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Biology and Impacts of Pacific Island Invasive Species. 8. *Eleutherodactylus planirostris*, the Greenhouse Frog (Anura: Eleutherodactylidae)[1]

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Abstract: The greenhouse frog, *Eleutherodactylus planirostris*, is a direct-developing (i.e., no aquatic stage) frog native to Cuba and the Bahamas. It was introduced to Hawai'i via nursery plants in the early 1990s and then subsequently from Hawai'i to Guam in 2003. The greenhouse frog is now widespread on five Hawaiian Islands and Guam. Infestations are often overlooked due to the frog's quiet calls, small size, and cryptic behavior, and this likely contributes to its spread. Because the greenhouse frog is an insectivore, introductions may reduce invertebrates. In Hawai'i, the greenhouse frog primarily consumes ants, mites, and springtails and obtains densities of up to 12,500 frogs ha^{-1}. At this density, it is estimated that they can consume up to 129,000 invertebrates ha^{-1} $night^{-1}$. They are a food source for the nonnative brown tree snake in Guam and may be a food source for other nonnative species. They may also compete with other insectivores for available prey. The greatest direct economic impacts of the invasions are to the nursery trade, which must treat infested shipments. Although various control methods have been developed to control frogs in Hawai'i, and citric acid, in particular, is effective in reducing greenhouse frogs, the frog's inconspicuous nature often prevents populations from being identified and managed.

The greenhouse frog, *Eleutherodactylus planirostris* (Cope, 1862), is a direct-developing (i.e., no aquatic stage) frog native to Cuba and the Bahamas; it has established breeding populations on five islands in Hawai'i and on Guam, as well as on the U.S. mainland and at least four Caribbean localities (Kraus 2009). In general, its invasions have not been well studied, even though the greenhouse frog is one of the most successful amphibian invaders (Bomford et al. 2009). This may be because the species is not often noticed, due to its small size (<30 mm), inconspicuous advertisement call (Kraus and Campbell 2002), and easily overlooked soil-deposited eggs. Because the greenhouse frog does not require standing water for transport, establishment, or persistence, additional inadvertent translocations in the Pacific region are probable (Christy et al. 2007*a*).

The introduction of nonnative *Eleutherodactylus* spp. has affected the nursery trade in Hawai'i. In addition, the nonnative Puerto Rican coqui, *E. coqui*, can negatively impact Hawaiian ecosystems through predation on invertebrates and by altering nutrient cycles (Beard 2007, Sin et al. 2008, Choi and Beard 2012). There may be similar impacts from the greenhouse frog. High densities of the greenhouse frog may also facilitate the establishment and spread of other nonnative species in the Pacific, in particular the brown tree snake, *Boiga irregularis* (Mathies et al. in press).

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Thus, it is important to know how the greenhouse frog impacts Pacific islands, and the state of management of its invasion.

NAME

Eleutherodactylus planirostris (Cope, 1862)

Phylum Chordata, class Amphibia, order Anura, family Eleutherodactylidae

Synonyms: *Hylodes planirostris* Cope, 1862; *Lithodytes* (=*Eleutherodactylus*) *ricordii* Cope, 1875; *Eleutherodactylus ricordii planirostris* Shreve, 1945; *Eleutherodactylus planirostris planirostris* Schwartz, 1965.

As the Latin meaning of the genus name implies, *Eleutherodactylus* Duméril & Bibron frogs have individual (nonwebbed) fingers and toes. The name *planirostris* comes from the Latin "rostrum" (snout) and "planum" (level, flat). There are 185 species in the genus, distributed throughout the West Indies, the southern United States, Mexico, Belize, and Guatemala (Hedges et al. 2008). Hedges et al. (2008) suggested that *E. planirostris* should be classified in the subgenus *Euhyas* Fitzinger because of differences in liver shape, no external vocal sac, and more terrestrial behavior than the more arboreal species classified in the subgenus *Eleutherodactylus*. The family-level classification of this group, currently Eleutherodactylidae, has been highly unstable in the last decade; it was routinely placed in Leptodactylidae before recent molecular assessments of frog phylogeny (Hedges et al. 2008). Commonly known as the greenhouse frog, it is often found in plant nurseries, gardens, and greenhouses (Schwartz and Henderson 1991). Previous common names of the greenhouse frog that are no longer in use include Ricord's frog, cricket toad, Bahaman tree frog, and pink-snouted frog (Wright and Wright 1949).

DESCRIPTION AND ACCOUNT OF VARIATION

Species Description

A small species of *Eleutherodactylus*, the greenhouse frog is sexually dimorphic. On the island of Hawai'i, maximum snout-vent length (SVL) for females was 27 mm (mean = 22, $n = 176$) and 21 mm (mean = 17, $n = 100$) for males across 10 sites, with females 30% to 40% longer than males (Olson and Beard 2012). These sizes are similar to those in their native Cuba and nonnative Florida, where females have a maximum SVL range of 26.5–28 mm and males a maximum SVL range of 17.5–21 mm (Schwartz 1974, Meshaka et al. 2004).

There are two basic color phases: (1) a mottled tan and brown phase (Figure 1), and (2) a mottled tan and brown phase with two yellow dorsolateral stripes extending from the eye along the length of the body (Figure 2) (Lynn 1940). The mottled pattern is recessive to the dominant striped pattern, and in Cuba, there is a 3 : 1 ratio of striped to mottled individuals (Goin 1947). A population from Gainesville, Florida (USA), exhibited a 1 : 1 ratio, which may have been a result of a bottleneck (Goin 1947) or selective pressure (Woolbright and Stewart 2008). Only mottled individuals were found in recent studies across the islands of Hawai'i, Lāna'i, and Maui (Olson and Beard 2012; R. Choi, unpubl. data). In museum specimens from Hawai'i, the predominant pattern was also mottled, with only 14% exhibiting striped patterns (12 out of 155 specimens), and all striped individuals were collected from O'ahu (Bishop Museum, Honolulu, Hawai'i, [Fred Kraus, pers. comm.]). Hundreds of greenhouse frogs have been collected across Guam, and only mottled frogs have been found (Diane Vice, unpubl. data).

Distinguishing Features

In Cuba, 85% of the native frog species are in the *Eleutherodactylus* genus (55 out of 66 species). The greenhouse frog was originally thought to be the species *E. ricordii* and later classified as a subspecies of *E. ricordii*. The two subspecies were then split into separate species after they were found to be syntopic in eastern Cuba (Schwartz 1974); thus several early references to Florida populations were called *E. ricordii* but were actually *E. planirostris*. Two species, *E. goini* and *E. casparii*, were

Figure 1. Adult female *Eleutherodactylus planirostris* in Hawai'i showing mottled color phase. (Photo: Christina A. Olson)

at one time considered subspecies of *E. planirostris* (Schwartz 1974, Díaz and Cádiz 2008).

Of the frogs introduced to Hawai'i, the greenhouse frog most resembles *E. coqui*, the Puerto Rican coqui frog. Features that distinguish the coqui are its light tan color, golden eyes, wider snout, and larger toe pads (Beard et al. 2009). The coqui is also larger than the greenhouse frog, with a maximum SVL for females of 49 mm and for males of 39 mm (Beard et al. 2009). Most notably, the breeding call is different. The greenhouse frog produces short, irregular, soft chirps (Schwartz 1974) with sound pressure levels around 35–45 dB at 0.5 m (K.H.B., unpubl. data), which are often mistaken for a cricket or bird; the coqui produces a loud, two-note "ko-kee" call that can reach sound pressure levels of 80–90 dB at 0.5 m (Beard and Pitt 2005). In Guam, there are no other *Eleutherodactylus* species, but it may be confused with non-native newly metamorphosed cane/marine toads (*Bufo marinus*), which also have been introduced to Hawai'i; however, the greenhouse frog lacks the cane toad's large, conspicuous parotid glands.

Combinations of physical traits important for identifying the greenhouse frog include the following:

(1) Size: SVL for reproductive males 14 to 21 mm; for gravid females 17 to 27 mm in Hawai'i (Olson and Beard 2012).
(2) Body color: Venter is white to light gray and dorsal is tan pink to dark

Figure 2. A recently hatched juvenile *Eleutherodactylus planirostris* from Florida (Sarasota County) showing size and striped color phase. (Photo: Christina A. Olson)

reddish brown (Ashton and Ashton 1988, Bartlett and Bartlett 2006). There is a dark S-shaped line from top of tympanum to arm insertion (Wright and Wright 1949).

(3) Body shape: Head as broad as body, snout truncated and extending slightly beyond the lower jaw (Wright and Wright 1949).
(4) Eye color: Black pupil with a reddish iris (Wright and Wright 1949).
(5) Foot features: Toes are long and slender, lack webbing, and have very small, terminal disks (Wright and Wright 1949).
(6) Tympanum: White or coral red, approximately half the size of the eye (Wright and Wright 1949).

ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACT

Detrimental Aspects

Greenhouse frogs and their eggs are frequently moved unintentionally with plants or landscape materials and therefore may affect industries involved with this movement, such as the floriculture industry, which is the largest single agricultural commodity for the state of Hawai‘i (HASS 2005). Although there is no information available on the amount nursery owners spend to control greenhouse frogs, treatment can be necessary to maintain pest-free status and may increase shipment costs and reduce trade. Interisland and international plant shipments from the island of Hawai‘i, in particular, are supposed to be inspected and treated before shipment. Infested plant shipments may be refused entry or destroyed (Raloff 2003).

In addition to economic impacts to agricultural industries, several resorts in Hawai‘i have attempted to manage greenhouse frogs because they are found in swimming pools and irrigation boxes; large populations may similarly affect homeowners (W.C.P., unpubl. data). Although government funds have not specifically been allocated to target greenhouse frogs in Hawai‘i, county, state, and federal governments have incurred costs to control coqui frogs. Greenhouse frog populations are probably indirectly controlled at sites targeted for coqui eradication and control, which cost public agencies $4 million in 2006, but expenditures have declined in recent years (Anonymous 2010).

Beneficial Aspects

In general, there is little concern over the spread of greenhouse frogs (Kraus and Campbell 2002). Because of its quiet call, many residents in Hawai‘i do not consider the frog a nuisance, and some have expressed preferences for the greenhouse frog over the coqui (C.A.O., pers. obs.). Some residents find the frogs and their calls pleasant, and frogs have been intentionally moved to gardens or homes. Some who move frogs incorrectly believe that all frogs control harmful invertebrates, such as mosquitoes and termites (Fullington 2001, Singer 2001). A diet study of the greenhouse frog conducted in Hawai‘i indicates that this is unlikely; only two mosquitoes and no termites were found out of 7,494 identified prey items (Olson and Beard 2012).

Ambivalence and inability to detect new infestations may facilitate the spread of greenhouse frogs. For example, both the coqui and greenhouse frog were introduced to Guam in 2003 (Christy et al. 2007*b*). The coqui was quickly eradicated, but the greenhouse frog established and spread throughout the island with little alarm (Daniel Vice, pers. comm.). This may have occurred because the coqui was easier to detect (because of its louder call) while populations were still small enough to treat, but it may also have occurred because there was less concern about greenhouse frog invasions, in general.

Regulatory Aspects

In Hawai‘i, all frogs (they are all nonnative) are listed as State Injurious Species, and it is illegal to transport or release frogs into the wild. The requirement to treat plants before shipment has initiated primarily to combat coqui frogs, but the presence of any frog in a shipment would trigger legal requirements to restrict movement (Hawai‘i Department of Agriculture 150A-2, Hawai‘i Revised Statutes). Plant shipments from Hawai‘i to Guam, the continental United States, and other countries require a phytosanitary certificate that certifies shipments are pest-free, and shipments may be inspected visually or by listening for calling frogs during the daytime. However, this often does little to prevent movement of greenhouse frogs or their eggs, because the small frogs and their eggs are not easily detected and the soft nighttime, intermittent chirps of calling males may not be heard (Keevin Minami, pers. comm.). Further spread could be reduced if all shipments were treated whether or not frogs or eggs are detected.

Environmental Impacts

Because the greenhouse frog is an insectivore (Goin 1947, Stewart 1977), their greatest threat in Pacific ecosystems is to the invertebrate communities. To determine impacts to invertebrate communities, the greenhouse frog diet was determined at 10 sites on the island of Hawai‘i (Olson and Beard 2012). Greenhouse frogs were found to primarily consume leaf-litter invertebrates and were estimated to consume up to 129,000 invertebrates ha^{-1} $night^{-1}$ (Olson and Beard 2012). Because the study did not identify stomach contents to species, it is unknown how much of the total diet comprised native species. The diet did include mites (19% of the total number of all items consumed), springtails (17%), spiders (3%), beetles (2%), flies (2%), and booklice (2%), all of which are invertebrate orders that contain native species found in Hawai'i (Olson and Beard 2012). Overall, 42% of the species identified in the diet were nonnative ants (32%), isopods (8%), and amphipods (1%) (Olson and Beard 2012). All ant species are nonnative to Hawai'i, and species identified in the diet included the big-headed ant (*Pheidole megacephala*), the Argentine ant (*Linepithema humile*), and the yellow crazy ant (*Anoplolepis gracilipes*). Studies indicate that these ant species, in particular, consume and negatively impact native invertebrates (Krushelnycky et al. 2005). Thus, the frog introduction may indirectly benefit these native invertebrates.

Native fauna may be threatened by introduced *Eleutherodactylus* through pathways besides predation. It was hypothesized that the coqui may compete with native insectivores, such as endemic birds, for prey because of its potential to invade high-elevation forests in Hawai'i (Kraus et al. 1999, Beard and Pitt 2005). Kraus et al. (1999) considered this to be of less concern for the greenhouse frog because: (1) at that time, greenhouse frogs were only found in lower elevations and were thus thought less likely to impact native invertebrates and their native predators, which primarily reside in high-elevation forests, and (2) the greenhouse frog forages in the leaf litter and thus is less likely to compete with native birds that forage in the canopy. However, it has since been found that the greenhouse frog may invade higher elevations than the coqui (Olson et al. 2012). Furthermore, diet studies of the coqui and greenhouse frog indicate that both species predominantly consume leaf-litter invertebrates in Hawai'i (Beard 2007, Olson and Beard 2012), but no specific study has been conducted to determine if either species competes with native insectivores in Hawai'i.

It was also hypothesized that large populations of introduced frogs in Hawai'i may facilitate the spread of other invasive species by providing an abundant prey source that does not naturally occur (Kraus et al. 1999). Beard and Pitt (2006) conducted diet analysis on mongoose and rat on the eastern side of the island of Hawai'i and found that *Eleutherodactylus* spp. made up a small or negligible part of their diets. In Guam, another invasive species, the brown tree snake, preys on introduced greenhouse frogs (Mathies et al. in press), although their percentage in brown tree snake diets has not yet been determined. This suggests that if the brown tree snake is introduced to Hawai'i it may use the greenhouse frog as a prey source, which may facilitate the snake's establishment and spread (Mathies et al. in press).

Greenhouse frogs may also impact ecosystem processes, such as nutrient cycling. For example, many invertebrates that the greenhouse frog consumes play important roles in ecosystem processes, such as decomposition of plant material. Sin et al. (2008) found that herbivory rates were lower, and plant growth and leaf litter decomposition rates were higher in Hawaiian sites with than without coqui because of coqui excrement rather than changes to the invertebrate community. Similar effects may occur at sites invaded by the greenhouse frog because of either changes in the invertebrate community or other pathways.

GEOGRAPHICAL DISTRIBUTION

The native range of the greenhouse frog comprises several islands in the Caribbean (Heinicke et al. 2011). The greenhouse frog is found island-wide on Cuba except at the highest elevations (1,100 m), with a maximum elevation of 720 m (Díaz and Cádiz 2008); on the islands of Little Bahama Bank, South Bimini, New Providence, and Eleuthera in the Bahamas (Schwartz and Henderson 1991); and on the islands of Grand Cayman and Cayman Brac in the Caymans (Seidel and Franz 1994). It has now spread to several localities outside its native range throughout the southeastern United States and the Caribbean (Table 1). The most likely pathway for initial introduction to those new areas was via cargo or the nursery trade (Stewart 1977, Wilson and Porras 1983).

The first record of the greenhouse frog in the Pacific basin is from the island of Hawai'i in 1994, although its initial introduction may

TABLE 1

Nonnative Distribution of the Greenhouse Frog

Location	Approximate Date of First Known Occurrence	Additional Information and References
North America		
United States		
Florida		Widespread throughout the peninsula in human-altered and natural habitats; possibly introduced naturally, such as on driftwood (Goin 1947, Meshaka et al. 2004, Heinicke et al. 2011)
Florida Keys	1863	
Miami	1899	
Gainesville	1933	
Tampa	1938	
Jacksonville	1943	
Louisiana	1975	First record is from a city park in New Orleans; currently found in 10 parishes in the southern part of the state (Meshaka et al. 2009)
Alabama	1982	Found in Baldwin County (Carey 1982)
Georgia	1998	Found in five counties in the southern part of the state (Jensen et al. 2008)
Oklahoma	2000	One population found in a tropical building of Tulsa Zoo (Somma 2010)
Mississippi	2003	Found in the city of Gulfport (Dinsmore 2004)
Mexico, Veracruz	1974	Schwartz (1974)
Caribbean islands		
Jamaica	1937	Found throughout the island, except Hellshire Hills and the Portland Ridge Peninsula (Hedges 1999)
Grenada	1999	Kraus et al. (1999)
Caicos Islands	Unknown	North Caicos Island (Schwartz and Henderson 1991)
Miskito Cays	Unknown	Heinicke et al. (2011)
Pacific islands		
Hawai‘i	1994	Kraus and Campbell (2002)
Guam	2003	Christy et al. (2007*a*)

have occurred at an earlier date (Kraus and Campbell 2002). It is thought to have arrived via nursery plants (Kraus et al. 1999), possibly from Florida. This is assumed because the greenhouse frog first appeared in nurseries that imported plants from Florida, and it had relatively abundant populations in Florida nurseries around the time of introduction. It was particularly abundant in nurseries raising *Dracaena* species (Kraus et al. 1999). The greenhouse frog was then introduced to Guam from Hawai‘i via the nursery trade in 2003 (Christy et al. 2007*b*).

The greenhouse frog is now present on the islands of Hawai‘i (W.C.P., pers. obs.), Maui (Adam Radford, pers. comm.), O‘ahu (Katie Swift, pers. comm.), Kaua‘i (Keren Gunderson, pers. comm.), and Lāna‘i (Figure 3). The striped morph found on O‘ahu (mentioned earlier) may reflect a separate introduction on that island (Peacock et al. 2009, O’Neill and Beard 2010). Frogs were initially found in four localities on Guam (Tumon, Tamuning, Mangilao, and Manengon [Christy et al. 2007*a*]) and have rapidly spread to the entire island (Diane Vice, unpubl. data). A systematic presence/absence study sampled every 2 km on the major network on the island of Hawai‘i in 2009 (Olson et al. 2012) found males calling at 62 (14%) of the 446 points sampled. Occupancy modeling showed that population detection probabilities were low (<0.3), but three repeated visits improved detection to >0.7 (Olson et al. 2012).

It may be possible to determine genetically if Pacific greenhouse frogs came directly from Cuba or if the frogs are a secondary introduction from some area of their introduced range, such as Florida. Studies indicate that the

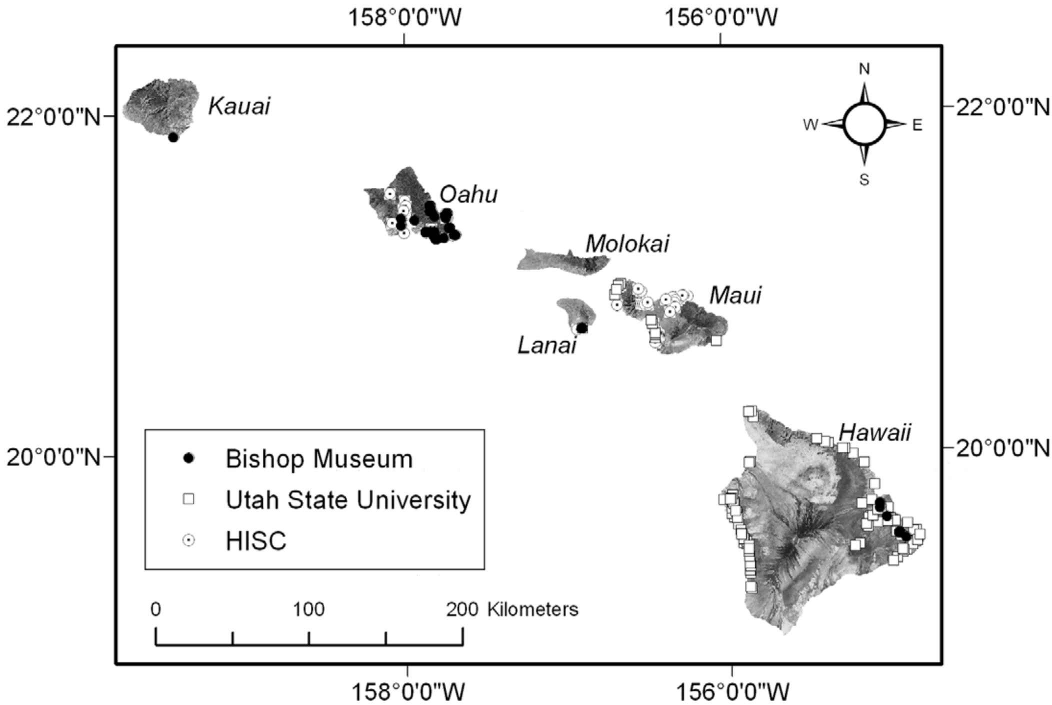

Figure 3. Map of reported locations of *Eleutherodactylus planirostris* on the islands of Hawai'i, Kaua'i, Lāna'i, Maui, and O'ahu including records from the Bishop Museum, Honolulu, Hawai'i; Utah State University 2008–2010; and the Hawai'i Invasive Species Council (HISC). (Source: Landsat imagery, http://hawaii.gov/dbedt/gis/)

greenhouse frogs found in Florida and those found in Hawai'i are originally from western Cuba and are distinct from populations found in eastern Cuba, the Bahamas, and the Caymans, and from other introduced populations in the Caribbean (Heinicke et al. 2011). In addition, genetic diversity is lower in Florida than in source populations (Heinicke et al. 2011).

HABITAT

Climatic Requirements and Limitations

Studies on climate requirements of the greenhouse frog indicate that, predominantly, the frog has established populations in nonnative ranges with mean annual and maximum warmest-month temperatures similar to those in Cuba (Bomford et al. 2009, Rödder and Lötters 2010). However, it is found in areas with seasonal daily minimum temperatures as low as 4°C to 8°C in the southeastern United States (Wray and Owen 1999, Tuberville et al. 2005), and it has been suggested that long-term residence in the Florida Keys may have allowed the greenhouse frog to evolve physiological and/or behavioral adaptations to cope with colder temperatures (Bomford et al. 2009, Heinicke et al. 2011). One study suggests that greenhouse frogs in Hawai'i may be limited to areas with mean annual temperatures >20°C; however, this may reflect its recent introduction, and the species may still spread to cooler areas (Rödder and Lötters 2010).

The greenhouse frog is not found on the highest peaks in Cuba (1,100 m) (Díaz and Cádiz 2008) or Jamaica (2,200 m), where greenhouse frogs are found only from sea level to 600 m (Stewart and Martin 1980). The range in the continental United States is limited to the southeastern coastal lowlands with an elevation <200 m. In Hawai'i, greenhouse frogs were detected at an elevation of 1,115 m (Olson et al. 2012). There may be suitable habitat types in Hawai'i above 1,115 m, although temperatures and precipitation decline at higher elevations (Price 1983).

Habitat Resource Requirements and Limitations

The greenhouse frog is typically found on the forest floor (Olson and Beard 2012) and up to 2 m off the ground (Duellman and Schwartz 1958, Stewart and Martin 1980). In Cuba, the greenhouse frog is often found in the leaf litter, under rocks, and in rock crevices at the mouth of caves (Garrido and Schwartz 1968). It is common in open grassy areas in Jamaica (Stewart and Martin 1980). In Florida, the greenhouse frog is found under rocks, fallen branches, and leaf litter, and in low-growing bromeliads and gopher tortoise burrows, as well as burrowing into moist soil (Goin 1947, Neill 1951, Lips 1991, Schwartz and Henderson 1991). In Hawai'i, it is found predominantly in the leaf litter as well as under manmade objects (i.e., flowerpots, water meters, and tarps) and rocks, and inside lava tubes (Olson and Beard 2012). The use of daytime retreat sites on or below the forest floor has been documented in Jamaica, Florida, and Hawai'i (Goin 1947, Stewart 1977, Olson and Beard 2012).

Although there are numerous descriptions of its habitat, there have been no studies investigating factors that limit the greenhouse frog. Overcast or rainy sky conditions are important factors in call activity (Meshaka and Layne 2005, Olson et al. 2012); thus precipitation may be an important factor limiting their distribution. Humidity is an important variable for egg development and hatching success (Goin 1947), although the greenhouse frog has higher tolerance for drier conditions than other *Eleutherodactylus* species (Pough et al. 1977). In Cuba and Florida, where there is a distinct wet and dry season, frogs breed more during the wet season (Meshaka and Layne 2005, Díaz and Cádiz 2008), and it is possible that the greenhouse frog has a breeding period limited to a wet season in Hawai'i as well (Olson et al. 2012).

Ecosystem and Community Types Invaded

In its native range, the greenhouse frog is common and well adapted to a wide diversity of habitats, including wet and dry forests, coastal and mountainous areas, rivers, streambeds, caves, rocky outcrops, gardens, and houses (Garrido and Schwartz 1968, Díaz and Cádiz 2008). In Florida, the greenhouse frog is common in wet and dry forests, open grasslands, coastal areas, and scrub habitats (Enge 1997, Meshaka et al. 2004). In Jamaica, it is most often found in drier habitats, such as open grasslands and scrub, as well as lawns, pastures, and roadsides (Stewart and Martin 1980).

Most populations in Hawai'i are found in lowland (0–500 m) habitats. Populations have become established along roadsides and in macadamia nut orchards, nurseries, pastures, residential gardens, resort areas, state forests, and state parks (Olson 2011). Most of the invaded habitats are dominated by nonnative plants; however, populations have also been found in native shrublands and forests dominated by the native 'ō'hia tree, *Metrosideros polymorpha* (Olson et al. 2012). In Guam, the greenhouse frog has invaded both urbanized and forested areas, including residential gardens and secondary scrub forests (Bjorn Lardner, pers. comm.).

PHYSIOLOGY AND GROWTH

Based on a study of greenhouse frogs in Florida, minimum body size for breeding males is 15.0 mm SVL and 19.5 mm for breeding females, and they reach sexual maturity after 1 yr (Goin 1947). Eggs are laid individually in or under moist soil, or under fallen leaves or rocks, and unlike other members of the genus, there is no guarding of the eggs. Clutch size ranges from 3 to 26 eggs ($n = 104$ clutches), with a mean of 16 (Goin 1947). In Hawai'i, clutches were found inside irrigation boxes with a mean number of eggs of 10.3 ($n = 3$ [K.H.B., unpubl. data]).

As in other *Eleutherodactylus*, fertilized eggs undergo direct development, meaning that there is no free-living tadpole phase, and complete metamorphosis occurs within the egg with young hatching as tiny froglets (Goin 1947). Eggs consist of three layers outside the vitelline membrane and are 5–6 mm in diameter at the time of hatching (Goin 1947). Eggs require 100% humidity to hatch and can be submerged in water for a period of up to 25 days and still remain viable (Goin 1947). Eggs hatch 13–20 days after deposition, and newly emerged hatchlings are 4.3–5.7 mm SVL (Goin 1947, Lazell 1989). Hatchlings have a small-spined tooth used to rupture the egg and a reduced tail, both of which detach soon after hatching (Goin 1947). Newly emerged hatchlings have the same stripe patterns as adults. One frog in captivity gained four times its original body mass and measured 6.9 mm SVL 30 days after hatching (Goin 1947).

The greenhouse frog has a high tolerance for warm and dry conditions compared with other *Eleutherodactylus* species. One study from Jamaica conducted on two species of native and two species of introduced frogs (including the greenhouse frog) indicated that both introduced species acclimated to and survived longer in higher temperatures than the native species (Pough et al. 1977). The preferred temperature of the greenhouse frog was 27.3°C ± 0.66°C, with its critical maximum temperature ranging from 36.4°C to 41.8°C (acclimated to 20°C: mean = 38.7°C ± 0.38°C, range = 36.4°C–40.0°C; acclimated to 30°C: mean = 40.5°C ± 0.35°C, range = 39.0°C–41.8°C). Critical water loss was at 34.9% ± 0.004 of initial body weight in 40%–50% relative humidity (RH), significantly higher than the critical water loss of the native species (24%–27% of initial body weight).

REPRODUCTION AND POPULATION DYNAMICS

The breeding season in Cuba is April through January (Meshaka and Layne 2005). In Florida, the breeding season is typically April to early September (Goin 1947, Meshaka and Layne 2005). It is unclear if the greenhouse frog has a distinct breeding season in Hawai‘i and Guam.

Eleutherodactylus spp. reach a calling peak at night between 1830 and 0500 hours, but call frequency and duration vary by species (Drewry and Rand 1983). There is no information available on the calling times for the greenhouse frog (Goin 1947). Meshaka and Layne (2005) found that calling in central Florida most frequently took place when air temperature was 23°C–30°C and RH was 84%–100%. Males call from the ground or on vegetation under 1 m in height (Díaz and Cádiz 2008). In Hawai‘i, males call from under debris and stone fences, as well as from subterranean lava tubes (Olson 2011).

Greenhouse frog density was estimated in a macadamia nut orchard on the eastern side of the island of Hawai‘i in June 2009 using mark-recapture techniques of adult frogs in a 50 by 50 m plot (Olson and Beard 2012). Over seven nights, 651 adults were captured and densities were estimated at 4,564 (4,148–5,101, 95% CI) frogs ha^{-1}. Multiplying this estimate by the preadult to adult ratio of 1.7, it was estimated that the total population density was 12,522 frogs ha^{-1} (Olson and Beard 2012). Mark-recapture methods were also used to estimate densities at two additional sites in natural areas on the eastern side of the island of Hawai‘i in January 2010, with estimates of 2,400 (1,720–3,760, 95% CI) and 5,300 (3,728–8,048, 95% CI) frogs ha^{-1} (C.A.O., unpubl. data).

Greenhouse frogs often use coconut husk piles as diurnal retreats in Jamaica. A husk pile removal study was conducted at four sites in northern Jamaica, and the site with highest density was estimated to have 4,635 frogs ha^{-1} (including two native and two nonnative species) (Stewart and Martin 1980). Overall abundance of frogs in husk piles was higher in the dry season than in the wet season for all species. Greenhouse frog abundance was lower in husk piles dominated by the native frog species and higher in the coastal sites than in the upland sites.

RESPONSE TO MANAGEMENT

Chemical Control

Most control options for greenhouse frogs were developed for coqui frogs. For example, chemical controls are used to control coquis over large areas in Hawai‘i (Tuttle et al. 2008) and are equally effective against greenhouse frogs (Pitt and Sin 2004*a*). Currently, only citric acid can be used legally to control *Eleutherodactylus* spp. in Hawai'i, although several other chemicals have been identified as effective frog toxicants (Pitt and Sin 2004*b*, Pitt and Doratt 2005, 2008). For example, hydrated lime is effective and was registered as a frog toxicant from 2005 to 2008. Citric acid is exempt from the requirements of the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) by regulation (40 CFR Section 152.25) because it is classified as a minimum-risk pesticide. A 16% citric acid solution is 100% effective for greenhouse frogs in the laboratory and is effective in the field (Pitt and Sin 2004*a*).

Few control efforts have been directed exclusively at greenhouse frogs. In 2003, we evaluated the ability to control greenhouse frogs at five Kaua'i resorts over a 5-month period (W.C.P., unpubl. data). Greenhouse frogs are often found in irrigation boxes used for landscape watering at resorts with arid landscapes. We evaluated the immediate and long-term effects of control on frog abundance in irrigation boxes. A 16% citric acid solution was applied bimonthly to infested irrigation boxes. As expected, frogs reinvaded irrigation boxes because citric acid does not have long-term residual effects on frogs (Pitt and Sin 2004*a*). The number of irrigation boxes at each resort varied from 33 to 411 ($\bar{x} = 185$). The application removed all frogs from 91% of irrigation boxes within 24 hr. After 5 months of treatments, 67% fewer irrigation boxes were infested.

Mechanical Control

Mechanical control techniques evaluated for coqui frogs may have similar effects on greenhouse frogs. These methods are directed toward nursery operations, quarantine areas, or residential areas. Hot water spray or vapor treatments are commonly used to treat plant shipments for a variety of pests. Hot water sprayed on plants at either 45°C for 1 min or 39°C for 5 min was effective against adult coqui frogs (Hara et al. 2010), and similar results are expected for greenhouse frogs, considering their similar thermal tolerances (Pough et al. 1977). Native habitat management, such as leaf litter removal, may reduce frog abundance and the likelihood that they will move into an area. Hand capture of coqui frogs is effective when few frogs are present (Beard et al. 2009) but may be more difficult with the more cryptic and harder to catch greenhouse frog. Traps and barriers developed for coquis (Figure 4) have not been tested to determine their effectiveness on greenhouse frogs, although barriers may be equally effective against both species.

NATURAL ENEMIES

In the Caribbean, three racer snakes (*Cubophis canterigerus* on Cuba, *C. caymanus* on Grand Cayman, and *C. vudii* in the Bahamas) and the Cuban treefrog (*Osteopilus septentrionalis*) are predators of greenhouse frogs (Meshaka 1996, Henderson and Powell 2009). Other predators of *Eleutherodactylus* species in the Caribbean include invertebrates, frogs, lizards, snakes, birds, and mammals (Henderson and Powell 1999). The ringneck snake (*Diadophis punctatus*), a small (8–38 cm) fossorial species, is a predator in Florida (Wilson and Porras 1983, Lazell 1989). In Guam, the invasive brown tree snake consumes greenhouse frogs (Mathies et al. in press). There are no records of Hawaiian species consuming greenhouse frogs. Documented parasites in Cuba include nematodes (Henderson and Powell 2009).

No studies have been conducted on the potential for biological control, and the release of organisms to combat the frog likely will have little success in substantially reducing populations and could have many unintended consequences. In many areas, greenhouse frogs are abundant in the presence of numerous predators, parasites, and competitors (Henderson and Powell 2009). For example, brown tree snakes are extremely abundant on Guam and prey on greenhouse frogs; however, frogs continue to spread across the island despite predation pressure (Rodda and Savige 2007, Mathies et al. in press).

Pathogens have a low potential for controlling greenhouse frogs in Hawai'i primarily because viruses and diseases are most effective when applied to small populations of species with low reproductive capacity (Brauer and

Figure 4. Photograph of a fine-mesh frog barrier attached to chain-link fence. The frog barrier is 1 m high with the bottom apron buried under gravel and an upper lip extending 25 cm out from the barrier at a 90° angle. (Photo: William C. Pitt)

Castillo-Chavez 2001, Daszak et al. 2003). In addition, most major frog diseases infect tadpole stages and greenhouse frogs would be less affected (Daszak et al. 2003). One disease organism that has been implicated in frog population declines worldwide, the chytrid fungus, is already established in frog populations in Hawai'i (Beard and O'Neill 2005). Although there are no native frogs in Hawai'i and thus none at risk of infection, there is a chance that a frog infected with a disease could be transported to other states or countries. Thus, releasing a disease organism may affect frog populations elsewhere and could restrict trade.

PROGNOSIS

Greenhouse frogs are widespread in Hawai'i and Guam. Control efforts on Hawai'i are targeted toward the coqui frog, and there have been no efforts to control the greenhouse frog on Guam; thus, it is unlikely that they will be controlled with current methods. Many alternative control measures have been evaluated and found to have low probability of success, including biological control, sterilization, and pathogen release. The best method to control greenhouse frogs is to reduce their spread to new areas with good management techniques, such as inspecting cargo and plant materials, treating plant materials with citric acid solution or hot water, using barriers, and not transporting material that is known to be infested.

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Literature Cited

Anonymous. 2010. Hawai'i's coqui frog management, research and education plan. Draft. Hawai'i Invasive Species Council, Honolulu. www.hawaiiinvasivespecies.org/hisc/pdfs/201003coquiplan.pdf.

Ashton, R. E., and P. S. Ashton. 1988. Handbook of reptiles and amphibians of Florida: Part 3. The amphibians. Windward Publishing, Miami.

Bartlett, R. D., and P. Bartlett. 2006. Guide and reference to the amphibians of eastern and central North America. University of Florida Press, Gainesville.

Beard, K. H. 2007. Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii. Copeia 2007:281–291.

Beard, K. H., and E. M. O'Neill. 2005. Infection of an invasive frog *Eleutherodactylus coqui* by the chytrid fungus *Batrachochytrium dendrobatidis* in Hawaii. Biol. Conserv. 126:591–595.

Beard, K. H., and W. C. Pitt. 2005. Potential consequences of the coqui frog invasion in Hawaii. Divers. Distrib. 11:427–433.

———. 2006. Potential predators of an invasive frog (*Eleutherodactylus coqui*) in Hawaiian forests. J. Trop. Ecol. 22:345–347.

Beard, K. H., E. A. Price, and W. C. Pitt. 2009. Biology and impacts of Pacific island invasive species. 5. *Eleutherodactylus coqui*, the Coqui frog (Anura: Leptodactylidae). Pac. Sci. 63:297–316.

Bomford, M., F. Kraus, S. C. Barry, and E. Lawrence. 2009. Predicting establishment success for alien reptiles and amphibians: A role for climate matching. Biol. Invasions 11:713–724.

Brauer, F., and C. Castillo-Chavez. 2001. Mathematical models in population biology and epidemiology. Springer-Verlag, New York.

Carey, S. D. 1982. Geographic distribution: *Eleutherodactylus planirostris.* Herpetol. Rev. 13:130.

Christy, M. T., C. S. Clark, D. E. Gee II, D. Vice, D. S. Vice, M. P. Warner, C. L. Tyrrell, G. H. Rodda, and J. A. Savidge. 2007*a*. Recent records of alien anurans on the Pacific island of Guam. Pac. Sci. 61:469–483.

Christy, M. T., J. A. Savidge, and G. H. Rodda. 2007*b*. Multiple pathways for invasion of anurans on a Pacific island. Divers. Distrib. 13:598–607.

Choi, R. T., and K. H. Beard. 2012. Coqui frog invasions change invertebrate communities in Hawaii. Biol. Invasions. 14:939–948. doi:10.1007/s10530-011-0127-3.

Cope, E. D. 1862. On some new and little known American Anura. Proc. Acad. Nat. Sci. Phila. 14:151–594.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2003. Infectious disease and amphibian population declines. Divers. Distrib. 9:141–150.

Díaz, L. M., and A. Cádiz. 2008. Guía taxonómica de los anfibios de Cuba Abc taxa 4: vi + 294 pp. + audio compact disk.

Dinsmore, A. 2004. Geographic distribution: *Eleutherodactylus planirostris* (greenhouse frog). Herpetol. Rev. 35:403.

Drewry, G. E., and A. S. Rand. 1983. Characteristics of an acoustic community: Puerto Rican frogs of the genus *Eleutherodactylus.* Copeia 1983:941–953.

Duellman, W. E., and A. Schwartz. 1958. Amphibians and reptiles of southern Florida. Bull. Fla. State Mus. Biol. Sci. 3:181–324.

Enge, K. M. 1997. A standardized protocol for drift-fence surveys. Technical Report No. 14, Florida Game and Fresh Water Fish Commission, Tallahassee.

Fullington, G. 2001. Another voice for the coqui. Hawai'i Island Journal, 1–15 October, 4.

Garrido, O. H., and A. Schwartz. 1968. Anfibios, reptiles y aves de la península de Guanahacabibes. Poeyana 53:1–68.

Goin, C. J. 1947. Studies on the life history of *Eleutherodactylus ricordii planirostris* (Cope) in Florida: With special reference to the local distribution of an allelomorphic color pattern. University of Florida Press, Gainesville.

Hara, A. H., C. M. Jacobsen, S. R. Marr, and R. Y. Niino-DuPont. 2010. Hot water as a potential disinfestation treatment for an invasive anuran amphibian, the coqui frog, *Eleutherodactylus coqui* Thomas (Leptodactylidae), on potted plants. Int. J. Pest Manage. 56:255–263.

HASS. 2005. Hawai'i Agriculture Statistics Service. Statistics of Hawai'i Agriculture. Hawai'i Department of Agriculture, USDA National Agriculture Statistics Service, Honolulu. http://www.nass.usda.gov/Statistics_by_State/Hawaii/index.asp.

Hedges, S. B. 1999. Distribution patterns of amphibians in the West Indies. Page 633 *in* W. E. Duellman, ed. Patterns of distribution of amphibians: A global perspective. The Johns Hopkins University Press, Baltimore.

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.

Heinicke, M. P., L. M. Diaz, and S. B. Hedges. 2011. Origin of invasive Florida frogs traced to Cuba. Biol. Letters 7:407–410.

Henderson, R. W., and R. Powell. 1999. West Indian herpetoecology. Pages 223–268 *in* B. I. Crother, ed. Caribbean amphibians and reptiles. Academic Press, San Diego.

———. 2009. Natural history of West Indian reptiles and amphibians. University Press of Florida, Gainesville.

Jensen, J. B., C. D. Camp, G. W. Gibbons, and M. J. Elliott. 2008. Amphibians and reptiles of Georgia. University of Georgia Press, Athens.

Kraus, F. 2009. Alien reptiles and amphibians: A scientific compendium and analysis. Springer, Dordrecht.

Kraus, F., and E. W. I. Campbell. 2002. Human-mediated escalation of a formerly eradicable problem: The invasion of Caribbean frogs in the Hawaiian Islands. Biol. Invasions 4:327–332.

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

Krushelnycky, P. D., L. L. Loope, and N. J. Reimer. 2005. The ecology, policy, and management of ants in Hawaii. Proc. Hawaii. Entomol. Soc. 37:1–25.

Lazell, J. D. 1989. Wildlife of the Florida Keys: A natural history. Island Press, Washington, D.C.

Lips, K. R. 1991. Vertebrates associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in South-central Florida. J. Herpetol. 25:447–481.

Lynn, W. G. 1940. The herpetology of Jamaica. Bull. Inst. Jam. Sci. Ser. 1:1–12.

Mathies, T., W. C. Pitt, and J. A. Rabon. In press. *Boiga irregularis* (Brown treensnake): Diet. Herpetol. Rev.

Meshaka, W. E., Jr. 1996. Diet and colonization of buildings by the Cuban treefrog (*Osteopilus septentrionalis*) (Anura: Hylidae). Caribb. J. Sci. 32:59–63.

Meshaka, W. E., Jr., J. Boundy, and A. A. Williams. 2009. The dispersal of the greenhouse frog, *Eleutherodactylus planirostris* (Anura: Eleutherodactylidae), in Louisiana, with preliminary observations on several potential exotic colonizing species. J. Kans. Herpetol. 32:13–16.

Meshaka, W. E., Jr., B. P. Butterfield, and J. B. Hauge. 2004. The exotic amphibians and reptiles of Florida. Krieger Publishing Co., Malabar.

Meshaka, W. E., Jr., and J. N. Layne. 2005. Habitat relationships and seasonal activity of the greenhouse frog (*Eleutherodactylus planirostris*) in southern Florida. Fla. Sci. 68:35–43.

Neill, W. T. 1951. A bromeliad herptofauna in Florida. Ecology 32:140–143.

Olson, C. A. 2011. Diet, density, and distribution of the introduced greenhouse frog, *Eleutherodactylus planirostris*, on the island of Hawaii. M.S. thesis, Utah State University, Logan.

Olson, C. A., and K. H. Beard. 2012. Diet of the invasive greenhouse frog in Hawaii. Copeia 2012:121–129. doi:10.1643/CE-11-008.

Olson, C. A., K. H. Beard, D. N. Koons, and W. C. Pitt. 2012. Detection probability of two introduced frogs in Hawaii: Implications for assessing non-native species distributions. Biol. Invasions. 14:889–900. doi:10.1007/s10530-011-0125-5.

O'Neill, E. M., and K. H. Beard. 2010. Genetic basis of a color pattern polymorphism in the coqui frog *Eleutherodactylus coqui*. J. Hered. 101:703–709.

Peacock, M. M., K. H. Beard, E. M. O'Neill, V. Kirchoff, and M. B. Peters. 2009. Strong founder effects and low genetic diversity in introduced populations of Coqui frogs. Mol. Ecol. 18:3603–3615.

Pitt, W. C., and R. E. Doratt. 2005. Efficacy of hydrated lime on *Eleutherodactylus coqui* and an operational field-application assessment on the effects on non-target invertebrate organisms. QA 1243 Final Report. USDA, APHIS, WS, National Wildlife Research Center, Hilo, Hawai'i.

———. 2008. Dermal toxicity of sodium bicarbonate to control *Eleutherodactylus* frogs in Hawaii. QA 1541 Final Report. USDA, APHIS, WS, National Wildlife Research Center, Hilo, Hawai'i.

Pitt, W. C., and H. Sin. 2004*a*. Dermal toxicity of citric acid based pesticides to introduced *Eleutherodactylus* frogs in Hawaii. QA 992 Final Report. USDA/APHIS/WS, National Wildlife Research Center, Hilo, Hawai'i.

Pitt, W. C., and H. Sin. 2004*b*. Invertebrate non-target hazard assessment of caffeine application for control of *Eleutherodactylus* frogs. QA 978 Final Report. USDA, APHIS, WS, National Wildlife Research Center, Hilo, Hawai'i.

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

Price, S. 1983. Climate. Pages 59–66 *in* R. W. Armstrong, ed. Atlas of Hawaii. University of Hawai'i Press, Honolulu.

Raloff, J. 2003. Hawaii's hated frogs: Tiny invaders raise a big ruckus. Sci. News 163:11–13.

Rodda, G. H., and J. A. Savidge. 2007. Biology and impacts of Pacific island invasive species. 2. *Boiga irregularis*, the brown tree snake (Reptilia: Colubridae). Pac. Sci. 61:307–324.

Rödder, D., and S. Lötters. 2010. Explanative power of variables used in species distribution modelling: An issue of general model transferability or niche shift in the invasive greenhouse frog (*Eleutherodactylus planirostris*). Naturwissenschaften 97:781–796.

Schwartz, A. 1974. *Eleutherodactylus planirostris* (Cope). Pages 154.151–154.154 *in* Cat. Am. Amphib. Reptiles. Society for the Study of Amphibians and Reptiles.

Schwartz, A., and R. W. Henderson. 1991. Amphibians and reptiles of the West Indies: Descriptions, distributions, and natural history. University Press of Florida, Gainesville.

Seidel, M. E., and R. Franz. 1994. Amphibians and reptiles (exclusive of marine turtles) of the Cayman Islands. Pages 407–433 *in* M. A. Brunt and J. E. Davies, eds. The Cayman Islands: Natural history and biogeography. Kluwer Academic Publishers, The Netherlands.

Sin, H., K. H. Beard, and W. C. Pitt. 2008. An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. Biol. Invasions 10:335–345.

Singer, S. R. 2001. Viewpoint: Save the "Hawaiian" coqui! Hawai'i Island Journal, 16–20 September, 4–5.

Somma, L. A. 2010. *Eleutherodactylus planirostris*. http://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=61.

Stewart, M. M. 1977. The role of introduced species in a Jamaican frog community. Pages 113–146 *in* Actas del IV Simposium Internacional de Ecologica Tropical, Panama City.

Stewart, M. M., and G. E. Martin. 1980. Coconut husk-piles—a unique habitat for Jamaican terrestrial frogs. Biotropica 12:107–116.

Tuberville, T. D., J. D. Willson, M. E. Dorcas, and J. W. Gibbons. 2005. Herpetofaunal species richness of southeastern national parks. Southeast. Nat. 4:537–569.

Tuttle, N. C., K. H. Beard, and R. Al-Chokhachy. 2008. Aerially applied citric

acid reduces an invasive frog. Wildl. Res. 35:676–683.
Wilson, L. D., and L. Porras. 1983. The ecological impact of man on the South Florida herpetofauna. University of Kansas, Lawrence.
Woolbright, L. L., and M. M. Stewart. 2008. Spatial and temporal variation in color pattern morphology in the tropical frog, *Eleutherodactylus coqui*. Copeia 2008:431–437.
Wray, K., and R. Owen. 1999. New records of amphibians for Nassau County, FL. Herpetol. Rev. 30:237–238.
Wright, A. H., and A. A. Wright. 1949. Handbook of frogs and toads of the United States and Canada. Comstock Publishing Co., Ithaca, New York.