almost exclusively during the hottest times of day; few were encountered early and late in the day or on cool rainy days. In contrast, *S. fantasticus fuga* was active in leaf litter from shortly after dawn until dusk regardless of weather conditions.

Transect data (Table 1) yielded mean population density estimates of 1,338.0 ± 385.1 *G. pleii*/ha (0–3,440/ha) at Cabrits National Park and estimates of 127.0 ± 127.0 *G. underwoodi*/ha (0–1,270/ha) and 1,210.0 ± 823.0 *S. fantasticus fuga*/ha (0–7,650/ha) at Batali Beach. Mean densities for

Table 1. Transect data (Gp = *Gymnophthalmus pleii*, Gu = *G. underwoodi*, Sf = *Sphaerodactylus fantasticus fuga*).

Site Transect	Length (m)	N Gp	N Gu	N Sf	Density	Elevation (m)	Litter type	Litter depth (cm)	Bare ground (%)	Shade (%)	Relative soil moisture	Notes
Cabrits												
1	12.5	1	—	—	800	11	Mixed	1.4 ± 0.7	0	60	moist	20 m to coast
2	17.9	3	—	—	1,680	23	Mixed	1.1 ± 0.4	0	60	dry	next to trail
3	30.5	1	—	—	330	31	Mixed	3.1 ± 0.5	0	70	dry	next to trail
4	32.0	11	—	—	3,440	51	Mixed	2.6 ± 0.4	0	30	dry	undergrowth to 10 cm
5	25.0	1	—	—	400	59	Mixed	1.2 ± 0.3	30	40	dry	on path
6	12.0	2	—	—	1,670	64	Mixed	2.0 ± 0.3	0	30	dry	courtyard ruins
7	13.0	3	—	—	2,310	62	Mixed	3.1 ± 0.7	0	50	dry	undergrowth to 10 cm
8	14.0	0	—	—	0	64	Mixed	2.6 ± 04	0	60	dry	next to trail
9	54.5	15	—	—	2,750	21	Mixed	2.0 ± 0.4	10	40	dry	undergrowth to 20 cm
10	20.0	0	—	—	0	38	Mixed	1.3 ± 0.5	0	40	dry	undergrowth to 20 cm
Batali												
1	34.5	—	0	0	0	<10	*Mangifera*	1.9 ± 0.7	30	80	dry	rotting mangos
2	17.3	—	0	0	0	<10	*Mangifera*	4.7 ± 1.1	0	90	dry	rotting mangos
3	15.8	—	2	0	1,270	<10	Mixed	2.7 ± 0.9	0	60	dry	leaves and dead vines
4	15.0	—	0	0	0	<10	Mixed	8.7 ± 2.7	0	70	dry	most litter dead vines
5	17.0	—	0	7	4,120	<10	*Coccoloba*	4.3 ± 1.6	10	80	dry	all sand, 10 m to coast
6	30.0	—	0	0	0	<10	Mixed	1.0 ± 0.4	50	90	dry	30 m off coast
7	34.5	—	0	0	0	<10	*Mangifera*	1.7 ± 0.7	0	90	dry	rotting mangos
8	17.3	—	0	0	0	<10	*Mangifera*	4.5 ± 1.3	0	90	dry	rotting mangos
9	17.0	—	0	13	7,650	<10	*Coccoloba*	4.4 ± 1.5	0	90	dry	all sand, 10 m to coast
10	30.0	—	0	1	330	<10	Mixed	1.3 ± 0.4	0	60	dry	all sand

transects during which lizards of each species actually were observed were 1,672.5 ± 398.1 *G. pleii*/ha, 1,270 ± 0.0 *G. underwoodi*/ha, and 4,033.3 ± 2113.5 *S. fantasticus fuga*/ha.

Of the *G. pleii* subjected to desiccation, 12 were adults and seven were juveniles; of the *S. fantasticus fuga*, 19 were adults and five were juveniles; however, all *G. underwoodi* were juveniles comparable in size to *S. fantasticus fuga* (i.e., SVL < 30 mm). Mean snout–vent lengths (SVL) and masses of lizards were 33.7 ± 2.0 mm (19.6–49.5 mm) and 1.020 ± 0.156 g (0.372–2.220 g) for *G. pleii* (N = 19), 22.7 ± 1.0 mm (19.7–26.6 mm) and 0.248 ± 0.031 g (0.141–0.366 g) for *G. underwoodi* (N = 4), and 23.4 ± 0.8 mm (17.0–28.6 mm) and 0.376 ± 0.032 g (0.105–0.591 g) for *S. fantasticus fuga* (N = 24). Regression of log-SVL and log-desiccation rate (mg/g/h; Fig. 2) was significant for *G. pleii* (df = 1, F = 21.6, P = 0.0002), *S. fantasticus* (F = 25.9, P < 0.0001), and for all three species combined (F = 74.3, P < 0.0001), but not for *G. underwoodi* (F = 1.9, P = 0.30). Log-desiccation rates (mg/g/h) among species (Fig. 3) did not differ significantly (ANCOVA, with log-SVL as covariate, df = 2, F = 0.88, P = 0.42). However, rates for *G. pleii* were significantly lower than those for *G. underwoodi* (Fisher's PLSD, P = 0.0006) and *S. fantasticus* (P < 0.0001), whereas those of *G. underwoodi* and *S. fantasticus* (P = 0.23) did not differ significantly. The desiccation rate of the one *G. underwoodi* collected at an elevation >300 m was 43.81 mg/g/hr.

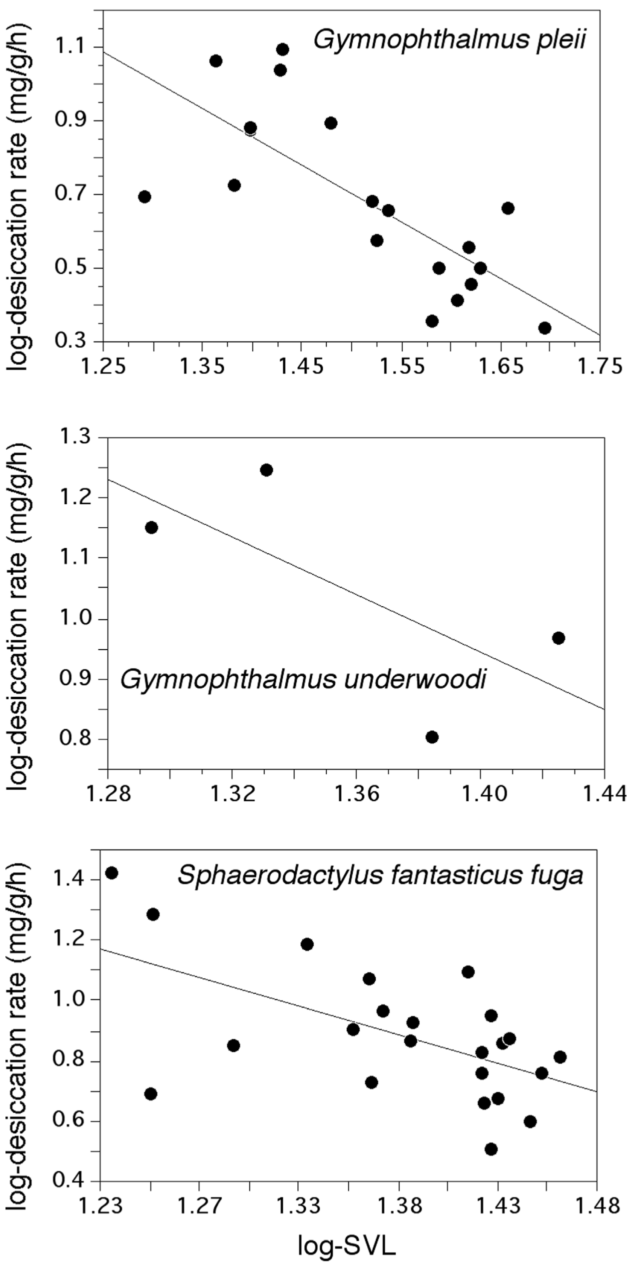

Figure 2. Size (log-SVL) was negatively correlated with rates of water loss (log-mg/g/hr).

Discussion

We cannot discern whether differences in activity, habitat associations, or desiccation rates reflect the different phylogenetic histories of the three species (especially between the gymnophthalmids and the sphaerodactylid) or whether they represent different ecological adaptations to slightly dissimilar microhabitats encountered in geographically proximate and climatically similar environments. Regardless of the underlying cause, all three species of these diurnal, litter-dwelling lizards must cope with the problems associated with small mass and living in what appear to be harsh, desiccating habitats.

Differences in the extent of peak activity periods almost certainly are reflections of habitat associations (Table 1), with *Gymnophthalmus* spp. exhibiting an apparent preference for hotter and drier conditions. Sites at Cabrits National Park, where only *G. pleii* occurred, were considerably drier than those at Batali Beach. At the latter locality, *G. underwoodi* was prevalent in relatively open xeric woodlands ~50–100 m inland from the coast, whereas *S. fantasticus fuga* was found in greatest abundance about ~10 m from the coast in shaded situations associated with seagrapes (*Coccoloba uvifera*), the large leaves of which make for litter capable of conserving moisture to a greater extent than the smaller leaves of species in the drier forest farther inland.

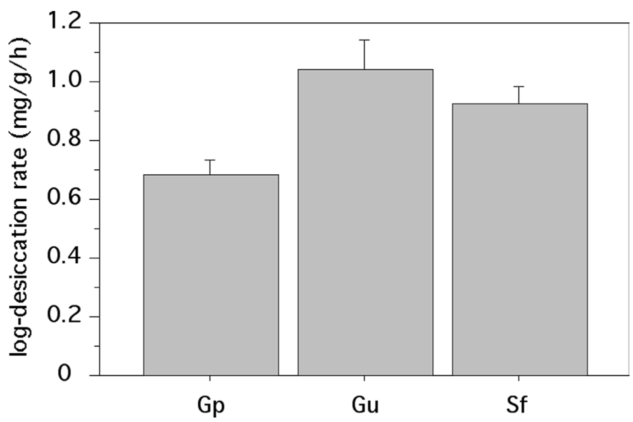

Figure 3. Mean log-desiccation rate (mg/g/hr) in three small species of litter-dwelling lizards in Dominica (Gp = *Gymnophthalmus pleii*, Gu = *G. underwoodi*, Sf = *Sphaerodactylus fantasticus fuga*).

Gymnophthalmus pleii was observed solely at Cabrits National Park. In contrast, *G. underwoodi* was observed in several locations, including open secondary forest along the trail to Kachibona Lake at an elevation of >300 m. The two species were never found in the same areas. This suggests that the unisexual *G. underwoodi*, an excellent colonizer and presumably a recent arrival to Dominica, might have been able to displace *G. pleii* from at least some habitats, as suggested by Breuil (2009) for Martinique.

No previous population density estimates exist for *G. pleii*. The only other population density estimate for *G. underwoodi* was by Daltry (2007), who recorded as many as five *G. underwoodi*/m^2 on Great Bird Island (Antigua). Our relatively low estimate for *G. underwoodi* should be considered very conservative. In June 2007, two of us (RP and RWH) noted considerably greater numbers of individuals at the same site. Also, when collecting animals outside sampling transects and during concurrent surveys for other species in the area (e.g., Daniells et al. 2008, Ackley et al. 2009, Rudman et al. 2009), *G. underwoodi* was regularly encountered in suitable habitats at rates that probably exceeded one lizard/m^2.

Population density estimates for *S. fantasticus fuga* were substantially lower than the 10,000/ha recorded by Breuil (2002) for *S. fantasticus karukera* on Grand Terre (Guadeloupe) and the 7,900/ha for a closely related species on Grand Îlet, Îles des Saintes (*S. phyzacinus*, which until recently was considered a subspecies of *S. fantasticus*; Thorpe et al. 2008, Powell et al. 2010). Our estimates also were substantially lower than the maxima recorded for other West Indian congeners in Henderson & Powell (2009), which range as high as 67,600/ha for *S. macrolepis* in continuous seagrape (*Coccoloba uvifera*) habitats on Guana Island in the British Virgin Islands (Rodda et al. 2001). Although we found dwarf geckos and *G. underwoodi* in similar adjacent habitats, we never found them in syntopy. Consequently, whether the low densities recorded for *S. fantasticus fuga* reflect local conditions, the species' relatively recent colonization of the island, or competitive displacement by *G. underwoodi* cannot be discerned.

Smaller animals lost water faster than larger individuals, supporting the general contention that body mass increases exponentially with an increase in surface area, so that larger lizards have relatively less surface area through which they lose water. Although not as low as those recorded by Leclair (1978) on Martinique, for which slightly different methods might explain the difference, desiccation rates were lowest for *G. pleii*, reflecting the larger body sizes of lizards in the sample and the fact that these lizards occupied and presumably were adapted to drier and hotter habitats than those in which the other two species were sampled. Conversely, the similar desiccation rates for *G. underwoodi* and *S. fantasticus fuga* probably reflect the comparable body sizes of the animals sampled and the similar habitats in which they occurred at Batali Beach. However, one *G. underwoodi* collected in a more humid area at a higher elevation (>300 m on the trail to Kachibona Lake) exhibited a much higher desiccation rate (43.81 mg/g/hr) than those of conspecifics from Batali Beach (mean = 11.88 ± 2.53 mg/g/hr), suggesting that populations of *G. underwoodi* might adapt to desiccating habitats such as those near the coast by becoming more resistant to water loss.

Confounding in these comparisons is the fact that all tested *G. underwoodi* were juveniles (SVL <30 mm). In 2007, two of us (RP & RWH) noted large numbers of adults at the same sampling site at Batali Beach — where only one adult was caught in 2008. That discrepancy cannot be explained. Consequently, however, the desiccation rates for juvenile *G. underwoodi* may not be representative of adults, which were not tested and which are comparable in size to *G. pleii*.

These data tend to support the predictions that populations of these three species with largely similar niches are essentially allopatric and that larger individuals would exhibit lower rates of water loss. Support for the third prediction, that *Gymnophthalmus* spp. would exhibit lower desiccation rates than *Sphaerodactylus fantasticus fuga*, was equivocal. *Gymnophthalmus pleii* was found in the most xeric conditions and did have the lowest rates of water loss. However, the difference between *G. underwoodi* and *S. fantasticus fuga* was not significant, but whether that can be attributed to the use of similar habitats or similarity in body sizes between the dwarf geckos and juvenile *G. underwoodi* cannot be determined.

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