# Colour and pattern polymorphism in *Eleutherodactylus johnstonei* on Grenada

JENNIFER M. SANDER[1], JENNIFER M. GERMANO[2], ROBERT POWELL[3]*, and ROBERT W. HENDERSON[4]

[1] *Department of Natural Sciences and Mathematics, Lee University, Cleveland, TN 37320, USA*
[2] *School of Interdisciplinary Studies, Miami University, Oxford, OH 45056, USA*
3Department of Biology, Avila University, Kansas City, MO 64145, USA
[4] *Section of Vertebrate Zoology, Milwaukee Public Museum, Milwaukee, WI 53233, USA*
*corresponding author

THE genus *Eleutherodactylus* is the most species-rich vertebrate genus in the world, including more than 143 species currently known from the West Indies (Powell et al., 1996; Powell & Henderson, 1999). Two species occur on Grenada, one endemic (*E. euphronides*) and one introduced (*E. johnstonei*). The latter is a well-adapted coloniser and a resource generalist (Kaiser & Hardy, 1994). In addition to Grenada, this species is established on all of the major Lesser Antillean islands except Dominica. Other colonies are well established in various locales in Central and South America (Kaiser & Hardy, 1994).

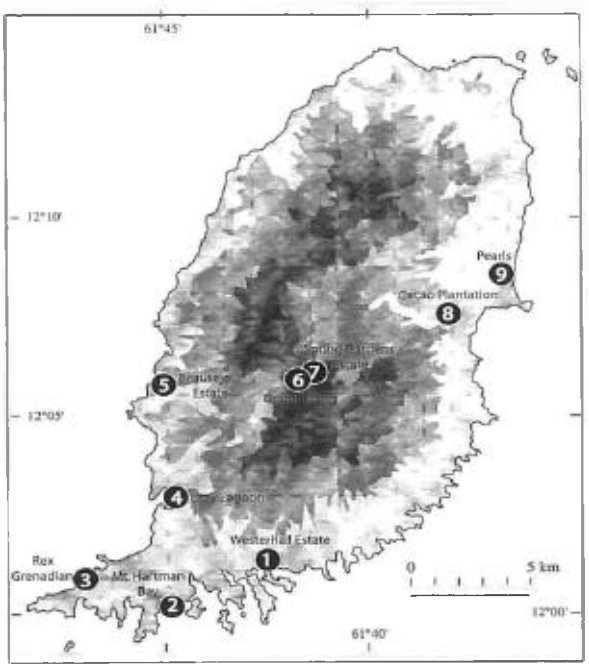


**Figure 1.** Map of Grenada showing collecting localities. Contour lines are at 120 m, 365 m, and 610 m.

Many species of *Eleutherodactylus* exhibit considerable colour and pattern polymorphism (e.g., Savage & Emerson, 1970; Sifers et al., 2001). Published descriptions of *E. johnstonei* include such phrases as: 'dorsal ground color brown to grayish tan; dorsal pattern variable but usually with at least 1 chevron (sometimes followed by a second) in scapular region; often with prominent dorsolateral stripes and/or pale median dorsal hairline; single crural crossbar bordered with paler color; no red on hindlimbs or groin ... venter creamy, often with stippling on throat; postanal triangle frequently present' (Schwartz & Henderson, 1991) and 'dorsal coloration is brown to grayish-brown, with a great variety of dorsal patterns. Most specimens have a scapular chevron, often in combination with one or more other pattern elements, such as a second chevron, a pale median hairline, or prominent pale dorsolateral stripes ... single crural crossbar, hidden surfaces of hindlimbs and groin irregularly patterned, but never colored red' (Kaiser & Hardy, 1994). Herein we quantify colour and pattern polymorphism from an ecological perspective.

We collected 146 *E. johnstonei* from nine different localities of varying elevations and habitats on Grenada from 5th–22nd June 2002. We examined eleven pattern characteristics: dorsal ground colour (quantified from pale to dark brown using a scale of 1-4), mottling on dorsum

(present or absent), middorsal line (present or absent), dorsolateral lines (present or absent, and colour on a scale of 1-4), number of scapular chevrons (0, 1, or 2), colour of chevrons in shades of brown (quantified from 1-4), interorbital bar (absent, broken, or full), canthal line (present or absent), supratympanic line (present or absent), ventral colour and pattern (light or dark and stippled or not), and colour of iris. We measured snout-vent length (SVL) to the nearest 0.5 mm. For those characters with three character states, we compared presumed genotypic frequencies to those expected at Hardy-Weinberg equilibrium. Most frogs were released at the exact site of collection, but voucher specimens from each locality were deposited in the Bobby Witcher Memorial Collection (BWMC) at Avila University (06880, 06884-06910, 06916-7, 06940-1, 06960, 06962-7). For all statistical tests, we used Statview 5.0 (SAS Institute, Cary, North Carolina); for all tests, $\alpha = 0.05$.

Collecting sites (Fig. 1) were: Site 1, a mixed agricultural/residential area at Westerhall Estate, 18 m above sea level (ASL); Site 2, a dry forest at Mt. Hartman Point, <5 m ASL; Site 3, a public beach area at the Rex Grenadian resort, <10 m ASL; Site 4, an urban area with decorative plantings and a weed-overgrown boundary fence at the Lazy Lagoon Guest House in St. George's, 9 m ASL; Site 5, a residential area, Beausejour Estate, 46 m ASL; Site 6, a relatively undisturbed rainforest at Grand Etang Forest Reserve, 544 m ASL; Site 7, a banana/nutmeg/cacao plantation at Spring Gardens Estate, 447 m ASL; Site 8, a cacao plantation monoculture near L'Esterre, 169 m ASL; and, Site 9, an area of mixed agriculture and forest remnants near the abandoned airport at Pearls, 12 m ASL. Because samples from sites 2 and 3 were very small, site-specific data are included in totals but were omitted from comparisons with other sites.

| Pattern Element | | Site Number (see Text), Sample Sizes in Parentheses | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 (13) | 2 (2) | 3 (1) | 4 (12) | 5 (30) | 6 (19) | 7 (29) | 8 (32) | 9 (8) | Total (146) |
| Dorsal Colour | Light | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 5 |
| | Medium-Light | 7 | 2 | 0 | 6 | 20 | 17 | 14 | 20 | 4 | 90 |
| | Medium-Dark | 3 | 0 | 1 | 5 | 3 | 2 | 13 | 10 | 4 | 46 |
| | Dark | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 5 |
| Number of Chevrons | 0 | 1 | 0 | 0 | 2 | 2 | 3 | 7 | 4 | 0 | 17 |
| | 1 | 5 | 0 | 0 | 7 | 22 | 10 | 17 | 20 | 4 | 87 |
| | 2 | 7 | 2 | 1 | 3 | 6 | 6 | 3 | 8 | 4 | 40 |
| Chevron Colour | Light | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Medium-Light | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| | Medium-Dark | 7 | 2 | 0 | 4 | 17 | 15 | 12 | 19 | 4 | 80 |
| | Dark | 5 | 0 | 1 | 7 | 9 | 1 | 8 | 9 | 4 | 44 |
| Interorbital Bar | Full | 9 | 2 | 1 | 6 | 26 | 13 | 17 | 21 | 6 | 101 |
| | Broken | 3 | 0 | 0 | 2 | 3 | 3 | 5 | 7 | 2 | 25 |
| | Absent | 1 | 0 | 0 | 4 | 1 | 3 | 5 | 4 | 0 | 18 |
| Dorsolateral Lines | Absent | 9 | 2 | 1 | 9 | 22 | 14 | 20 | 27 | 8 | 112 |
| | Present | 4 | 0 | 0 | 3 | 8 | 5 | 7 | 5 | 0 | 32 |
| Mottled Dorsum | No | 13 | 2 | 1 | 7 | 29 | 19 | 26 | 32 | 8 | 136 |
| | Yes | 0 | 0 | 0 | 5 | 1 | 0 | 1 | 0 | 0 | 7 |
| Middorsal Line | Absent | 12 | 0 | 1 | 12 | 3 | 5 | 20 | 27 | 8 | 115 |
| | Present | 1 | 2 | 0 | 0 | 0 | 14 | 7 | 5 | 0 | 29 |
| Dorsolateral Line Colour | Light | 2 | 0 | 0 | 1 | 5 | 2 | 1 | 0 | 0 | 11 |
| | Medium-Light | 1 | 0 | 0 | 2 | 2 | 1 | 1 | 2 | 0 | 9 |
| | Medium-Dark | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 |
| | Dark | 1 | 0 | 0 | 0 | 1 | 2 | 4 | 2 | 0 | 10 |

**Table 1.** Colour and pattern polymorphism in *Eleutherodactylus johnstonei* from Grenada.

Dorsal colour and pattern in *E. johnstonei* are extremely variable (Table 1, Fig. 2). Dorsal colour ranges from light to dark brown, and pattern elements change in colour, type, and distribution. Few characteristics are invariable: all of the frogs examined had dark brown canthal lines, dark brown supratympanic lines, a bronze upper iris, a pale and stippled venter, and all scapular chevrons were darker in colour than the dorsum. However, dorsolateral lines could be either lighter or darker than the dorsal ground colour, in contrast with statements in Kaiser & Hardy (1994). In the absence of scapular chevrons, dorsolateral lines

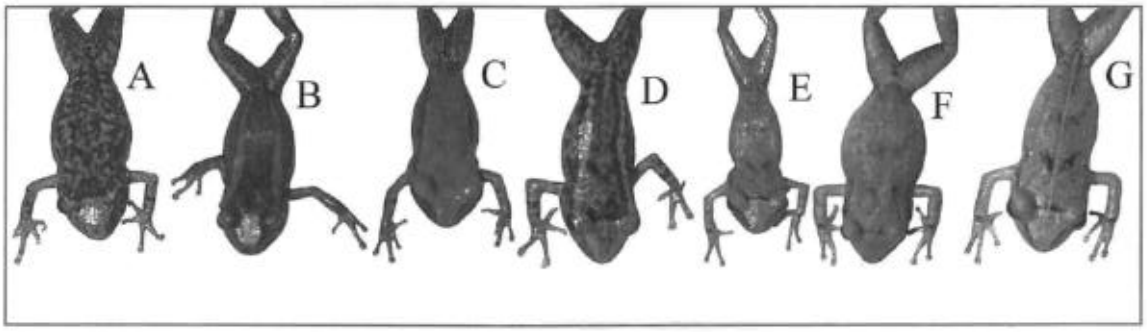


**Figure 2.** Representative pattern polymorphism in *Eleutherodactylus johnstonei* from Grenada (note that individuals are not figured in the same scale): A. site 4, SVL 24.0 mm, dorsal colour medium-dark, 1 dark chevron, interorbital line full, mottled dorsum; B. site 4, SVL 24.5 mm, dorsal colour medium-dark, chevrons absent, interorbital line absent, medium-dark dorsolateral lines; C. site 7, SVL 22.0 mm, dorsal colour medium-light, chevrons absent, interorbital line broken, medium-dark dorsolateral lines; D. site 4, SVL 17.5 mm, dorsal colour medium-light, 1 dark chevron, interorbital line full, medium-light dorsolateral lines, mottled dorsum; E. site 4, SVL 21.0 mm, dorsal colour light, 1 medium-dark chevron, interorbital line full; F. site 1, SVL 21.5 mm, dorsal colour medium-light, 1 medium-dark chevron, interorbital line full; G. site 1, SVL 19.5 mm, dorsal colour medium-light, 2 medium-dark chevrons, interorbital line full, middorsal line present.

were always present, although both were present in some individuals.

Only two characters were suitable for comparisons with expected Hardy-Weinberg frequencies. For number of chevrons, all frogs ($\chi^2 = 10.6$, $P = 0.05$) and frogs from sites 5 ($\chi^2 = 15.0$, $P = 0.0006$), 7 ($\chi^2 = 15.4$, $P = 0.0005$), and 8 ($\chi^2 = 7.0$, $P = 0.03$) differed significantly from expected values. For interorbital bar, all frogs ($\chi^2 = 24.4$, $P < 0.0001$) and frogs from sites 1 ($\chi^2 = 12.7$, $P = 0.002$), 5 ($\chi^2 = 19.0$, $P < 0.0001$), 6 ($\chi^2 = 20.4$, $P < 0.0001$), 7 ($\chi^2 = 10.0$, $P = 0.007$), and 8 ($\chi^2 = 18.1$, $P < 0.0001$) differed significantly from expected values.

An ANOVA revealed no significant variation (all $P > 0.05$) between animals collected at different sites, although pairwise comparisons (Fisher's PLSD) indicated that dorsolateral line colour frequencies at Beausejour and Pearls differed significantly ($P = 0.03$).

Contingency test comparisons of frequencies for each character state at each site with those for all sites suggested that significant differences were associated with small sample sizes, i.e., small samples were much more likely not to include rare character states. For example, two frogs at site 5 had light chevrons, which were not found at any other site. Frogs with pale markings also were pale in dorsal colour, suggesting the presence of a causative gene present only in the population at this site. Similarly, mottling as the primary pattern element was found only at site 4 (in five individuals), although indistinct mottling in addition to other primary pattern elements was present in two specimens from other sites.

*Eleutherodactylus johnstonei* is likely native to the Antigua Bank (Kaiser, 1997), but has occurred on some other Lesser Antillean islands for over a century. Grenada is the type locality for the species, but, according to Barbour (1914), it was introduced there from Barbados in about 1885. Thus, with the exception of Barbados, *E. johnstonei* has had a longer history on Grenada than on any other West Indian island onto which it has been introduced. Individuals on Grenada are extremely variable, and variability does not appear to be associated with habitats at various elevations and subjected to varying degrees of human disturbance. We have no basis for suggesting that Grenadian populations originated as a consequence of a single or of multiple invasion events, but the ecological versatility of the species has allowed it to exploit essentially all available habitats. During audio surveys conducted while driving from Pearls (site 9), over the central mountain range at elevations exceeding 500 m (site 6), to St. George's (site 4) and from

Westerhall Estate (site 1) to St. George's, we were out of earshot of calling *E. johnstonei* for only 20 sec as we passed through an all-concrete area of the city. Its ubiquity on the island (Germano et al., 2003) precludes any restriction of gene flow between populations that could result in local variation responding to localised selective pressures.

## ACKNOWLEDGEMENTS

Mr. Rolax Frederick, Department of Forestry and National Parks, Ministry of Agriculture, Lands, Forestry, and Fisheries was instrumental in granting us the appropriate permits to work in Grenada. Fieldwork was supported by Grant No. DBI-9732257, awarded by the National Science Foundation to RP.

## REFERENCES

Barbour, T. (1914). A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. *Mem. Mus. Comp. Zoöl.* **44**, 205-359.

Germano, J. M., Sander, J. M., Henderson, R. W. & Powell, R. (2003). Herpetofaunal communities in Grenada: a comparison of variously altered sites, with an annotated checklist of Grenadian amphibians and reptiles. *Carib. J. Sci.* **39**, 68-76.

Kaiser, H. (1997). Origins and introductions of the Caribbean frog, *Eleutherodactylus johnstonei* (Leptodactylidae): management and conservation concerns. *Biodiv. Conserv.* **6**, 1391-1407.

Kaiser, H. & Hardy, J. D., Jr. (1994). *Eleutherodactylus johnstonei. Cat. Amer. Amphib. Rept.*, No. 581.

Powell, R. & Henderson, R. W. (1999). Addenda to the checklist of West Indian amphibians and reptiles. *Herpetol. Rev.* **30**, 137-139.

Powell, R., Henderson, R. W., Adler, K. & Dundee, H. A. (1996). An annotated checklist of West Indian amphibians and reptiles. In *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*, pp. 51-93 + 8 pls. Powell, R. & Henderson, R. W. (eds.). Ithaca: *Soc. Study Amphib. Rept. Contrib. Herpetol.* Vol. 12.

Savage, J. M. & Emerson, S. B. (1970). Central American frogs allied to *Eleutherodactylus bransfordii* (Cope): a problem of polymorphism. *Copeia* **1970**, 623-644.

Schwartz, A. & Henderson, R. W. (1991). *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. Gainesville: Univ. Florida Press.

Sifers, S. M., Yeska, M. L. & Powell, R. (2001). *Eleutherodactylus abbotti*. Pattern polymorphism. *Herpetol. Rev.* **32**, 180-181.