

Colour and pattern polymorphism in *Pristimantis shrevei* and *Eleutherodactylus johnstonei* (Leptodactylidae) on St. Vincent, West Indies

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THE genus *Eleutherodactylus*, with more than 700 species, had been considered to be the most speciose vertebrate genus (Pough *et al.*, 2004). A recent revision (Heinicke *et al.*, 2007), however, revealed three major clades, two of which are represented in the West Indies. A “Caribbean clade” (*Eleutherodactylus*) contains four subgenera and 170 currently recognised species, including all but two West Indian forms. A “South American clade” (*Pristimantis*) contains nearly 400 species, two of which occur on the St. Vincent and Grenada island banks. All of these frogs lay eggs in humid places outside of water and exhibit direct development, with froglets emerging as small replicas of adults (Rivero, 1998). They often exhibit colours and patterns that render them cryptic (Pough *et al.*, 2004), although many species exhibit considerable polymorphism (e.g., Savage & Emerson, 1970; Sifers *et al.*, 2001, Sander *et al.*, 2003). Schwartz & Henderson (1991) used phrases such as “... dorsal pattern variable ...” and “... frequently present”, and Kaiser & Hardy (1994) noted “... a great variety of dorsal patterns”.

Two eleutherodactylines, *Pristimantis shrevei* and *Eleutherodactylus johnstonei* (Figure 1), occur on St. Vincent. *Pristimantis shrevei* is endemic and occurs primarily at higher elevations (> 350 m), whereas *E. johnstonei* presumably is introduced (Kaiser & Hardy, 1994), albeit well-established, and occurs at low and high elevations. The former is most abundant in relatively natural habitats, where *E. johnstonei* often is less commonly encountered (C. A. Rodríguez Gómez, pers. comm.). However, in heavily altered situations, especially at lower elevations, ecologically

versatile *E. johnstonei* dominates and *P. shrevei* is absent (Mallery *et al.*, 2007).

As in many eleutherodactylines (e.g., Schwartz & Henderson, 1991; Sifers *et al.*, 2001), both Vincentian species are extremely variable in colour and pattern. Sander *et al.* (2003) documented considerable variation in *E. johnstonei* from Grenada, identifying colour and pattern elements that occurred in varying frequencies in populations at different locations. We examined colour, patterns, and sizes of frogs taken from sites on St. Vincent at high to moderate elevations, where both species were present, and at low elevation, where we found only *E. johnstonei*, to determine if variability was influenced by elevation.

From 1st–20th June 2006, we captured 25 *P. shrevei* and 43 *E. johnstonei* from five sites on St. Vincent (Fig. 2): (1) La Soufriere Volcano trail (elevation 961 m), (2) Vermont Nature Trail natural forest (411 m), (3) Hermitage Forest Reserve (342 m), (4) Vermont Nature Trail plantation forest (297 m), and (5) Bambareux Beach Resort (< 10 m). Frogs were kept individually at ambient temperatures (ca. 27°C) for no more than six days before release at the original site of capture. We measured snout-vent length (SVL) to the nearest 0.1 mm using a Vernier caliper and mass to the nearest 0.1 g with a Pesola spring scale (Pesola AG, Baar, Switzerland). Each individual was photographed with a digital camera (Nikon Cool Pix 5600; Nikon USA, Melville, New York) to record colour and pattern. Photographs were taken in a darkened room, as individuals often are much darker when exposed to daylight. We specifically noted the following



Figure 1. Adult male *Pristimantis shrevei* (left) and adult female *Eleutherodactylus johnstonei* from the Hermitage Nature Trail (342 m), St. Vincent. All photographs © R. Powell.

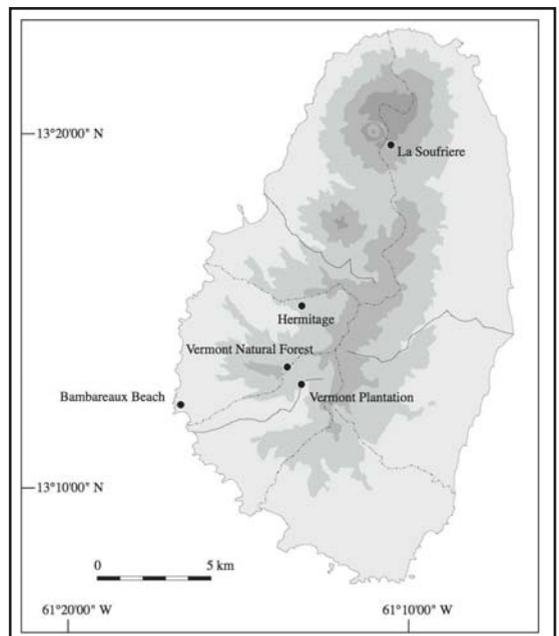
characteristics: dorsal, lateral, and ventral ground colour, colour of iris, snout, and toe pads, and presence/absence, extent, and colour of dorsal mottling, middorsal line, dorsolateral lines, dorsal chevrons, interorbital line, canthal lines, supratympanic, tympanic, and subtympenic lines, post-anal triangle, and vertical bars on fore- and hindlimbs. For statistical tests, we used Statview 5.0 (SAS Institute, Cary, North Carolina). All means are presented \pm one standard error; $\alpha = 0.05$.

Female and male *P. shrevei* from sites 1 and 2 did not differ significantly in SVL (Mann-Whitney U, $Z = -0.28$, $P = 0.78$; $Z = -0.94$, $P = 0.35$; respectively) or body mass (males, $Z = -0.23$, $P = 0.82$; females, $Z = -1.17$, $P = 0.24$), allowing us to pool our samples from those sites (Table 1). Females were significantly longer and heavier than males (SVL, $Z = -3.35$, $P = 0.0008$; weight, $Z = -3.48$, $P = 0.0005$). Size and body mass were significantly correlated in both sexes (Kendall correlation, females, $Z = 2.21$, $P = 0.03$; males, $Z = 4.58$, $P < 0.0001$).

Results were essentially similar for *E. johnstonei* (Table 1). No significant differences existed in SVL between females or males from high and low elevations (Mann-Whitney U, $Z = -1.64$, $P = 0.10$; $Z = -0.44$, $P = 0.66$; respectively), nor did either males or females from different elevations differ significantly in body mass (males, $Z = -0.76$, $P = 0.45$; females, $Z = -0.22$, $P = 0.83$). Female *E. johnstonei* were significantly larger and heavier than males (SVL, $Z = -3.47$, $P = 0.0005$; weight, $Z = -3.70$, $P = 0.0002$). As expected, SVL and body mass were significantly correlated in both males (Kendall correlation, $Z = 3.239$, $P = 0.0012$) and females ($Z = 3.97$, $P < 0.0001$).

Pristimantis shrevei from both of the sites where we found these frogs (Table 2) was extremely variable in colouration and pattern (Fig. 3). We found no consistent differences between either of our sites, nor were any traits found exclusively in either males or females. Characteristics common to most frogs

Figure 2. Map of St. Vincent showing collecting localities: (1) La Soufrière Volcano trail (elevation 961 m), (2) Vermont Nature Trail natural forest (411 m), (3) Hermitage Forest Reserve (342 m), (4) Vermont Nature Trail plantation forest (297 m), and (5) Bambareaux Beach Resort (< 10 m).



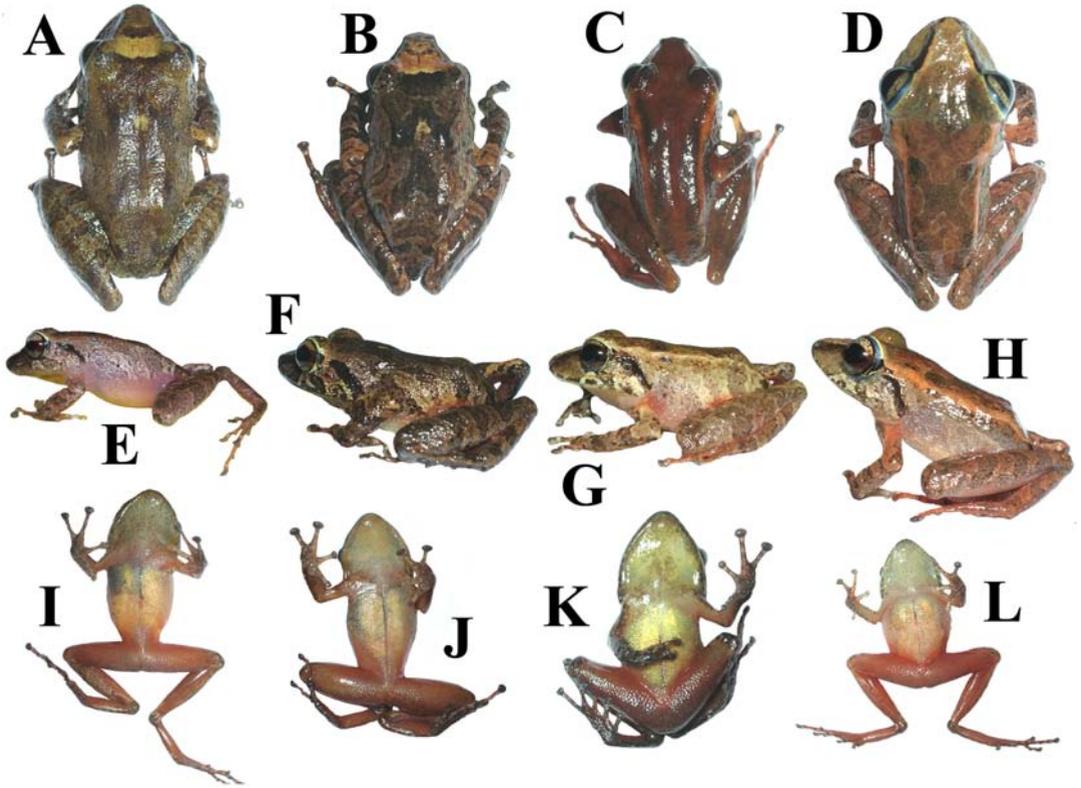


Figure 3. Representative colour and pattern polymorphism in *Pristimantis shrevei* from St. Vincent (note that individuals are not figured in the same scale): **A.** Gravid female (SVL 29.0 mm) from site 2 with a complete interorbital bar and a light bar on the top of the snout, two dorsal chevrons, and distinct bars on hindlimbs; **B.** Male (SVL 13.0 mm) from site 2 with a line on the top of the snout and interorbital bar present, distinct bars on hind- and forelimbs; **C.** Male (SVL 20.0 mm) from site 2 with dorsolateral lines, toe pads darker than toes, interorbital line absent; **D.** Male (SVL 19.0 mm) from site 2 with distinct bars on hindlimbs, inverted chevrons on dorsum, and full interorbital and canthal lines; **E.** Male (SVL 29.0 mm) from site 2 with broken bars on forelimbs, ivory coloration of the iris, and a strong supratympanic line; **F.** Male (SVL 18.5 mm) from site 2 with a supratympanic line, distinct bars on lips and hindlimbs; **G.** Male (SVL 18.0 mm) from site 2 with distinct bars on lips and supratympanic line followed by a lighter line; **H.** Male (SVL 19.0 mm) from site 2 with a weak bars on lips, distinct bars on fore- and hindlimbs, and distinct canthal and dorsolateral lines; **I.** Gravid female (SVL 24.0 mm) from site 1 with heavy mottling on grey throat and reddish colour on hind- and forelimbs; **J.** Male (SVL 19.0 mm) from site 1 with weak mottling on green throat and dark red on hindlimbs; **K.** Male (SVL 18.5 mm) from site 2 with a yellowish belly and mottling limited to the centre of the throat; **L.** Male (SVL 18.0 mm) from site 2 with a reddish belly and white throat.

included predominately yellow venters, and a greenish throat with a distinct yellowish cast; some individuals had white, grey, or yellow throats, but always with a yellowish tinge. Varying degrees of brown stippling on the throat were universally present, albeit sometimes reduced to margins and few scattered specks. The ground colour of the iris was above and below a dark horizontal line running through the pupil ranged from near white through ivory to pale brown, often with a slightly golden tinge. Areas above and below the line were

essentially similar in colour. The horizontal line itself was dark brown, frequently with a reddish cast.

Pattern elements that were almost universally present, albeit less well defined in some individuals, included: (1) a dark brown to black canthal line continuous with the line through the orbit and continuing as a comparably dark supratympanic line set off by a lighter line passing through the tympanum; (2) interorbital bars (complete or broken) were present in all but two of the females (one each from sites 1 and 2) and three of the males (all from

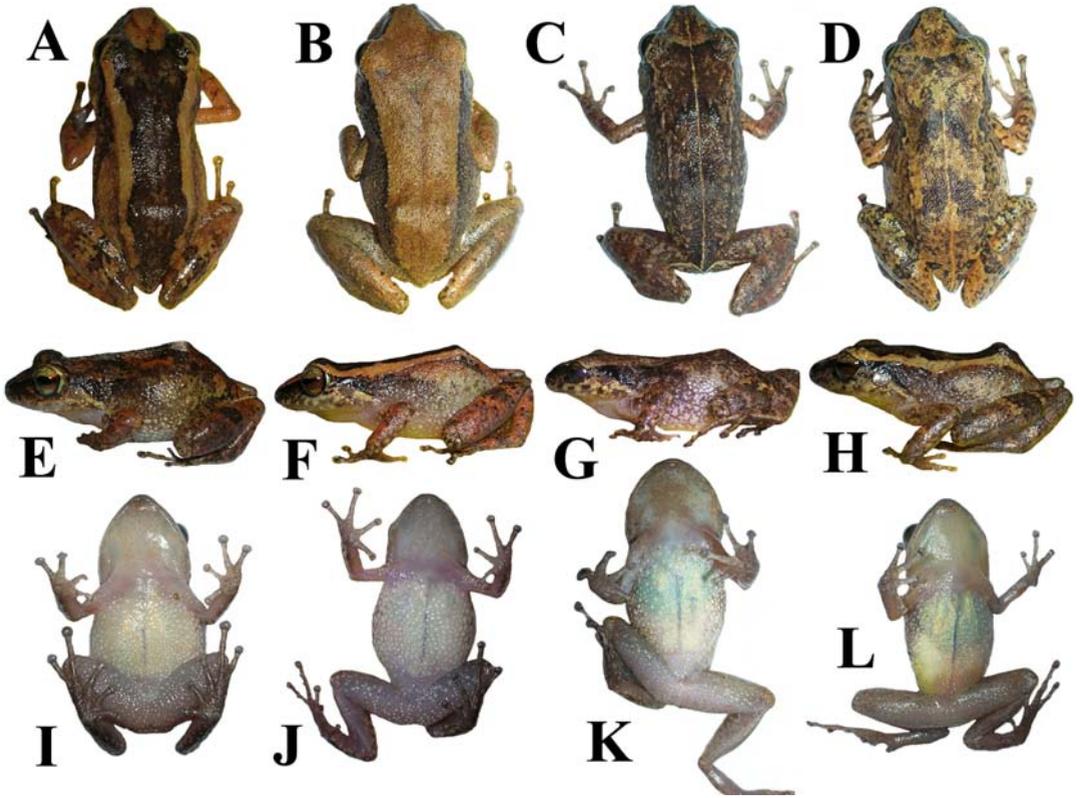


Figure 4. Representative colour and pattern polymorphism in *Eleutherodactylus johnstonei* from St. Vincent (note that individuals are not figured in the same scale): **A.** Male (SVL 22.0 mm) from site 4 with distinct dorsolateral lines, dorsum darker than sides, and bars on hindlimbs broken; **B.** Female (SVL 30.0 mm) from site 3 with dorsum lighter than sides and no interorbital bar or middorsal line; **C.** Gravid female (SVL 27.0 mm) from site 5 with a light middorsal line, broken interorbital bar, and top of the snout lighter than dorsum; **D.** Male (SVL 20.0 mm) from site 5 with heavy mottling on the dorsum, dorsal chevrons, and middorsal line; **E.** Male (SVL 21.0 mm) from site 5 with no bars on lips and light tympanic above a faint subtympanic line; **F.** Male (SVL 21.0 mm) from site 4 with distinct bars on lips, broken bars on fore- and hindlimbs and dorsolateral lines; **G.** Male (SVL 21.5 mm) from site 4 with a supratympanic line, light tympanic line, and strong bars on the lips; **H.** Gravid female (SVL 22.0 mm) from site 4 with dorsolateral lines and distinct bars on hindlimbs; **I.** Male (SVL 19.9 mm) from site 5 with faint mottling on the throat and white belly; **J.** Male (SVL 19 mm) from site 5 with brown mottling on grey throat; **K.** Female (SVL 30.0 mm) from site 3 with mottling limited to margins and centre of throat; **L.** Gravid female (SVL 19.0 mm) from site 4 with a slightly yellowish belly.

site 2). Post-anal triangles occurred in all frogs. No individuals in our samples had middorsal lines. Most individuals had strong to indistinct vertical bars on the upper lips; three individuals that did not have bars on the upper lips instead had varying numbers and sizes of brown specks. Most frogs had two dark chevrons on the dorsum, but four had one chevron and six had none.

The ground colour of the dorsal and lateral fields, the top of the snout in front of the interorbital bar, and limbs ranged from grey and

light brown to very dark brown, often with a yellowish, orange, or reddish cast. Dorsal ground colour was usually the same as the lateral colour, but was occasionally darker or lighter. The top of the snout was usually lighter, but infrequently the same as the dorsum. Dorsolateral lines were in most cases absent, but when present, they were usually lighter than the dorsum; in only one individual were the dorsolateral lines darker than the dorsum. Toe pads varied in colour from very light brown through dark brown, sometimes with a

<i>Pristimantis shrevei</i>			
Female SVL	Female Body Mass	Male SVL	Male Body Mass
Site 1: La Soufrière Volcano Trail			
25.9 ± 1.9	1.6 ± 0.2	18.0 ± 0.6	0.6 ± 1.7
24.0-27.9	1.4-1.8	17.0-19.0	0.6-0.7
N = 2	N = 2	N = 3	N = 3
Site 2: Vermont Nature Trail Natural Forest			
28.5 ± 1.0	2.1 ± 0.3	17.8 ± 1.0	0.6 ± 0.1
27.0-31.0	1.4-2.5	13.0-29.0	0.2-1.8
N = 4	N = 4	N = 16	N = 16
<i>Eleutherodactylus johnstonei</i>			
Site 2: Vermont Nature Trail Natural Forest			
27.0 ± 0.0	2.6 ± 0.0	21.5 ± 0.5	0.7 ± 0.1
27.0	2.6	21.0-22.0	0.6-0.8
N = 1	N = 1	N = 2	N = 2
Site 3: Hermitage Nature Trail			
29.5 ± 0.5	2.1 ± 0.2		
29.0-30.0	1.9-2.2		
N = 2	N = 2		
Site 4: Vermont Nature Trail Plantation Forest			
22.2 ± 1.2	1.0 ± 0.1	20.2 ± 0.4	0.7 ± 0.1
19.0-25.0	0.5-1.4	18.2-22.0	0.5-1.1
N = 5	N = 5	N = 13	N = 13
Site 5: Bambareux Beach Resort			
24.0 ± 1.7	1.2 ± 0.2	19.5 ± 0.2	0.7 ± 2.9
17.5-27.0	0.6-1.4	18.0-21.0	0.4-0.8
N = 5	N = 5	N = 15	N = 15

Table 1. Sizes (mm) and body masses (g) of *Pristimantis shrevei* and *Eleutherodactylus johnstonei* from various sites on St. Vincent. Each entry includes the mean ± 1 SE, range, and sample size.

distinct greyish cast; colour in all but one frog from site 1 was darker than the toe itself. Eight individuals from site 2 had a light bar on the snout, with bars ranging from wide and complete to narrow and broken; one individual had a light spot on the snout.

Although *E. johnstonei* is at least equally polymorphic (Table 3, Fig. 4), we found no consistent differences between sites, nor were any traits found exclusively in either males or females.

Nearly all *E. johnstonei* have essentially white venters with varying degrees of brown stippling on the throat. Venters of a few individuals had a slight yellowish tinge, and throat stippling was sometimes reduced to margins and few scattered, medial flecks.

The ground colour of the iris above and below a horizontal line running through the pupil ranged from yellowish-white and gold through brown, the latter often with a golden tinge. Sometimes the area below the line was darker or lighter than that above the line. The horizontal line itself was dark brown, frequently with a reddish cast.

Pattern elements that were almost universally present, albeit less well defined in some individuals, included a dark brown to black canthal line continuous with the line through the orbit and continuing as comparably dark supratympanic line set off by a lighter line passing through the tympanum. In most (34 of 43) individuals, an additional complete or broken dark subtympanic line was present under the lighter one. The ground colour of the dorsal and lateral fields, the top of the snout in front of the interorbital bar, and limbs ranged from grey and light brown to very dark brown, often with a yellowish, orange, or reddish cast. Dorsal ground colour was in most cases

the same as the lateral colour, but was occasionally darker or lighter. The top of the snout was usually lighter than the dorsum. Nine individuals from site 5 had middorsal lines, all of which were narrow, lighter than the dorsum, and split posteriorly to continue laterally onto the backs of the thighs. Dorsal chevrons, when present, were darker than the ground colour. Limbs varied in relation to dorsal and lateral colour and were variously marked with bars that were sometimes broken into stippling or dots. Toe pad colour was set off by a light (proximal) and dark band from the colour of the toe. Pads varied in colour from nearly white and light brown through dark brown, sometimes with a distinct reddish tinge. In most cases, colour was essentially similar to the colour of the toes. Most individuals had weak vertical bars on the upper lips, seven had distinct bars, whereas 12 had only specks or no dark markings whatsoever.

Females and males, respectively, of both species and from all sites were essentially equal in size and weight. As is common in frogs (Duellman & Trueb, 1986), females of both species and from all sites were significantly larger than males. Our samples of both species essentially corresponded to previously published descriptions (e.g., Schwartz & Henderson, 1991), although we found greater variation in dorsal ground colours and noted some previously undescribed variations and combinations of colour and pattern elements (e.g., yellow/orange dorsal and lateral colouration and transverse bars on the snout in *P. shrevei*, and variable light tympanic lines above dark subtympenic lines that may or may not be present, variation in extent and distinction of labial bars, and variability in the colour of toe pads in both species).

Despite belonging to deeply divergent clades, both *P. shrevei* and *E. johnstonei* share many similar characteristics and are both exceedingly variable in colour and pattern, often rendering the distinction between them superficially difficult. The easiest way to distinguish one species from the other is by means of the consistently present reddish coloration on the ventral side of the hindlimbs in *P. shrevei* (Schwartz & Henderson, 1991).

Both species remain abundant, although the distribution of *P. shrevei* was restricted to higher elevations, where *E. johnstonei* was less frequently encountered (C. A. Rodríguez Gómez, pers. comm.). The former may once have been found in forests throughout the island, only to have been displaced to at least some extent from the lowlands by deforestation for agricultural purposes during the colonial era, with the subsequent introduction of *E. johnstonei* facilitating that process. Specimens of closely related *P. euphronides* on Grenada were collected historically from areas where the species is no longer found (e.g., Schwartz & Henderson, 1991; Kaiser *et al.*, 1994); this may provide some support for the contention that both *P. euphronides* and *P. shrevei* were once more widely distributed on their respective islands. However, suspect locality data may render that evidence inconclusive (many specimens originating on islands prior to the onset of the 20th century were attributed to the major ports from which they were shipped; e.g., Dixon, 1981).

Pattern Element	Site (Sample Size)		
	1 (5)	2 (20)	Total (25)
Dorsal Colour			
Darker than side	0	8	8
Lighter than side	1	3	4
Same as side	4	9	13
Colour Top of Snout			
Lighter than dorsum	4	17	21
Same as dorsum	1	3	4
Colour of Toe Pads			
Darker than toes	4	16	20
Lighter than toe	1	0	1
Same as toe	0	4	4
Dorsolateral Lines			
Darker than dorsum	0	1	1
Lighter than dorsum	0	7	7
Absent	5	12	17
Dorsum			
Mottled	1	1	2
Uniform	4	19	23
Dorsal Chevrons			
Two	2	13	15
One	1	3	4
Absent	2	4	6
Bars on Hindlimbs			
Distinct	2	15	17
Broken	2	5	7
Absent	1	0	1
Bars on Forelimbs			
Distinct	2	12	14
Broken	2	7	9
Absent	1	1	2
Subtympenic Line			
Present	0	2	2
Broken	0	1	1
Weak	0	2	2
Absent	5	16	21
Bars on Lips			
Present	3	12	15
Weak	1	7	8
Specks	1	2	3

Table 2. Frequencies of pattern elements in *Pristimantis shrevei* from two sites on St. Vincent. Site 1 = La Soufrière Volcano Trail (961 m); 2 = "Upper" Vermont Nature Trail (natural forest, 411 m).

Eleutherodactylus johnstonei has effectively colonised the island, and is phenomenally abundant in many areas, especially in more dramatically altered lowland habitats. During the 20 days we spent on St. Vincent, we were never out of earshot of calling *E. johnstonei* at night, although the relatively few

Pattern Element	Site and Sample Size				
	2 (3)	3 (2)	4 (18)	5 (20)	Total (43)
Dorsal Colour					
Darker than sides	0	0	4	3	7
Lighter than sides	2	2	4	3	11
Same as sides	1	0	10	14	25
Colour Top of Snout					
Darker than dorsum	1	0	2	1	4
Lighter than dorsum	1	0	10	12	23
Same as dorsum	1	2	6	7	16
Colour of Toe Pads					
Darker than toes	1	0	3	4	8
Lighter than toes	1	0	6	7	14
Same as toes	1	2	9	9	21
Dorsolateral Lines					
Lighter than dorsum	0	0	8	1	9
Absent	3	2	10	19	34
Dorsum					
Mottled	3	0	6	8	17
Uniform	0	2	12	12	26
Dorsal Chevrons					
Two	1	0	2	12	15
One	1	0	11	6	18
Absent	1	2	5	2	10
Bars on Hindlimbs					
Distinct	1	0	9	5	15
Broken	2	1	8	10	21
Absent	0	1	1	5	7
Bars on Forelimbs					
Distinct	0	0	6	7	13
Broken	2	1	9	7	19
Absent	1	1	3	6	11
Interorbital Bar					
Full	2	0	13	8	23
Broken	1	0	2	6	9
Absent	0	2	3	6	11
Subtympanic Line					
Present	0	0	3	8	11
Broken	0	2	11	10	23
Absent	3	0	4	2	9
Bars on Lips					
Present	1	0	4	2	7
Weak	2	1	12	10	24
Specks	0	0	2	4	6
Absent	0	1	1	4	6

Table 3. Frequencies of pattern elements in *Eleutherodactylus johnstonei* from four sites on St. Vincent. Site 2 = "Upper" Vermont Nature Trail (natural forest, 411 m); site 3 = Hermitage (natural forest, 342 m); site 4 = "lower" Vermont Nature Trail (plantation forest, 297 m); site 5 = Bambareaux Beach (lowland forest, < 10 m).

individuals at the higher elevations on La Soufrière were inconspicuous among the much more numerous *P. shrevei*. We also frequently heard *E. johnstonei* singing by day in sheltered locations in dense forest, streambeds, leaf litter, and even in urban alleys. In contrast, we heard calling *P. shrevei* only in the evenings (18:00–21:30 h).

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Notes on the poorly known colubrid snake *Rhadinaea anachoreta* Smith & Campbell

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SMITH & Campbell (1994) described *Rhadinaea anachoreta* from two localities in the Sierra de Caral and Sierra de Santa Cruz of northeastern Guatemala. That description was based on two adult males and one adult female, one of which was “badly mutilated.” Campbell (1998) reported the species from Tikal, in the northern Petén of Guatemala, but did not mention the number or sex of the specimens from that locality. Campbell (1998) increased the known range of ventrals from 139 to 151 from over that of 139 to 147 given by Smith & Campbell (1994), but all of his other data were the same as that given by Smith & Campbell. Campbell’s (1998) colour description appears to

be taken from a preserved specimen, as was the colour description provided by Smith & Campbell (1994). Townsend *et al.* (2005) recorded the species from the department of Cortés in northwestern Honduras, based on one “desiccated” unsexed adult. All data provided by Townsend *et al.* (2005) are in agreement with the previously published data for the species. The only colour description of the Honduran specimen provided by Townsend *et al.* (2005) was also taken in preservative.

On 10th October 2006, I collected a specimen of *Rhadinaea anachoreta* in the top portion of a rotten tree stump about 0.5 m above the ground in a shade-tolerant coffee farm at Cerro Negro,