Frogs of Dominica, with notes on habitat use by two species of *Eleutherodactylus*

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ABSTRACT - One species of *Leptodactylu*s and three species of *Eleutherodactylus* have been recorded from Dominica, a Lesser Antillean island of recent volcanic origin. The Mountain Chicken Frog (*Leptodactylus fallax*) is native and listed on the IUCN Red List as "critically endangered" due mainly to overhunting, habitat loss, and the effects of chytridiomycosis. *Eleutherodactylus amplinympha* and *E. martinicensis* are native, and the former is an island endemic. *Eleutherodactylus johnstonei* is invasive and thought to have arrived on the island in the aftermath of Hurricane David in 1979. However, it has not been found during recent surveys. Using timed 50- and 100-m transects, we surveyed five sites at different elevations and subjected to varying levels of human and natural disturbances to assess frog numbers, microhabitat associations, and perch heights. Both *E. amplinympha* and *E. martinicensis* used available habitat, demonstrating no apparent bias for particular perches or microhabitats. Both species are polymorphic, but no variation in colour or pattern appears to be specific to either species.

DOMINICA, with a topography dominated by nine currently dormant volcanoes, is one of the Windward Islands in the Lesser Antilles. Although monocultures such as banana (*Musa*) and coconut (*Cocos*) are abundant, natural island habitats are proportionately more abundant than on any other West Indian island. This is largely attributable to the lack of level lowlands suitable for sugar plantations and the prevalence of steep slopes that preclude most agriculture (bananas are a notable exception). Natural areas as well as those disturbed by human activities, provide habitats for the 20 species of terrestrial frogs and reptiles known to occur on the island (Malhotra & Thorpe, 1999; Malhotra et al., 2007; Daniells et al., 2008).

Four species of frogs have been recorded from Dominica. *Leptodactylus fallax* (Leptodactylidae; Fig. 1), locally known as the Crapaud or Mountain Chicken, is native. The species also occurs on Montserrat, and once may have occurred on St. Christopher (Johnson, 1988), Guadeloupe, Martinique, St. Lucia, and St. Kitts (Gibson & Buley, 2004). Because of its large size (maximum male SVL 158.7 mm, [Heyer, 1979]; maximum female SVL 210 mm, [Daltry & Gray, 1999]), Mountain Chickens are hunted for food and considered to be delicacies, especially among tourists (Fa et al., 2004). The IUCN Red List designates the species as "critically endangered" (Fa et al., 2004) due to declining populations attributable to over-hunting, anthropogenic habitat losses, volcanic eruptions, hurricanes, and effects of chytridiomycosis (Kaiser & Day, 1995; Fa et al., 2004). On Dominica, this fungal disease reduced populations by 70% between 2002 and 2004 (ZSL, 2008).

Three species of *Eleutherodactylus* (Eleutherodactylidae) have been reported on Dominica. Like most *Eleutherodactylus*, they are small brown frogs characterised by dark canthal and supratympanic lines or bars, light and dark banding on the hindlegs, and two- or three-note rising whistle-like calls. The three species known from Dominica are part of a monophyletic group of Greater Antillean origin and are one another's

closest relatives (Kaiser et al., 1994a). All are highly polymorphic and can be difficult to distinguish without genetic evidence.

Eleutherodactylus martinicensis (Fig. 2), locally called Tink Frogs, have tubercles on dorsal surfaces, pink on the inner thighs and venters, slender bodies, and relatively small toepads. Males have bi-lobed glandular vocal sacs and produce a two-note call, which is almost indistinguishable from that of *E. johnstonei* (Kaiser, pers. comm.; Malhotra & Thorpe, 1999). Malhotra & Thorpe (1999) also indicated that *E. martinicensis* has a stippled venter and distinctly spotted throat, but ventral stippling is evident on both *E. martinicensis* and *E. amplinympha* when exposed to daylight (when frogs generally appear to be much darker), but disappears at night (Kaiser et al., 1994a; pers. obs.). The largest recorded male and female were 32 and 47 mm SVL, respectively (Kaiser & Hardy, 1994b). The species is considered native (Hedges et al., 2004a) and is abundant on Dominica. It can be found in disturbed as well as pristine habitats (Ackley et al., 2009), including rainforests, dry woodlands, banana and coconut plantations, gardens, and along streams and roadsides in both lowland and upland areas from sea level to 1,250 m (Henderson & Powell, 2009). Despite this, the IUCN Red List classifies *E. martinicensis* as "near threatened" (Hedges et al., 2004a) because it inhabits less than 5,000 Km^2 and because of the threat of invasive predators, such as cats, rats, and mongooses (which have not become established on Dominica), the effects of pesticides, and possible competition from *E. johnstonei*.

Eleutherodactylus amplinympha (Fig. 3) was first recorded as a species distinct from *E. martinicensis* in 1992 (Kaiser & Henderson, 1994), but was not formally described until 1994 (Kaiser et al., 1994a). The species is endemic to Dominica, where it is called the Gounouj. These frogs have slender bodies, pointed snouts, relatively long hind limbs, and comparatively large toepads. Males have bi-lobed glandular vocal sacs and produce a three-note rising call. The largest recorded male is 26.4 mm SVL. Females often exceed 35 mm SVL (Kaiser et al., 1994a) and the largest female recorded had a SVL >50 mm (Malhotra & Thorpe, 1999). The species is restricted to montane habitats at elevations of 300-1,200 m (Hedges, 1999) and are most abundant at elevations over 700 m in rain and cloud forests, palm brakes, and moss mats on the slopes of Morne Diablotin (Kaiser & Henderson, 1994) and Morne Macaque (Kaiser et al., 1994a). Because of its restricted distribution, high probability of habitat decline due to human expansion, hurricanes, and volcanism, the species is listed as "endangered" on the IUCN Red List (Hedges & Powell, 2004).

Eleutherodactylus johnstonei has a smooth dorsal surface, rounded snout, and relatively small toepads. Males have single-lobed glandular vocal sacs and produce a two-note call (Kaiser, pers. comm.; Malhotra & Thorpe, 1999). The largest male and female snout-vent lengths (SVL) recorded are 25 mm and 35 mm, respectively (Kaiser & Hardy, 1994a). These frogs are often associated with disturbed habitats and artificial sites that include roadsides, gardens, plantations, and open areas cleared by hurricanes from sea level to ~1,300 m (Henderson & Powell, 2009). These frogs are remarkable colonisers, with populations on many Lesser Antillean islands as well as Jamaica, Bermuda, Trinidad, Curaçao, and the Neotropical mainland (e.g., Lever, 2003). This species is considered introduced on Dominica. Crombie (in Kaiser, 1992) proposed that the species arrived on the island after Hurricane David in 1979. Johnson (1988) noted the severe damage caused by the hurricane, which presumably provided the disturbed areas *E. johnstonei* exploited during colonisation. Because amphibians are generally intolerant of exposure to salt water, Kaiser (1992) stated that the species probably was not transported by the hurricane. More likely, Dominican *E. johnstonei* arrived as stowaways among vegetables and other supplies from neighbouring islands that were providing aid (Kaiser, 1997). Uncertainty about the origin of these Dominican frogs presumably led Hedges et al. (2004b) to list *E. johnstonei* as a native Dominican species on the IUCN Red List. On some islands, populations established in lowland habitats that have been disturbed by human activity have expanded into more pristine habitats at higher elevations. On St. Vincent (Mallery et al., 2007) and Grenada (Germano et al., 2003) in particular, these frogs have become ubiquitous

Leptodactylus fallax.
Photograph © Arlington James.

Leptodactylus fallax.
Photograph © Jeffrey W. Ackley.

Figure 1. *Leptodactylus fallax* (Leptodactylidae), locally known as the Crapaud or Mountain Chicken, is native to Dominica. Photograph © Arlington James.

Eleutherodactylus martinicensis.
Photograph © Robert Powell.

Eleutherodactylus martinicensis.
Photograph © Robert Powell.

Figure 2. *Eleutherodactylus martinicensis*, locally called Tink Frogs, are exceedingly variable in colour and pattern. ▲▼ Photographs © Robert Powell. ▲

Eleutherodactylus martinicensis.
Photograph © Robert Powell.

Figure 3. *Eleutherodactylus amplinympha* is endemic to Dominica, where it is called the Gounouj.
Photograph © Robert Powell.

and may be displacing populations of endemic frogs, *Pristimantis shrevei* and *P. euphronides* (Kaiser, 1997). S.B. Hedges (in Johnson, 1988) also suggested that female *E. junori* on Jamaica have difficulty finding males because the calls of introduced *E. johnstonei* are so loud. However, introduced populations may have failed to become established on Dominica (Kaiser & Hardy, 1994a). The species has not been encountered during recent surveys (e.g., Quick, 2001; Alexander, 2007; A. James, pers. comm.) and is therefore no longer included by the Department of Forestry, Commonwealth of Dominica, on lists of Dominican species (A. James, in litt., 3.VIII.2008).

METHODS AND MATERIALS

From 6–22 June 2008, we surveyed frog numbers and microhabitat use along 1,000 m in 11 timed transects at five sites on the leeward slopes of Dominica (Fig. 4). We characterised microhabitat use by the perches on which frogs were observed within transects. We surveyed each of nine 100-m transects for 30 min and two 50-m transects for 15 min, sampling each transect twice on non-consecutive nights.

Site Descriptions

We described sites based on elevation, temperature and humidity data, variety of microhabitats, and levels of human disturbance. We used a HOBO® Tidbit® v2 Submersible Temperature Logger (accurate to 300 m) to record temperature at site 5 and HOBO® Temperature/RH Data Loggers U23-001 to record temperature and humidity data at sites 1 and 3-5.

Site 1 consisted of two 100-m transects within Syndicate Park Reserve in Morne Diablotin National Park (approximately 540 m above sea level). From 10-19 June 2008, mean temperature and relative humidity were 22.2 ± 1.0°C (19.7-26.7°C) and 94.0 ± 3.4% (80.3-98.4%), respectively. Based on the relatively sparse density of the canopy, the forest at this site was "young." Understorey growth consisted mainly of small broadleaf shrubs. *Selaginella* sp., bromeliads, and other epiphytes were abundant, as were woody debris and leaf litter. Human activity was largely restricted to established trails with a few wooden bridges, log steps, and signs. Disturbance was minimal.

Site 2 consisted of one 100-m and two 50-m transects in an agricultural field across a road from the entry to Syndicate Reserve. Elevation, mean temperature and relative humidity data are the same as for site 1. Almost all native trees had been cleared and the relatively open field planted with citrus and banana (most no more than 3 m tall) and pineapple. Patches of grassy and herbaceous growth (mostly dead) and piles of woody debris were scattered throughout the site. Evidence of pesticide use and other human disturbance was abundant. Plastic jugs (one of motor oil), extensive trenches, and a dirt road were present within the transects.

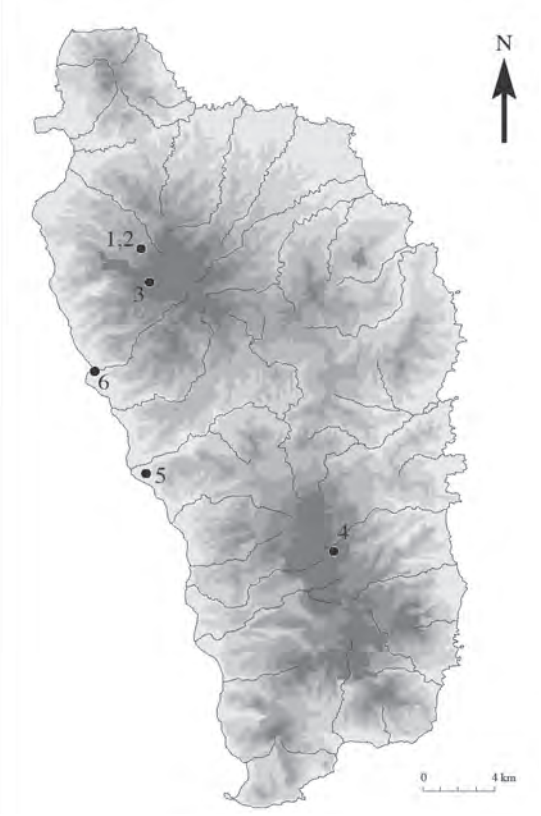

Figure 4. Map of Dominica showing locations of study sites (see text). Contour intervals = 300 m.

Site 3 consisted of two 100-m transects along the trail to Kachibona Lake in old-growth forest (approximately 755 m). From 8-23 June 2008, mean temperature and relative humidity were 21.5

± 1.5°C (18.9-28.0°C) and 88.1 ± 7.6% (66.2-98.4%), respectively. Topography was decidedly uneven, with both steeply sloped (ca. 30°) and relatively level sections. Canopy was nearly complete and undergrowth was correspondingly sparse. The area was characterised by broadleaf shrubs, woody debris, leaf litter, exposed rocks and patches of bare soil, with the more level stretches also supporting scattered *Selaginella* sp., palms, ferns, broadleaf razor grass, and herbaceous growth. Human disturbance was minimal. Only a small path had been cleared and a few trees had been painted or otherwise marked to show the direction of the path.

Site 4 consisted of two 100-m transects along the trail to Boeri Lake in Morne Trois Pitons National Park (approximately 865 m). From 9-16 June 2008, mean temperature and relative humidity for the period sampled was 21.0 ± 0.8°C (18.7-24.3°C) and 98.4 ± 1.7% (91.6-99.9%), respectively. Abundant condensation allowed for lush vegetation such as bromeliads, other epiphytes, *Selaginella* sp., mosses, grassy and herbaceous growth, ferns, palms, *Heliconia* sp. and Ginger to grow along with trees and saplings and other broadleaf shrubs. Woody debris and leaf litter covered the substrate. Human disturbance was minimal. Log steps, ditches and signs served to identify a trail.

Site 5 consisted of two 100-m transects in a coconut (*Cocos nucifera*) grove at sea level. From 11-21 June 2008, mean temperature was 27.6 ± 2.7°C (23.0-33.0°C). From 17-21 June 2008, mean temperature and relative humidity within a husk pile (on which frogs were frequently encountered) were 25.2 ± 0.7°C (24.4-26.7°C) and 104.1%, respectively. Regularly spaced coconut trees and piles of *Cocos* debris (husks, fronds etc.) were interspersed by stands of grasses, scattered herbaceous growth and small (ca. 2 m) broadleaf shrubs. Evidence of human disturbance was abundant, with the cleared site paralleling the main coastal road.

Microhabitats

We identified six microhabitat categories: (1) broadleaves, (2) tree or sapling trunks, (3) ferns, (4) low herbaceous growth, (5) leaf litter, and (6) woody debris, each of which included different perch types. The broadleaf category included broadleaf shrubs, broadleaf razor grass, banana, bromeliads, other epiphytes, Ginger, *Heliconia* sp. and pineapple plants. The tree or sapling trunks category included trunks of trees (>10 cm diameter at breast height [DBH]), saplings (<10 cm DBH), tree ferns, and coconut (*Cocos*) palms. The ferns category included leaves and branches from both tree and ground ferns. The low herbaceous growth category included grassy and herbaceous growth, mosses, *Selaginella* sp., and ground orchids. The leaf litter category included leaf litter, coconut husks, soil, and rock. The woody debris category included dead branches, fallen logs, sticks and tree stumps. Not all elements in each microhabitat category were found at every site.

For all sites, we counted frogs only if seen. Due to the lush overhead microhabitat provided by bromeliads, other epiphytes, and ferns, especially at site 4, frog counts may have been overly conservative as several frogs were heard calling from unobservable elevated perches and were not included in our data. For statistical tests, we included only those data for frogs whose sex we could positively determine due to large body size or the presence of eggs (seen through the body wall) in females or male calling behaviour.

Size and Morphology

We collected frogs at sites 1 and 3-6 (Fig. 4). Site 6, along the Batali River, was at sea level and experienced regular human disturbances. For all frogs examined, we characterised pattern and colour, measured snout-vent length (SVL), head length (HL), head width (HW), eye diameter (ED), eye-narial distance (EN), diameter of the tympanum (TD), interorbital distance (IOD), femoral length (FL), tibial length (TL), length of the foot (LF), and fourth-toe length (FTL) using SPI 2000 dial calipers (Forestry Suppliers, Jackson, Michigan, USA) and Mitutoyo Absolute digimatic digital calipers (Mitutoyo America Corp., Elk Grove Village, Illinois, USA), and weight using an Ohaus HH 120D digital scale (Ohaus Corp., Pine Brook, New Jersey, USA) and Pesola 10-g and 30-g spring scales (Pesola AG, Baar, Switzerland). All data were log-transformed prior to statistical analyses. We used Statview 5.0 (SAS Institute, Cary, North

Carolina, USA) for all statistical tests. For all analyses, alpha = 0.05.

RESULTS AND DISCUSSION

Elevational Effects

We encountered only *E. amplinympha* along the trail to Boeri Lake (site 4), which was the highest elevation site sampled. We never observed *E. amplinympha* and *E. martinicensis* together, although a very few *E. amplinympha* were heard calling from the trail to Kachibona Lake (site 3). All frogs at sites 1, 2 and 5 were *E. martinicensis.* We encountered no *E. johnstonei*. This is consistent with other studies (Kaiser et al., 1994a, 1994b; Kaiser & Henderson, 1994; Malhotra & Thorpe, 1999; Evans & James, 1997; Alexander, 2007) that found *E. amplinympha* only in upland pristine habitats and *E. martinicensis*, more of an ecological generalist, abundant in both upland and lowland habitats, regardless of disturbance level. Our failure to encounter *E. johnstonei* is consistent with recent surveys (e.g. Quick, 2001; Alexander, 2007) and supports the conclusion that *E. johnstonei* failed to establish a permanent presence on Dominica.

Habitat Availability and Use

Frequencies of perch types did not differ significantly between any two sites (Wilcoxon Signed Rank, all $P \geq 0.35$). Frequencies of perch type use also did not differ significantly from frequencies of perch type availability at any site (Wilcoxon Signed Rank, all $P \geq 0.24$). Neither *E. amplinympha* nor *E. martinicensis* appeared to favour any particular perches. At site 1, nine of 15 frogs were on broadleaves at heights of 0.50-1.75 m and four were on tree or sapling trunks at heights of 0.25-1.67 m. At site 2, five of six frogs were on broadleaves at heights of 0.25-2.00 m. At site 3, 10 of 31 frogs were on trunks at heights of 0.5-1.0 m and nine were on broadleaves at heights of 0.25-1.00 m. At site 4, two of six frogs were on litter at ground level and all of the others were on different perch types. At site 5, 26 of 29 frogs were on elevated perches at heights of 0.2-2.0 m. Most were on broadleaves. Disparity between perch type use versus availability might have been greater if larger sample sizes for sites 2 and 4 had been available. Site 2 consisted mainly of low (albeit dead) herbaceous vegetation. The lush vegetation at Site 4 provided potential perch sites extending from the ground well into the canopy. Several frogs were heard calling from the canopy, but were not seen and therefore not counted. Had these frogs been observed, trunks and epiphytes might have accounted for a larger percentage of perches utilised than those nearer the ground.

Perch Height

Perch heights differed significantly between sites (ANOVA, df = 4, F = 5.51, P = 0.0006; Fig. 5), with significant differences (Fisher's PSLD) between sites 1 and 5 (P = 0.0007), 2 and 5 (P = 0.001), and 3 and 5 (P = 0.0008). Site 5 consisted mainly of low broadleaf growth, litter, and coconut (*Cocos*) tree trunks, but had been purposefully cleared of most understorey and woody debris. Consequently, frogs were largely restricted to low and very high perches. Sites 1-3 had many moderately sized broadleaf shrubs and copious amounts of woody debris that were used by frogs. When data for all sites were combined, perch heights did not differ significantly between species (Mann-Whitney U, Z = -0.03, P = 0.97) or between male and female *E. martinicensis* (Z = -0.15, P = 0.88).

Size and Morphology (Table 1)

Female *E. martinicensis* are larger than males. Although log-SVL only approached significance (ANOVA, df = 1, F = 3.81, P = 0.06), log-weight and all other measured variables differed significantly (ANCOVA with log-SVL as the covariate, all $P \leq 0.02$). The sole female *E. amplinympha* in our sample was larger in all measurements than any conspecific male. Males of the two species did not differ significantly in log-SVL (ANOVA, df = 1, F = 0.52, P = 0.48) and, although limb measurements for *E. amplinympha* were longer than in *E. martinicensis*, no other measured variables differed significantly (ANCOVA with log-SVL as the covariate, all $P \geq 0.19$), except log-weight, for which male *E. amplinympha* were proportionately lighter than *E. martinincensis* (P = 0.03). The sole female *E. amplinympha* in our sample exceeded the mean measurements for female *E. martinicensis*.

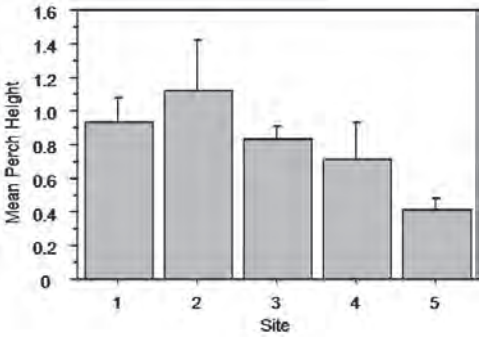

Figure 5. Mean perch heights (± one SE) of frogs at five study sites on Dominica.

Polymorphism

Both *E. martinicensis* and *E. amplinympha* demonstrated considerable polymorphism (e.g. Kaiser et al., 1994a; Alexander, 2007). Dorsal pattern elements, which were either present or absent, included a wide or narrow mid-dorsal line, narrow dorsolateral lines, a wide interorbital line, or a darker mid-dorsal region contrasting with lighter sides. Dorsal background colours ranged from light and dark brown to olive, bronze, brass, or even red. Mid-dorsal, dorsolateral, and interorbital lines were usually orange or cream and were sometimes bordered in black or dark brown. Tubercles on dorsal surfaces may or may not be present. No single dorsal pattern was unique to either species. Pattern variants may merely reflect genetic diversity, although Woolbright & Stewart (2007) associated specific variants of *E. coqui* with different microhabitats on Puerto Rico. Our sample sizes were insufficient for associating any effects of microhabitat on dorsal patterns.

ACKNOWLEDGEMENTS

Peter J. Muelleman, Patrick A. Turk, Natalie N. Wyszynski and Nelson J. Vélez Espinet helped in the field. Robert W. Henderson and John S. Parmerlee, Jr. helped take morphological and polymorphic data, and provided useful comments

	Species			
	E. martinicensis		*E. amplinympha*	
Measurement	Male (N = 13)	Female (N = 18)	Male (N = 8)	Female (N = 1)
Snout-vent length	22.5 ± 1.1	29.7 ± 2.3	23.4 ± 0.6	39.5
Head width at jaw	9.3 ± 0.3	12.7 ± 0.7	9.1 ± 0.2	15.6
Head length[1]	9.8 ± 0.3	13.0 ± 0.6	9.7 ± 0.5	15.8
Eye diameter	3.2 ± 0.1	4.0 ± 0.2	3.2 ± 0.1	4.3
Eye-naris distance	2.7 ± 0.1	3.7 ± 0.2	2.7 ± 0.1	4.5
Tympanum diameter	1.6 ± 0.1	2.1 ± 0.1	1.8 ± 0.1	2.2
Interorbital distance	2.8 ± 0.2	3.7 ± 0.2	2.8 ± 0.1	4.9
Femur length[2]	9.1 ± 0.3	12.2 ± 0.6	9.7 ± 0.3	14.8
Tibia length[3]	10.8 ± 0.4	14.3 ± 0.6	11.3 ± 0.4	18.7
Foot length[4]	14.9 ± 0.5	20.5 ± 1.1	15.5 ± 0.4	25.5
4th toe length	2.8 ± 0.1	3.9 ± 0.2	2.8 ± 0.1	4.7
Weight	1.0 ± 0.1	2.5 ± 0.3	0.7 ± 0.1	3.0

[1] jaw to tip of snout, [2] venter to knee, [3] knee to heel, [4] heel to tip of longest toe

Table 1. Measurements taken from nine *Eleutherodactylus amplinympha* and 31 *E. martinicensis* from Dominica. Measurements were taken from either side of adult animals and recorded in mm except weight, which was recorded in g. Means are presented ± one SE.

on a previous draft of this manuscript. Arlington James, Forest Officer, Forestry, Wildlife, and Parks Division, Ministry of Agriculture & the Environment, Commonwealth of Dominica, issued permits to conduct research in Dominica and was incredibly helpful in assisting our efforts. This project was funded by a grant from the National Science Foundation (USA) to Robert Powell (DBI-0242589).

REFERENCES

Ackley, J.W., Muelleman, P.J., Carter, R.E., Henderson, R.W. & Powell, R. (2009). A rapid assessment of herpetofaunal diversity in variously altered habitats on Dominica. *Applied Herpetology* **6**, 171-184.

Alexander, K. (2007). A photographic field guide to the reptiles and amphibians of Dominica, West Indies. Unpublished report, Texas A&M University Study Abroad, College Station, Texas http://dominica.tamu.edu/student%20projects/projects_by_year.htm.

Daltry, J.C. & Gray, G. (1999). Effects of volcanic activity on the endangered Mountain Chicken Frog (*Leptodactylus fallax*). *Froglog* **32**, 1-2.

Daniells, E.A., Ackley, J.W., Carter, R.E., Muelleman, P.J., Rudman, S.M., Turk, P.A., Vélez Espinet, N.J., White, L.A. & Wyszynski, N.N. (2008). An annotated checklist of the amphibians and reptiles of Dominica, West Indies. *Iguana* **15**, 130-141.

Evans, P.G.H. & James, A. (1997). *Dominica Nature Island of the Caribbean: Wildlife Checklists*. Roseau, Dominica: Ministry of Tourism.

Fa, J., Hedges, B., Ibéné, B., Breuil, M., Powell, R. & Magin, C. (2004). *Leptodactylus fallax*. In 2007 IUCN Red List of Threatened Species. <www.iucnredlist.org>.

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

Gibson, R.C. & Buley, K.R. (2004). Maternal care and obligatory oophagy in *Leptodactylus fallax*: A new reproductive mode in frogs. *Copeia* **2004**, 128-135.

Hedges, S.B. (1996). Historical biogeography of West Indian vertebrates. *Ann. Rev. Ecol. Syst.* **27**, 163-196.

Hedges, S.B. (1999). Distribution Patterns of Amphibians in the West Indies. In: *Patterns of Distribution of Amphibians: A Global Perspective*, pp. 211-254. W.E. Duellman (Ed.). Baltimore, Maryland: The Johns Hopkins University Press.

Hedges, S.B. & Powell, R. (2004). *Eleutherodactylus amplinympha*. In: 2007 IUCN Red List of Threatened Species. <www.iucnredlist.org>.

Hedges, S.B. Ibéné, B. Breuil, M. & Powell, R. (2004a). *Eleutherodactylus martinicensis*. In: 2007 IUCN Red List of Threatened Species. <www.iucnredlist.org>.

Hedges, S.B. Ibéné, B. Koenig, S. La Marca, E. Ibáñez, R. & Hardy, J. (2004b). *Eleutherodactylus johnstonei*. In: 2007 IUCN Red List of Threatened Species. <www.iucnredlist.org>.

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

Henderson, R.W. & Powell, R. (2009). *Natural History of West Indian Amphibians and Reptiles*. Gainesville, Florida: University Press of Florida.

Heyer, W.R. (1979). Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smith. Contrib. Zool.* **301**, 43 pp.

Johnson, T.H. (1988). Biodiversity and conservation in the Caribbean: Profiles of selected islands. International Council for Bird Preservation Monograph **1**, 143 pp.

Kaiser, H. (1992). The trade-mediated introduction of *Eleutherodactylus martinicensis* (Anura: Leptodactylidae) on St. Barthélémy, French Antilles, and its implications for Lesser Antillean biogeography. *J. Herpetol.* **26**, 264-273.

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

Kaiser, H. & Day, M.L. (1995). Abiotic disturbances in the Lesser Antilles. *Froglog* **15**. <www.open.

ac.uk/daptf/froglog/FROGLOG-15-2.html>.

Kaiser, H. & Hardy, J.D., Jr. (1994a). *Eleutherodactylus johnstonei*. *Cat. Amer. Amphib. Rept.* **581**, 1-5.

Kaiser, H. & Hardy, J.D., Jr. (1994b). *Eleutherodactylus martinicensis*. *Cat. Amer. Amphib. Rept.* **581**, 1-4.

Kaiser, H. & Henderson, R.W. (1994). The conservation status of Lesser Antillean frogs. *Herpetol. Nat. Hist.* **2** (2), 41-56.

Kaiser, H. Green, D.M. & Schmid, M. (1994a). Systematics and biogeography of Eastern Caribbean frogs (Leptodactylidae, *Eleutherodactylus*), with the description of a new species from Dominica. *Can. J. Zool.* **72**, 2217-2237.

Kaiser, H. Sharbel, T.F. & Green, D.M. (1994b). Systematics and biogeography of Eastern Caribbean *Eleutherodactylus* (Anura: Leptodactylidae): Evidence from allozymes. *Amphibia-Reptilia* **15**, 375-394.

Lever, C. (2003). *Naturalized Reptiles and Amphibians of the World*. New York: Oxford University Press.

Malhotra, A. & Thorpe, R.S. (1999). *Reptiles and Amphibians of the Eastern Caribbean*. London: Macmillan Education Ltd. 134 pp.

Mallery, C.S., Jr. Marcum, M.A. Powell, R. Parmerlee, J.S., Jr. & Henderson, R.W. (2007). Herpetofaunal species of the leeward slopes and coasts of St. Vincent: A comparison of sites variously altered by human activity. *Applied Herpetology* **4**, 313-325.

Quick, B. (2007). A field guide to the herpetofauna on Dominica, W. I. Unpublished report, Texas A&M University Study Abroad, College Station, Texas http://dominica.tamu.edu/student%20projects/projects_by_year.htm.

ZSL (Zoological Society of London). (2008). Chytridiomycosis and the Caribbean. <www.zsl.org/conservation/animals/amphibians/mountain-chicken,830,AR.html>.