The Grenada Frog (*Pristimantis euphronides*): An Endemic Species in Decline and the Combined Effects of Habitat Loss, Competition, and Chytridiomycosis

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The island of Grenada, West Indies is home to only two endemic terrestrial vertebrates, the Grenada Dove (*Leptotila wellsi*) and the Grenada Frog (*Pristimantis euphronides*). The Grenada Dove is featured on the national emblem and is considered to be a national treasure, while the Grenada Frog is virtually unknown to Grenadians. It is listed as Endangered on the IUCN Red List because of its limited range and competition with Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*). The invasive *E. johnstonei* is practically ubiquitous on the island. Its calls saturate Grenada's nights, and it is the frog with which most Grenadians are familiar.

Grenada is the southernmost island in the Lesser Antilles. It is approximately 311 km^2 and is the largest island on the Grenada Bank. In addition to *P. euphronides* and *E. johnstonei*, it is home to The Windward Island Ditch Frog (*Leptodactylus validus*) and the Cane Toad (*Rhinella marina*), both of which are introduced.

Pristimantis euphronides was formerly considered to be a member of the genus *Eleutherodactylus*, in part because one of the characters that defined that genus was that they are direct developers. Direct developers bypass the tadpole stage and develop directly into froglets inside of the egg. *Pristimantis euphronides* belongs to the recently erected family Strabomantidae (Hedges et al. 2008). Although the Strabomantidae are widely distributed in South and Central America, only two species are endemic to the West Indies, the Grenada Frog and the St. Vincent Frog

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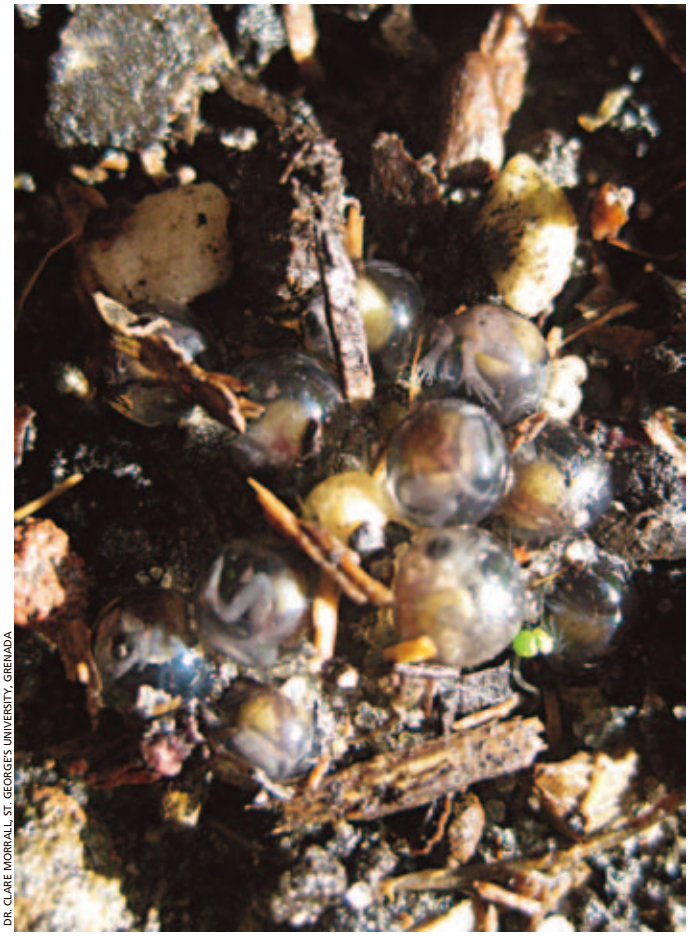
A Grenada Frog (*Pristimantis euphronides*) on Maidenhair Fern at Cable and Wireless.



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Direct-developing terrestrial eggs of Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*) — note the froglets in the eggs.

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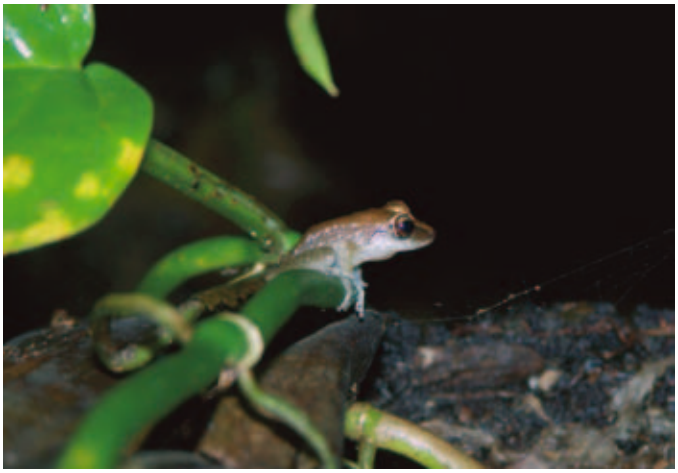
Hatchling Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*) — note the fingertips for scale.

(*Pristimantis shrevei*). The Grenada Frog is a relatively small frog; males attain a maximum snout-vent-length (SVL) of 27 mm, with an average of 22.7 mm. Females grow substantially larger, reaching 39.4 mm SVL with an average of 28.3 mm (Kaiser et al. 1994).

Pristimantis euphronides inhabits forests at altitudes over 300 m (Henderson and Berg 2006). Since 2004, we have surveyed five sites for the species and, to date, have never encountered this frog at an elevation below 400 m. However, this may be due to the fact that our sites are accessible by road and therefore are subject to disturbance, both today and in the past. In 1999, Hedges indicated that the distribution of this species was limited to an area of 16 km²; it is likely less than that now. Causes for habitat constriction include changes in land use patterns, competition with invasive *E. johnstonei* (Sander et al. 2003, Schwartz 1967), and the effects of Hurricane Ivan in 2004. The species probably was once more widespread on the island but, during the past 8,000 years, the forested areas of Grenada have shrunk by 70%, mostly due to anthropogenic changes (www.earthtrends.wri.org).

Barbour (1914) described *Eleutherodactylus johnstonei* based upon a specimen collected at St. George's and given to him by Robert S. Johnstone, the Chief Justice of Grenada. The genus *Eleutherodactylus* was until recently included in the family Leptodactylidae, but is now assigned to the family Eleutherodactylidae (Hedges et al. 2008). The geographic origin of this species is unknown, but is believed to be the Leeward Islands (Pregill et al. 1994, Kaiser 1997, Lescure 2000). Barbour (1914) indicated that it arrived on Grenada in 1885 from Barbados. That was likely to have been a noticeable introduction, as its call is loud and dissimilar to any other anuran or insect on the island. Within 50 years, *E. johnstonei* had reached Grand Etang, 10 km inland. Fifty years later, it was widespread across the island, absent only from cool, undisturbed, high-elevation forests. Today *E. johnstonei* can be found in moist and dry coastal areas to high-elevation rainforest or acacia scrub. The species thrives across a broad range of altitudes, temperature regimes, vegetational communities, and levels of human disturbance. These invaders readily occupy houses and exploit cisterns that residents use for water storage during the dry season. Grenadians today con-



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A Grenada Frog (*Pristimantis euphronides*) at Les Avocats in 2010.

CRAIG S. BERG

Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*) generates a piercing call that reaches 91 decibels, roughly the volume of a lawnmower.

sider *E. johnstonei* a nuisance, largely attributable to its shrill call (other frog species on the island have less raucous calls). Its call is two-tone, one note at 2,000 Hz and another ascending note from 2,000–3,500 Hz (see fig. 1 in Watkins et al. 1970). The call reaches 91 decibels, roughly the volume of a lawnmower (Tárano and Fuenmayor 2009) and individuals can emit as many as 60 calls per minute (Kaiser and Hardy 1994).

One of the most widely distributed amphibians in the world, *Eleutherodactylus johnstonei* is third only to the Bullfrog (*Lithobates catesbeianus*) and the Cane Toad (*Rhinella marina*; Kaiser 1997; Kraus 2009; amphibiaweb.org) in size of total range. It has successfully invaded many different habitat types in the greater Caribbean (where it is known from 28 islands or island groups; Powell et al. 2011) and on mainland Central and South America. Before the 1970s, these frogs were found principally on islands that were British protectorates. The dissolution of the protectorates opened new trade routes between islands and greatly accelerated the frog's dispersal. Shipments of plants are frequently cited as sources of inadvertent introductions (e.g., Kraus et al. 1999, Hodge et al. 2003, Powell et al. 2011).

Eleutherodactylus johnstonei possesses many traits that might provide it with a competitive advantage over *P. euphronides* in disturbed habitats, whether anthropogenic or natural. Kaiser et al. (1994) hypothesized that competition with Johnstone's Whistling Frog was causing a range reduction of the Grenada Frog. In 2004, surveys were initiated to determine if, indeed, *P. euphronides* was in decline and, if so, the proximate causes of the decline. An additional goal was an attempt to detect any drastic decreases in frog populations that might be associated with the arrival of amphibian chytrid fungus on Grenada.

Materials and Methods

Since February 2004, we have been monitoring established survey sites by walking timed transects. We conduct 30-minute searches along 100-m transects. Each 100-m transect is divided into ten 10-m sections to facilitate a near constant survey pace. All surfaces within 2 m of the transect are scanned for frogs. We record species, age class, sex (if known), perch type and height, and section number within the transect. This allows us to compare frog numbers and species ratios at different sites and make same-site comparisons on a year-to-year basis. Microhabitat parameters are monitored by data-loggers that record soil surface temperature (Tidbit v2; www.onsetcomp.com), and air temperature/relative humidity (HOBO Pro v2; www.onsetcomp.com) at our survey sites. To date, five sites have been surveyed following this protocol, but only three sites (Grand Etang, Les Avocats, and Cable and Wireless) are currently being monitored. Each site was selected because it represented a distinct habitat type.

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Habitat at Grand Etang immediately after Hurricane Ivan in 2004 (top) and today (February 2011).

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Map of Grenada indicating localities mentioned in the text. Contour lines are at 120 m, 365 m, and 610 m.

Grand Etang National Park (St. Andrew Parish; 525 m).—Grand Etang is the type locality for the Grenada Frog. Hurricane Ivan devastated the forest along the mountain crest. Trees were snapped off at their trunks or completely uprooted. What was once a closed-canopy forest with many trees and tree ferns (*Cyathea* sp.) attaining heights of 30 m (Beard 1949) became an open and sun-drenched landscape. Ferns and tree ferns are to this day a major component of the flora, but Razor and Saber grasses (*Scleria* sp.), which were rare prior to Hurricane Ivan, now cover substantial portions of the forest floor. This site is bathed, almost nightly, by a mist formed from condensation as warm, moist tradewinds emanating from the Atlantic Ocean move up slope into the cool night air of Grenada's mountain ranges. Rain can be expected almost nightly, especially during the wet season.

Cable and Wireless Station (St. Andrew Parish; 705 m).—Cable and Wireless was considered to be a Grenada Frog bastion and one of a few places on the island where the topography is too treacherous to be cleared for agriculture (Kaiser and Henderson 1994, Sander et al. 2003, Henderson

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The moist upland forests at the Cable and Wireless station, one of a few places on the island where the topography is too treacherous to be cleared for agriculture.

and Berg 2006). Prior to Hurricane Ivan, the flora was composed of broadleaf trees and shrubs, tree ferns (*Cyathea* sp.), and other ferns. Today the vegetation is predominantly Saber Grass (*Scleria* sp.) and ferns. Because the elevation of this site is 175 m higher than Grand Etang, the air is cooler and rains or mists are nightly events.

Les Avocats Water Works (St. Davids Parish; 400 m).—Although Les Avocats is part of Grand Etang National Park, it is located between two mountain ridges that protected it from the full onslaught of Hurricane Ivan. Consequently, the forest at Les Avocats has retained most of its canopy. The ridges also hinder the development of the mists that blanket the other two sites. Tree ferns (*Cyathea* sp.) are rare; Bamboo (*Bambusa vulgaris*) and *Heliconia* sp. are common. Razor and Saber grasses (*Scleria* sp.) are absent.

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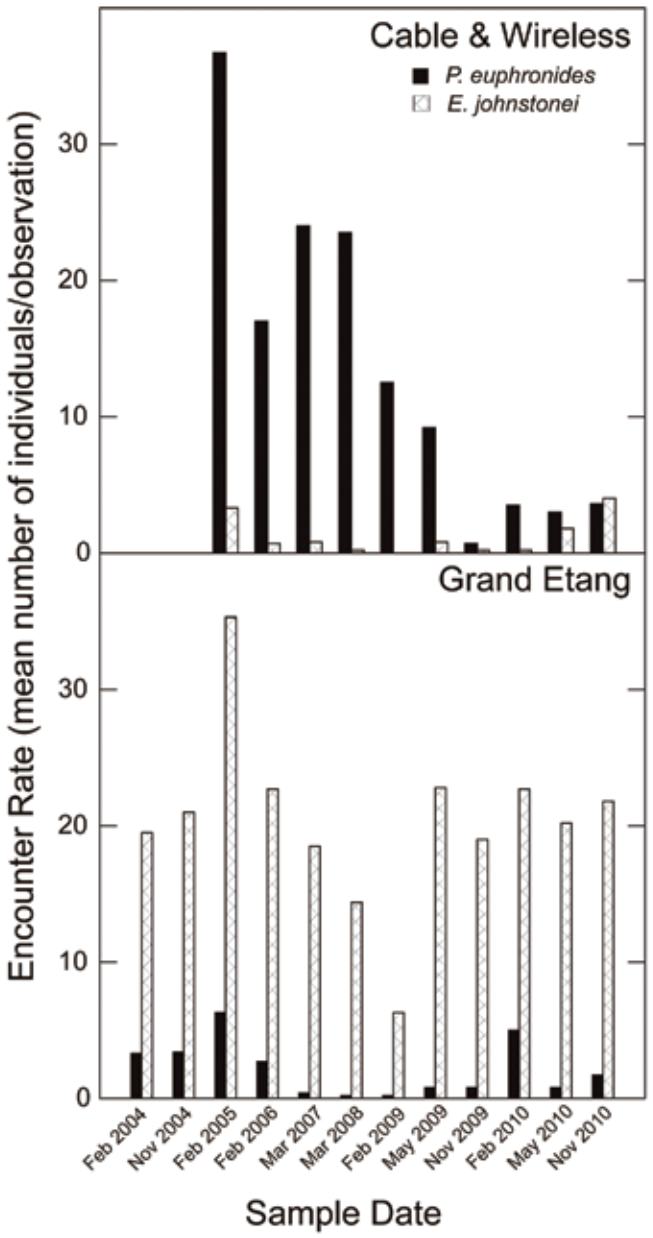
The senior author recording data on a Grenada Frog (*Pristimantis euphronides*) at Les Avocats.

Results

Results of our surveys show a decline in populations of *Pristimantis euphronides* and *Eleutherodactylus johnstonei*. The decline has been relatively consistent, occurring during both wet years and those of extreme drought. Amphibian populations are known to vacillate with environmental conditions, prey availability, and breeding-site availability. However, in hot and dry conditions, populations of *P. euphronides* declined whereas those of *E. johnstonei* maintained relatively stable numbers. The most remarkable decline was at Cable and Wireless, where environmental conditions are the most stable. This trend fits the pattern of declines attributable to pathogens.

We began to suspect that the deadly fungus *Batrachochytrium dendrobatidis* was contributing to declines in *P. euphronides*. In May 2009, we swabbed frogs, taking 80 samples from three species (Johnstone's Whistling Frog, Grenada Frog, Windward Island Ditch Frog) at four locations. Chytrid was found at all four sites and in all three species. It likely poses the most severe and imminent threat to the Grenada Frog, which is found only at high elevations where temperature and moisture regimes are ideal for the chytrid fungus.

Evidence of frog declines first emerged at Grand Etang in 2007, followed by a decline at Les Avocats in 2008 and at Cable and Wireless in 2009. This pattern would be expected of a pathogen arriving at a Grenadian



MIKE PAUERS

Graph showing encounter rates of Grenada Frogs (*Pristimantis euphronides*) and Johnstone's Whistling Frogs (*Eleutherodactylus johnstonei*) at two localities on Grenada between 2004 and 2010.

port, as the road that runs past our survey site at Grand Etang is the main road connecting Grenada's two major ports, St. George's and Grenville. This same road also brings busloads of tourists from cruise ships to view Grand Etang and walk along its forest trails. So, chytrid arriving via inter-island commerce (horticultural specimens, hitch-hiking frogs, construction materials, etc.) or in the mud-caked boots of eco-tourists would quickly be transported to and through Grand Etang. The frogs at Grand Etang and Les Avocats likely belong to the same meta-population and, if that is so, any pathogen infecting animals at Grand Etang would later appear at Les Avocats. Eventually, chytrid would make its way to Cable and Wireless.

We continue to collect samples from populations across the island in an effort to map the range of this deadly amphibian fungus. Most recently, we collected samples from the forest reserve at Mt. Stanhope. With combined stressors such as drought, habitat loss, reduced canopy cover, and competition with *E. johnstonei*, *P. euphronides* might not be able to withstand the additional pressure imposed by exposure to the chytrid fungus.

Discussion

Several traits would likely provide *Eleutherodactylus johnstonei* with a competitive advantage over *Pristimantis euphronides* in disturbed habitats. Johnstone's Whistling Frogs have exhibited tolerance of extreme temperature variation and desiccation. In a study of *Eleutherodactylus* on Jamaica, the introduced Johnstone's Whistling Frogs survived at temperatures to 40 °C and a 40% loss of their initial weight in water; by comparison, Jamaican endemics did not show comparable tolerances (Pough et al. 1977).

Direct developers do not rely on pools of water for ovopositioning sites, but rather sites that will remain moist throughout the developmental period. In the case of *E. johnstonei*, the female lays clutches of 5–30 eggs, which are typically attended by the male until hatching. During dry periods, the male grasps and broods the clutch. This action limits desiccation throughout development. Hatching occurs after 14–21 days. Because the male usually remains with the egg mass, females are free to feed and build the metabolic reserves necessary to produce another clutch of eggs. Clutches of *P. euphronides* are protected by the female until hatching. Because female *P. euphronides* have not been observed to feed (CSB, pers. obs.) while brooding, they need to build reserves necessary for producing another clutch. This difference in parental care could give *E. johnstonei* a reproductive advantage over *P. euphronides*.

Both species retreat beneath leaf litter and crevices in the substrate to avoid desiccation. These sites are used as diurnal retreats and during breeding and ovipositing. Eleutherodactylids vigorously protect nesting sites against other frogs (e.g., Townsend 1984, Bourne 1997). Both species would compete for appropriate ovopositioning sites (Lips and Donnelly 2005), and retreat availability is a limiting factor in eleutherodactylid population size (Stewart and Pough 1983).

In captivity, *P. euphronides* digs holes into the substrate whereas *E. johnstonei* does not (CSB, pers obs.). The soil at Les Avocats and Grand Etang consists of heavy clay, which is practically impenetrable. During the dry season, frogs must compete for available cavities, which are restricted to those that are formed naturally. The substrate at Cable and Wireless is composed of a thick layer of moss-covered decaying vegetation that enables *P. euphronides* to burrow. Because *P. euphronides* is able to dig into the substrate at Cable and Wireless, it does not need to compete with *E. johnstonei* for diurnal retreats and/or ovopositioning sites. At Les Avocats and Grand Etang, the numbers of *E. johnstonei* greatly exceed the numbers of *P. euphronides* and thus would likely swamp available ovoposition sites.

Eleutherodactylus johnstonei is known to share cover objects (Ovaska 1991) and may share them with *P. euphronides*. *Pristimantis euphronides* and *E. johnstonei* have been observed perching on the same plants and even on the same leaf (e.g., Germano et al. 2003). This close proximity could

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A Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*) in a natural crevice at Les Avocats.

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A female Grenada Frog (*Pristimantis euphronides*) attending a clutch of eggs.

indicate that the two species do not recognize each other as direct competitors for perch sites or prey. Close proximity is, however, likely to aid the transmission of chytrid.

Implications for Grenada and Other Islands

Insular endemics such as the Grenada Frog often rely on undisturbed forested areas. As of 2000, Grenada had lost 70% of its forests to agriculture or development. Managing for endemics may no longer be practical or possible without also protecting appropriate habitat. Assurance colonies can be maintained in *ex-situ* institutions, but the number of amphibian species requiring such efforts greatly exceeds the number of institutions that have the resources necessary to maintain bio-secure holding facilities. In order to ensure that threatened fauna survive in perpetuity, collaborative efforts on behalf of all stakeholders are necessary. Conservation action plans need to be developed to enable Caribbean forestry and wildlife departments to sustainably manage endangered ecosystems. Adequate training in amphibian biology and conservation initiatives is needed for local forestry/wildlife personnel.

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Literature Cited

Barbour, T. 1914. A contribution to the zoogeography of the West Indies with especial reference to amphibians and reptiles. *Memoirs of the Museum of Comparative Zoology* 44:209–359.

Beard, J.S. 1949. *Natural Vegetation of the Windward and Leeward Islands*. Oxford Forestry Memoirs No. 21. Clarendon Press, Oxford, England.

Bourne, G.R. 1977. Reproductive behavior of terrestrial breeding frogs *Eleutherodactylus johnstonei* in Guyana. *Journal of Herpetology* 31:221–229.

Germano, J.M., J.M. Sander, R.W. Henderson, and R. Powell. 2003. Herpetofaunal communities on Grenada: A comparison of altered sites, with an annotated checklist of Grenadian amphibians and reptiles. *Caribbean Journal of Science* 39:68–76.

Hedges, S.B. 1999. Distribution patterns of amphibians in the West Indies, pp. 211–254. In: W.E. Duellman (ed.), *Patterns of Distribution of Amphibians.* The Johns Hopkins University Press, Baltimore, Maryland.

Hedges S.B., W.E. Duellman, and M.P. Heinicke. 2008. New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa* (1737):1–182.

Henderson, R.W. and C.S. Berg. 2006. The herpetofauna of Grenada and the Grenada Grenadines: Conservation concerns. *Applied Herpetology* 3:197–213.

Hodge, K.V.D., E. J. Censky, and R. Powell. 2003. *The Reptiles and Amphibians of Anguilla, British West Indies*. The Valley Anguilla Trust.

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A Johnstone's Whistling Frog (*Eleutherodactylus johnstonei*) taking a meal.

Kaiser, H. 1997. Origins and introductions of the Caribbean frog, *Eleutherodactylus johnstonei* (Leptodactylidae): Management and conservation concerns. *Biodiversity and Conservation* 6:1391–1407.

Kaiser, H. and J.D. Hardy, Jr. 1994. *Eleutherodactylus johnstonei*. *Catalogue of American Amphibians and Reptiles* (581):1–5.

Kaiser, H. and R.W. Henderson. 1994. The conservation status of lesser Antillean frogs. *Herpetological Natural History* 2(2):41–56.

Kaiser, H., J.E. Hardy, and D.M. Green. 1994. Taxonomic status of Caribbean and South American frogs currently ascribed to *Eleutherodactylus urichi* (Anura: Leptodactylidae). *Copeia* 1994:780–796.

Kraus, F. 2009. *Alien Reptiles and Amphibians: A Scientific Compendium and Analysis*. Invading Nature: Springer Series in Invasion Biology 4. Springer, New York.

Kraus, F., E.W. Campbell, A. Allison, and T. Pratt. 1999. *Eleutherodactylus* frog introductions to Hawaii. *Herpetological Review* 30:21–25.

Lescure, J. 2000. Répartition passée de *Leptodactylus fallax* Müller, 1923 et d'*Eleutherodactylus johnstonei* Barbour, 1914 (Anoures, Leptodacylidés). *Bulletin de la Societe Herpétologie de France* 94:13–23.

Lips, K.R. and M.A. Donnelly. 2005. Lessons from the tropics, pp. 198–205. In: W. Lannoo (ed.), *Amphibian Declines: The Conservation Status of United States Species*. University of California Press, Berkeley and London.

Ovaska, K. 1991. Reproductive phenology, population structure, and habitat use of the frog *Eleutherodactylus johnstonei* in Barbados, West Indies. *Journal of Herpetology* 25:424–430.

Pough, F.H., M.M. Stewart, and R.G. Thomas 1977. Physiological basis of habitat partitioning in Jamaican *Eleutherodactylus*. *Oecologia* 27:285–293.

Powell, R., R.W. Henderson, M.C. Farmer, A.C. Echternacht, G. van Buurt, C.M. Romagosa, and G. Perry. 2011. Introduced amphibians and reptiles in the Greater Caribbean: Patterns of arrival and resulting distributions, pp. 63–143. In: A. Hailey, B. Wilson, and J. Horrocks (eds.), *Conservation of Caribbean Island Herpetofaunas*. Volume 1. Brill, Leiden, The Netherlands.

Pregill, G.K., D.W. Steadman, and D.R. Watters. 1994. Late Quaternary vertebrate faunas of the Lesser Antilles: Historical components of Caribbean biogeography. *Bulletin of the Carnegie Museum of Natural History* 30:iv + 55 pp.

Sander, J.M., H. Kaiser, and R. Powell. 2003. *Eleutherodactylus euphronides*. *Catalogue of American Amphibians and Reptiles* (764):1–3.

Schwartz, A. 1967. Frogs of the genus *Eleutherodactylus* in the Lesser Antilles. *Studies on the Fauna of Curaçao and Other Caribbean Islands* 24:1–62.

Stewart, M.M. and F.H. Pough. 1983. Population density of tropical forest frogs: Relationship to retreat sites. *Science* 221:570–572.

Tárano, Z. and E. Fuenmayor. 2009. Calling patterns in male responses to conspecific playbacks in the Johnstone's Whistling Frog *Eleutherodactylus johnstonei*. *Ethology* 115:747–757.

Townsend, D.S., M.M. Stewart, and F.H. Pough. 1984. Male parental care and its adaptive significance in a Neotropical frog. *Animal Behavior* 32:421–431.

Watkins, W.A., E.R. Baylor, and A.T. Bowen. 1970. The call of *Eleutherodactylus johnstonei*, the Whistling Frog of Bermuda. *Copeia* 1970:558–561.

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Group amplexing of large clusters (to >20 individuals) of Dennys' Treefrog (*Rhacophorus dennysi*) in Conghua, 150 km northeast of Dinghushan in March 2008, Guangdong Province, China.