



U.S. Department of Agriculture
Animal and Plant Health Inspection Service
Wildlife Services

U.S. Government Publication

9 Frogs (Coqui Frogs, Greenhouse Frogs, Cuban Tree Frogs, and Cane Toads)

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INTRODUCTION

Amphibians are perhaps most well known for their highly threatened status, which often masks appreciation for the great numbers of species that are widespread global invaders (Kraus 2009). Both purposeful and accidental introductions of amphibians have occurred worldwide. Motivations for purposeful amphibian introductions include their use as biocontrol agents and culinary ambitions (Storer 1925; Kraus 2009). However, there are an increasing number of amphibians that are being accidentally introduced and becoming widespread (Kraus 2009). These introductions are in some ways more disconcerting because they may be the most difficult to prevent in the future.

There are 19 nonnative amphibians that have become successfully established in 28 of the 50 U.S. states (Figure 9.1; Kraus 2009). The most successful nonnative amphibian is the bullfrog (*Lithobates catesbeianus*), which has become established in 19 states outside of its native range on the eastern side of the United States, followed by the Cuban greenhouse frog (*Eleutherodactylus planirostris*), which has established itself in six states, and five frog species, including the Puerto Rican coqui (*E. coqui*), which are now established in three states outside of their native range (Figure 9.1; Kraus 2009). The state with the most nonnative frogs is California with eight species, followed by Hawaii with six, and Florida and Arizona with four (Table 9.1; Kraus 2009). Many nonnative amphibians in the United States, particularly in the western United States, are from other parts of the United States, namely, east of the Mississippi River. However, there are also many nonnative amphibians with tropical or subtropical origins that are primarily successful in tropical and subtropical states, such as Florida and Hawaii, and territories, such as Guam.

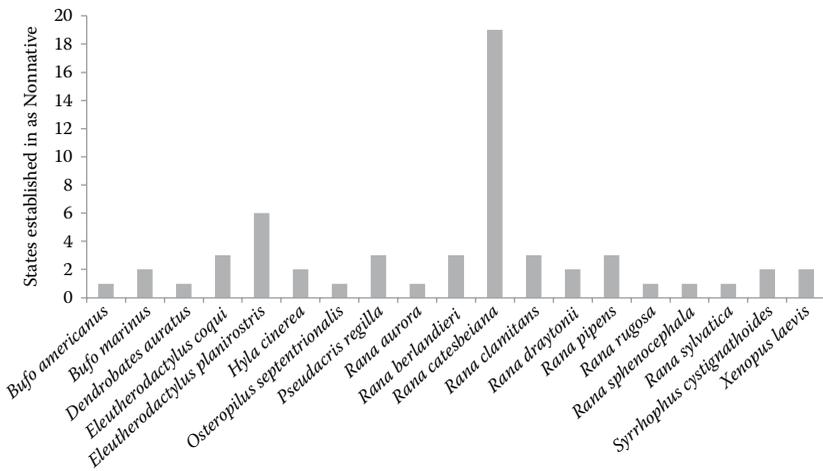


FIGURE 9.1 Number of U.S. states that have established nonnative frog species. (From Kraus, F., 2009, *Alien Reptiles and Amphibians: A Scientific Compendium and Analysis Series, Invading Nature—Springer Series in Invasion Ecology*, Dordrecht, Springer.)

TABLE 9.1
Number of Established Nonnative Frog Species by U.S. State

State/Territories	Number of Nonnative Frog Species
Alabama	1
Alaska	2
Arizona	4
California	8
Colorado	1
Florida	4
Georgia	1
Hawaii	6
Idaho	1
Illinois	1
Iowa	2
Kansas	1
Louisiana	2
Massachusetts	2
Minnesota	1
Mississippi	1
Missouri	1
Montana	1
Nebraska	1
Nevada	3
New Mexico	1
Oklahoma	1
Oregon	1
South Dakota	1
Texas	3
Utah	3
Washington	2
Wyoming	1
Territories	
American Samoa	1
Guam	5
Puerto Rico and islands	9
U.S. Virgin Islands	4

Source: Kraus, F., 2009, *Alien Reptiles and Amphibians: A Scientific Compendium and Analysis Series, Invading Nature—Springer Series in Invasion Ecology*, Dordrecht, Springer.

From an ecological perspective, the major concern with nonnative amphibians is a reduction in native species through competition or predation (Meshaka 2001; Beard and Pitt 2005) and the spread of chytrid fungus (Beard and O’Neill 2005), which has been devastating to amphibian populations around the world, including populations in the western United States (e.g., the boreal toad in Colorado and the



FIGURE 9.2 (a) Photograph of a coqui frog taken in Hilo, Hawaii. (Photo by Steve Johnson.) (b) Photograph of a greenhouse frog taken in Orlando, Florida. (Photo by Bob Fewster.) (c) Photograph of a Cuban tree frog taken in Lakeland, Florida. (Photo by Steve Johnson.) (d) Photograph of a cane toad taken in Lakeland, Florida. (Photo by Steve Johnson.)

mountain yellow-legged frog in California; Muths et al. 2003; Briggs et al. 2005). From an economic perspective, nonnative amphibians in the United States have lowered homeowner property values (Kaiser and Burnett 2006), cost the horticulture industry in terms of loss revenue and treating infestations (Beard et al. 2009), caused power outages (Johnson et al. 2010), and cost government agencies millions of dollars for management (Anonymous 2010). From a social perspective, nonnative amphibians have been blamed for noise pollution (Kalnicky et al. 2014) and producing toxic chemicals that harm humans and occasionally kill pets (Krakauer 1968; Reeves 2004).

Because this book is focused on terrestrial species, this chapter will review nonnative amphibians that are primarily terrestrial. For example, while the bullfrog is a notorious invader in the western United States (Kraus 2009), it will not be covered here because of its more aquatic lifestyle. Although salamanders, caecilians, and frogs are classified as amphibians, nearly 90% of all amphibian species are frogs, and indeed the most invasive amphibians are frogs. We will focus this chapter on two purely terrestrial species (Puerto Rican coqui and Cuban greenhouse frog; [Figure 9.2a,b](#)), meaning they do not require water for breeding, as well as two species that are primarily terrestrial but that use water bodies for breeding (Cuban tree frog and the cane toad; [Figure 9.2c,d](#)).

CASE STUDIES

COQUI FROGS (*ELEUTHERODACTYLUS COQUI*)

History of the Introduction and Spread

The coqui is endemic to the island of Puerto Rico but has been introduced to several areas in the United States. It was introduced to Florida in the early 1970s, likely via nursery plants (Austin and Schwartz 1975; Wilson and Porras 1983). It became established on the Puerto Rican islands of Culebra and Vieques and two U.S. Virgin Islands in the late 1970s and early 1980s (Rivero 1978; MacLean 1982). The coqui established in Hawaii in the late 1980s; it was brought over in nursery plants either from Puerto Rico or via Florida, which had populations in nurseries at the time (Kraus et al. 1999). The last reported population in Florida around the year 2000 (Meshaka et al. 2004). Florida populations may have died off because of cold winters. By 2001, the coqui had been collected from over 275 distinct locations throughout the islands of Hawaii, Maui, Oahu, and Kauai (Kraus and Campbell 2002). The coqui has been introduced to Guam and California from Hawaii (Campbell and Kraus 2002; Christy et al. 2007). In Guam, the few individuals introduced were quickly eradicated; in California, populations established outside of nurseries have not been confirmed.

While the coqui was once present on the four main Hawaiian Islands (Hawaii, Maui, Oahu, and Kauai), it currently only has established populations on the Big Island (Hawaii) and Maui. Genetic and morphological analyses indicate that populations on these islands started as two separate introductions; past populations on Oahu and Kauai came from the Big Island introduction (Peacock et al. 2009). Very diligent control operations were able to eradicate the coqui frog from Oahu and Kauai. Cooler climates, colder winters, and more manageable terrain might have played a role in these successful eradications, although there are continuing reports of individual calling frogs on these islands that are managed as incipient populations (Beachy et al. 2011; Pitt et al. 2012).

Currently, the coqui is widespread across the Big Island, particularly in the forested lowlands and on the windward side on the island, occupying over 30% of sites along major roads across the island (Anonymous 2010; Olson et al. 2012a). While there have been 36 different incipient populations reported on Maui (Kraus and Campbell 2002), after persistent control efforts, the coqui has been largely restricted to one last stronghold in Maliko Gulch on the north side of the island; however, calling individuals are occasionally reported in different parts of the island. The persistent Maliko Gulch population in Maui, as well as those on the Big Island, makes continuous monitoring, management, and control of incipient populations a reality on Maui as well as Oahu and Kauai.

Once established in Hawaii, interisland and within-island movement of nursery plants played a strong role in their spread, although hitchhiking on vehicles also likely contributed (Peacock et al. 2009; Everman and Klawinski 2013). Many new coqui populations begin adjacent to nurseries, such as the previously established Kauai population (K. Beard, pers. obs.). On the Big Island and Oahu, many landowners state that they started hearing coquis calling after they placed recently purchased nursery plants in their yards (Kalnicky et al. 2014). There were also intentional

introductions. In the early 2000s, people on the Big Island moved coquis to state parks where they deposited individuals near the parking areas in an effort to make the coqui too widespread to eradicate and as a misguided insect control effort (Beard and Pitt 2012).

Traits That Help Them Establish

The coqui is a small frog, with mean snout-vent length (SVL) around 34 mm for males and 40 mm for females (Beard 2007), which probably helps it establish because it may go undetected. It has direct development, meaning there is no free-living tadpole phase and metamorphosis occurs within the egg to produce froglets (Townsend and Stewart 1985, 1994). Coqui typically lay their eggs in leaf litter or rock crevices, but also can reproduce in man-made objects, such as nursery pots, as long as there is sufficient moisture (Beard et al. 2003). Direct development, along with year-round breeding, means that unlike some other frog species, the coqui does not require a landscape feature (such as a water body) or many other individuals, such as breeding chorus, to reproduce. Each clutch has, on average, 28 eggs (Townsend and Stewart 1994).

The coqui frog has male parental care, such that the male frog sits and guards the eggs before and a few days after hatch, which prevents desiccation and predation (Townsend et al. 1984). Because of this, if a male protecting a clutch is introduced, the eggs will be protected during transport, and tens of individuals could be introduced from a single introduction event. Genetic diversity of coquis was greatly reduced when they invaded the Big Island and Maui, yet they continued to establish successfully and reach extremely high densities (Peacock et al. 2009). Furthermore, findings from Peacock et al. (2009) suggest that a single clutch may be sufficient to establish a population.

The coqui is a generalist sit-and-wait predator (Woolbright and Stewart 1987; Beard 2007). In Hawaii, it consumes primarily leaf litter invertebrates, such as ants, amphipods, spiders, beetles, roaches, springtails, and mites, but shifts its diet at different sites based on availability (Beard 2007). The coqui is found in Hawaii and Puerto Rico from 0 m to 1200 m above sea level (as reviewed in Beard et al. 2009), and within this elevation range it is generally found anywhere that has adequate humidity and cover (Schwartz and Henderson 1991). In Hawaii, it is mostly found in lowland forests on the eastern side and in private residences. The elevation limit and associated minimal survival temperature of the coqui in Hawaii is unknown, but it has not established populations above 1200 m in the over 25 years since its introduction.

Scope of the Issues/Damage Caused by the Species

The coqui frog has one of the highest densities of any terrestrial frog species in the world. In its native Puerto Rico, densities are typically around 20,000 frogs/ha, but in some areas in Hawaii it has been documented to reach densities up to 90,000 frogs/ha and consume 690,000 invertebrates/ha/night (Woolbright et al. 2006; Beard et al. 2008). Because of its high densities and generalist feeding behavior, it was hypothesized to reduce invertebrates and change ecosystem functions (Beard and Pitt 2005). The coqui has been found to change invertebrate communities across the Big Island (Choi and Beard 2012). Leaf litter insects such as mites and ants,

in particular, are reduced where coquis invade, whereas flies increase (Choi and Beard 2012). Furthermore, coquis have been associated with increases in leaf litter decomposition rates, increased nutrient cycling rates, and faster growth rates of nonnative plants (Sin et al. 2008). While it has been hypothesized that coquis may compete with native insectivorous birds, recent research does not support this (Smith et al. 2017, Smith 2016). They have been hypothesized to bolster introduced mammal populations (Kraus et al. 1999), but this hypothesis has not yet been fully explored. Finally, because coquis do not appear to be affected by, but can be carriers of, chytrid fungus, their introductions could impact native amphibians by carrying this and other diseases (Beard and O'Neill 2005). This is not an issue in Hawaii, where there are no native amphibians, but could be important in other invaded areas.

From an economic perspective, the coqui has negatively influenced the floriculture industry and homeowners. The floriculture and nursery industry in Hawaii produces over \$100 million annually (Hara et al. 2010). For the floriculture industry, because coquis are mostly transported via plants, economic impacts include decreased sales, destruction of plant shipments, increased costs to control infestations, and increased quarantine procedures (Beard et al. 2009). Plant shipments from Hawaii to Guam, the continental United States, and other countries require a phytosanitary certificate that certifies shipments are pest-free. Interisland and international plant shipments from the Big Island, in particular, are supposed to be inspected and treated prior to shipment. This is often done by bathing plants using a hot water treatment (Hara et al. 2010). While some hotels and resorts have complained of potential loss of revenue, economic loss has only been documented for private landowners (Kaiser and Burnett 2006). Kaiser and Burnett (2006) found that complaints about the loud frog calls were related to housing prices, and that the closer the complaint to the marketed property, the greater the reduction in the housing price. While the Big Island housing unit drop in price associated with coqui establishment was almost always less than 1%, property values were estimated to drop \$7.6 million islandwide as a result of coquis. Furthermore, businesses, private landowners, and local, state, and federal government covered the cost of managing coquis. At its highest point in the late 2000s, public agencies were spending \$4 million per year to control the frogs (Anonymous 2010; Beard and Pitt 2012).

The primary public concern over the coqui has to do with its extremely loud mating call. The coqui produces a two-note mating call, which sounds like “ko-kee” (80–90 dB at 0.5 m) and exceeds the noise level set to minimize impacts for enjoyment of life (70 dB, Department of Health, Hawai'i Revised Statutes Section 324F-1; Beard and Pitt 2005). In Hawaii, there has been a lot of support by the general public in the form of coqui control groups to eradicate the coqui. These groups raised funds to rent or purchase control equipment, and invested endless hours of volunteer time monitoring and controlling populations (Anonymous 2010; Beard and Pitt 2012). Despite much local support in Hawaii for coqui suppression or eradication, there were also people that enjoyed the call of the coqui while others became accustomed to it (Kalnicky et al. 2014). More specifically, Kalnicky et al. (2014) found that people with more frogs on their property and those who owned property tended to have less-negative attitudes toward the frog. If tolerance for the species is in fact growing, that would hinder attempts to engage the general public in control efforts.

Historic and Current Management

Control efforts for coquis have primarily been performed in Hawaii, despite Guam and California placing restrictions for live plant importation from Hawaii as well as unlawful possession of coqui without permit (Hara et al. 2010). Since the frog's introduction to Hawaii, many control measures have been considered (Pitt et al. 2012). Some of the most effective measures identified for killing frogs were not approved for use because they were not deemed safe for nontargets or humans, or accepted by the general public (Pitt et al. 2012). Furthermore, most control measures were only found to work in limited situations, not across large areas with varying environmental conditions (Pitt et al. 2012).

Chemical control has been the most effective means of controlling coqui frogs. The U.S. Department of Agriculture (USDA) tested 90 chemical agents (agricultural pesticides and pharmaceutical and household products) and 170 chemical formulations as potential frog pesticides (reviewed in Pitt et al. 2012). Eight chemicals killed frogs, but only three were ever approved for control (Pitt et al. 2012). From 2001 to 2002, a 2% caffeine solution was approved for limited use and was very effective, but was not approved for widespread use because of human health concerns and a lack of public support (Pitt et al. 2012). From 2005 to 2008, a 6% hydrated lime solution was approved to control coquis but later discontinued because of caustic effects; it killed vegetation. Homeowners liked using hydrated lime because it was inexpensive (Pitt et al. 2012). In 2002, 16% citric acid, a food additive, was approved for widespread use and it is the only chemical currently approved for controlling frogs in Hawaii (Pitt et al. 2012). Citric acid has been used by landowners, government agencies, and nurseries to control coquis (Hara et al. 2010). For example, in 2005 alone, over 24,000 kg of citric acid was used to control coquis on Maui (L. Strohecker, pers. comm.). The successful eradication of hundreds of calling frogs on Oahu can be attributed to years of spraying citric acid using ground operations (Beachy et al. 2011).

Mechanical methods have also been evaluated for controlling coqui frogs, including hot water treatments, traps, vegetation management, hand capture, and barriers (Pitt et al. 2012). Frogs and their eggs are killed when exposed to hot water or steam applied for three minutes at 45°C (Hara et al. 2010). These methods are particularly important to prevent movement of coqui frogs via plant shipments because they often do not harm plants, unlike citric acid, which has phytotoxic effects. Traps have been developed that capture frogs, and thus they can be removed if diligently checked; however, frogs can use some traps to breed in, such as polyvinyl chloride (PVC) pipes (Stewart and Pough 1983), and they have not been effective at reducing populations (reviewed in Pitt et al. 2012). Vegetation management can reduce and help eradicate coqui frogs (Kalnicky et al. 2013). Experiments removing 100% of leaf litter and 100% understory vegetation showed marked reduction in coqui populations (Kalnicky et al. 2013). Removing tree canopies to create gaps in tree stands also reduced the coqui population (Klawinski et al. 2014). Hand capturing and erecting barriers can be effective in small areas, such as in and around greenhouses, on private yards, and with other incipient populations (reviewed in Pitt et al. 2012). For example, hand capturing prevented the coqui from establishing in Guam when they came over in a plant shipment from Hawaii (Beard et al. 2009). Investigating shipments for frogs as they come in may be the most critical step in stopping some introductions.

Biological controls have probably been the least explored. Chytrid is already established in coqui frog populations in Hawaii, and coquis are relatively resistant to the disease (Beard and O'Neill 2005). Research to identify parasites has not found one that reduces growth or survival (Marr et al. 2010). However, the high density of coqui frogs in their native range suggests that even if predators or parasites from Puerto Rico could be identified, they are unlikely to eradicate populations and biological controls bring associated risk (Pitt et al. 2012).

Combinations of management approaches can be important in the successful eradication of coqui frogs. The Kauai eradication, in particular, involved a great amount of vegetation removal, covering about 6 ha in addition to continual citric acid spraying (Pitt et al. 2012). However, once large populations are established in difficult terrain and in remote areas, even the most intensive efforts can make eradication impractical. For example, attempts to eradicate coquis from Manuka Natural Area Reserve on the Big Island and Maliko Gulch on Maui using large-scale citric acid helicopter drops, semipermanent spray systems, and ground operations have not been successful despite measurable reductions in coquis for periods of time (Tuttle et al. 2008; Anonymous 2010; Beard and Pitt 2012; Pitt et al. 2012). The terrain in these locations, including rock crevices and steep slopes, makes complete eradication of coquis from these areas unlikely because it is hard to spray all areas, and because coquis can hide from chemical spray in abundant crevices, particular during daytime spraying (K. Beard, pers. obs.). In the case of both the Oahu and Kauai eradications, the populations were isolated, the terrain was less difficult to maneuver through, and there were fewer rock crevices than the previously mentioned Big Island and Maui sites (K. Beard, pers. obs.). If the coqui invades other areas where the terrain is not as difficult and the sites are not as remote, methods developed to control coquis in Hawaii may work. Vegetation removal with citric acid spraying appears particularly effective at reducing populations.

GREENHOUSE FROGS (*ELEUTHERODACTYLUS PLANIROSTRIS*)

History of the Introduction and Spread

The greenhouse frog is native to Cuba and the Bahamas (four islands). It is one of the most widespread frog species in the world. Within the United States, it has become established in Hawaii (on five islands), Florida (widespread on the peninsula), Alabama (one county), Georgia (five counties), Louisiana (10 parishes), Mississippi (one city), and on Guam (widespread) (Olson et al. 2012b). Internationally its spread is beginning to be appreciated in Mexico, the Philippines, and on many Caribbean Islands (Kraus et al. 1999; Olson et al. 2014; Rogelio Cedeno-Vazquez et al. 2014). The first report of this frog in the United States occurred in Florida in the late 1800s; it is possible they established naturally, perhaps via driftwood (Goin 1947; Meshaka et al. 2004; Heinicke et al. 2011). The greenhouse frog is thought to have established itself in Hawaii in 1994 (Kraus and Campbell 2002). It first appeared in Hawaii in plants imported from Florida, and in Guam in 2003 in plants imported from Hawaii. Its spread is likely almost exclusively attributable to accidental introductions, primarily through the floriculture trade but also probably through cargo (Kraus et al. 1999).

In general, its introductions and spread have not been well studied (Olson et al. 2012b). Part of the reason for this may be its cryptic nature and relatively quiet mating call (Kraus and Campbell 2002). For example, *Eleutherodactylus planirostris* and *E. coqui* invaded Hawaii around the same time, and while there were many complaints about the coqui and a large effort was launched to control its spread, few funds were directly spent on controlling the greenhouse frog. This might explain why the greenhouse frog became more widespread on the Big Island than the coqui frog (Olson et al. 2012a). In a study designed to determine their distributions on the Big Island, greenhouse frogs were found to occupy 35% of sites along the major road systems around the island compared to 31% for the coqui (Olson et al. 2012a). While no systematic surveys have confirmed the distribution of greenhouse frog across the other Hawaiian Islands, they are thought to be widespread on Oahu, Kauai, and Maui (Olson et al. 2012b). Similarly, the greenhouse frog has become widespread in Florida and Guam. In Florida, greenhouse frogs are found throughout the peninsula and at a growing number of locations in the state's panhandle, predominantly in coastal areas (Krysko et al. 2011). Recent studies show that they are also spreading in Alabama (Alix et al. 2014) and Mississippi (Mann et al. 2015).

Traits That Help Them Establish

The frog is small (SVL on average 24 mm) and cryptic. It is brown in color and blends in with leaf litter and soil, where it is mostly found. Like the coqui frog, it has direct development; therefore, it does not need a water body to breed in; can lay eggs leaf litter, rock crevices, or soil; and unlike other members of the genus, there is no guarding of the eggs (reviewed in Olson et al. 2012b), which may increase the chances of an inadvertent introduction. Each clutch has, on average, 16 eggs (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 (Goin 1947).

While the greenhouse frog consumes a diversity of invertebrates including spiders, mites, springtails, and beetles in the leaf litter, the large majority of its diet is typically ants (Goin 1947; Stewart 1977; Olson and Beard 2012; Ferreria et al. 2015). This specialization on ants may assist their establishment into previously uninvaded areas, considering that ants comprise the majority of invertebrate biomass in tropical areas (Hölldobler and Wilson 1990). The greenhouse frog has invaded areas like Guam and Florida, with high potential predator densities (as reviewed in Olson et al. 2012b). However, this does not appear to have controlled frog establishment and spread.

The greenhouse frog has a high tolerance for warm and dry conditions compared to other *Eleutherodactylus* species; for example, it has established itself in Florida, whereas the coqui did not (Olson et al. 2012b). Furthermore, on the Big Island, the coqui and greenhouse frog overlap in about a third of their occupied sites; yet, the greenhouse frog is more often found in drier sites on the western side of the island (Olson et al. 2012a). In Florida and Hawaii, it is common in wet and dry forests, open grasslands and pastures, coastal areas, scrub habitats, nurseries, residential gardens, and resort areas (Meshaka et al. 2004; Olson et al. 2012a). Its distribution in its

nonnative range appears to reflect warmest-month temperatures in Cuba, but in the southeastern United States, it lives in areas as cool as 4°C (Tuberville et al. 2005; Rödder and Lötters 2010). In Hawaii, it has been detected from sea level up to 1115 m (Olson et al. 2012a).

The soft call of the greenhouse frog, with sound pressure levels around 35–45 dB at 0.5 m (K. Beard, unpublished data), prevents reporting of new infestations. A clear example of how the quieter call and more cryptic nature of the greenhouse frog, compared to the coqui frog, likely facilitated their range expansion is their comparative histories in Guam. When the coqui was introduced to Guam, its establishment was prevented very shortly after it came out of shipments. The greenhouse frog, on the other hand, established and rapidly spread (as reviewed in Christy et al. 2007; Olson et al. 2012b). In addition, through conversations with private landowners in Hawaii, most residents were aware when coquis were on their properties but many did not recognize the call of a greenhouse frog, and when they were informed that it was indeed a frog they said they did not mind the sound (K. Beard, unpublished data). Public opinion influences invasive species management in Hawaii; citizens have been very involved in control coqui frogs. The lack of public concern or awareness about the greenhouse frog likely contributed to its spread.

Scope of the Issues/Damage Caused by the Species

The greenhouse frog is most likely to impact leaf litter invertebrates where it invades because it only moves vertically several centimeters from the ground and has an insectivorous diet (Olson and Beard 2012). Assessments of ecological impacts of greenhouse frogs are most common in Hawaii, although their impacts are probably transferrable to other locations where they have invaded. Their densities have been estimated to reach up to 13,000 frogs/ha in Hawaii, and they have been estimated to consume 129,000 invertebrates/ha/night (Olson and Beard 2012). Also, in Hawaii, the greatest concern may be their potential to reduce rare or threatened populations of invertebrates. In other areas, where there are native frogs or other native species that depend on the leaf litter community, the greenhouse frog may compete with them for prey. The greenhouse frog may alter nutrient cycling, like the coqui frog (Sin et al. 2008), or serve as a food source for nonnative predators. Brown tree snakes in Guam are thought to consume greenhouse frogs (Mathies et al. 2012). Although they are likely consumed by a diversity of small carnivorous animals, documented predators of greenhouse frogs in the southeastern United States are exceedingly few (Meshaka et al. 2004; Jensen 2008; Dodd 2013).

Similar to the coqui frog, the greenhouse frog has impacted the floriculture industry in Hawaii. There is no summary of the amount of funds expended to control greenhouse frogs, but because intentional transport of frogs into the State of Hawaii is illegal (Kraus and Campbell 2002), it is very likely that nursery owners expend funds to keep their nurseries pest-free when they have infestations as well as treat shipments going off the island. Unfortunately, because greenhouse frogs are less obvious than coquis, greenhouse frogs and frog eggs are probably not detected as frequently in shipments as are the coqui. In addition, some resorts in Hawaii have attempted to reduce greenhouse frogs on their properties with moderate success, as described in the next section (Olson et al. 2012b).

Historic and Current Management

Unlike the coqui frog, the greenhouse frog has not been the target of large-scale control or eradication efforts in Hawaii or elsewhere that we know of. However, many of the same chemicals that were found to kill coquis are equally effective on greenhouse frogs (government documents supporting this are reviewed in Olson et al. 2012b). Specifically, 16% citric acid solution is 100% effective at killing greenhouse frogs in laboratory conditions (reviewed in Olson et al. 2012b). In addition, hydrated lime and caffeine are effective but currently not permitted for *Eleutherodactylus* control in Hawaii (Kraus and Campbell 2002; Pitt et al. 2012). In locations where coquis are sympatric with greenhouse frogs, both species were likely reduced by efforts targeting coquis. Because there have been almost no large-scale efforts to control greenhouse frogs, they have spread unabated in most places where they have been introduced. However, the chemical control measures developed for coqui frogs would be effective in controlling or reducing them (reviewed in Olson et al. 2012b) and should be considered as a management option.

Many of the mechanical controls described for coqui frogs would also work on greenhouse frogs. For example, hot water treatments are effective at killing *Eleutherodactylus* species (Hara et al. 2010) and should be required in any area shipping plant material where there are infestations. Traps may work on greenhouse frogs, and one of the most common locations to find greenhouse frogs at any site in Hawaii is an irrigation box (Ferreria et al. 2015). While hand captures of greenhouse frogs may be less effective than for coqui frogs because the greenhouse frog is smaller and more cryptic, hand capturing from irrigation boxes at several resorts in Hawaii did result in lower populations over time (as reviewed in Olson et al. 2012b). Leaf litter removal may be particularly effective for greenhouse frog control because they are often found close to the forest floor (Olson et al. 2012b; Kalnicky et al. 2013). While not tested on greenhouse frogs, barriers may also be effective in small areas (as reviewed in Olson et al. 2012b).

CUBAN TREE FROGS (*OSTEOPILUS SEPTENTRIONALIS*)

History of the Introduction and Spread

The Cuban tree frog, as its common name implies, is native to Cuba (including Isle of Pines) as well as the Cayman and Bahama islands (Schwartz and Henderson 1991). Individuals have been introduced to numerous islands of the West Indies and populations are established on several of these islands, including Puerto Rico and the U.S. Virgin Islands (Lever 2003; Kraus 2009). In the United States, Cuban tree frogs are only established in peninsular Florida; however, there are numerous isolated records of the species from many counties in the state's panhandle (Johnson 2007). Additional records of single frogs have been reported from other states, especially in the southeastern United States.

The first Cuban tree frogs from Florida were observed in the late 1920s in Key West, and they most likely were transported there inadvertently as stowaways in cargo on boats from Cuba (Barbour 1931). However, some authorities suggest Cuban tree frogs may have also colonized the Florida Keys naturally (Meshaka 2001). Based

on records maintained by the Florida Museum of Natural History at the University of Florida, by the early 1930s the frogs had made their way to the southern extreme mainland of Florida. Records into the 1950s are also confined to the southern tip of the peninsula, but 20 years later the frogs had been documented throughout much of the southern third of the peninsula. By the 1990s, Cuban tree frogs could be found as far north as Orlando, with records from several counties even further up the Atlantic Coast of Florida. By 2010, they had been recorded from every county in the peninsula and were established as far north as Cedar Key on Florida's Gulf Coast, Gainesville in north-central Florida, and Jacksonville on the Atlantic Coast.

Traits That Help Them Establish

Cuban tree frogs are the largest species of tree frog in the United States (Dodd 2013), and this facilitates their ability to consume large prey. They show pronounced sexual size dimorphism, and the largest male reported in Florida is 85 mm SVL and the largest female is 122 mm SVL (McGarrity and Johnson 2009). They are generalist predators that consume a great variety of invertebrates dominated by spiders, roaches, and beetles, as well as small vertebrates including native tree frogs (Meshaka 2001; Glorioso et al. 2012; Johnson, unpublished).

Females are quite fecund, and Meshaka (2001) reported clutch sizes from 1177 to 16,371 eggs based on a sample of 153 females from the Florida Everglades. They breed in a diversity of water bodies ranging from retention ponds to shallow cypress swamps (Dodd 2013). They also breed in ornamental fishponds, rain barrels, and swimming pools that are not well chlorinated. In northern and central Florida, they reproduce during the spring and summer, but may be reproductively active any time of the year in extreme southern Florida. Larval development (tadpole stage) to adult transformation can occur in the field in three to four weeks (Meshaka 2001).

In natural areas, Cuban tree frogs prefer closed canopy, forested habitats and tend to avoid more open habitats (McGarrity and Johnson 2010). They are common in moist tropical hardwood hammocks, bottomland forests, cypress swamps, and mangrove swamps, but also occur in pine rocklands, pine flatwoods, sandhills, and xeric hammocks (Meshaka 2001; Johnson 2007; Campbell et al. 2009; Rice et al. 2011). They also inhabit human-modified environments, such as Brazilian pepper stands, orange groves, agricultural landscapes, and urban/suburban neighborhoods. In urban and suburban settings, they are found on buildings and homes, and among landscape plants.

Cuban tree frogs have exceptionally large, sticky toe pads and are excellent climbers. Their affinity for human-modified environments (e.g., suburban settings), tendency to hide in confined spaces, and ability to climb well certainly facilitates their invasion of new habitats via human transport. The main invasion pathway for Cuban tree frogs within the state of Florida and beyond is via hitchhiking on vehicles and trailers, as well as on ornamental plants, especially palms (Meshaka 1996). They also have the ability to move rapidly from open, inhospitable areas to preferred habitats (McGarrity and Johnson 2010).

Tadpoles and adults tolerate a broad range of water temperatures. Meshaka (2001) reported finding Cuban tree frog tadpoles in water ranging from 12°C to 41°C. As expected, tadpoles in warm water reached metamorphosis much faster (three to four

weeks) than those in colder water (five to six months). Although prolonged exposure to below freezing temperatures in the wild is lethal to adults and can lead to local declines of Cuban tree frog populations (S. Johnson, unpub. data), they are surprisingly tolerant of short-term exposure to cold (Simpson 2013). Although several species of native snakes and birds are documented predators of Cuban tree frogs, Cuban tree frogs exhibit several antipredator behaviors (e.g., crypsis, large body size, and sheltering in confined spaces) and emit noxious skin secretions (Meshaka 2001) that likely make them less palatable than native tree frogs to potential predators.

Scope of the Issues/Damage Caused by the Species

Cuban tree frogs in Florida are a quintessential invasive species. They cause detrimental ecological and economic impacts, and they negatively affect quality of life for some Floridians. They readily consume small vertebrates and their large gape allows adult Cuban tree frogs of both sexes to capture and swallow native tree frogs (Wyatt and Forsy 2004; Glorioso et al. 2012). In fact, they are now the most commonly encountered tree frog in urban and suburban neighborhoods in much of peninsular Florida, likely due to their predation of native green and squirrel tree frogs (S. Johnson, pers. obs.). They may also depress populations of native tree frogs in natural areas. Cuban tree frogs reduced capture probability of native tree frogs and dominated captures in PVC pipe refuges at sites in south and central Florida during three different studies in which hundreds of frogs were encountered (Campbell et al. 2010; Waddle et al. 2010; Rice et al. 2011). These findings are even more astounding considering the fact that Cuban tree frogs prefer a more natural hiding place over a PVC pipe refuge, at least in an experimental setting (Hoffmann et al. 2009). Although there are no empirical data available, it seems possible, given their density in some natural areas and their broad diet, that Cuban tree frogs might compete for food with native species. Additionally, Cuban tree frog tadpoles were found to be superior competitors against two native species of tadpoles in controlled experiments (Knight et al. 2009), and Cuban tree frog tadpoles are documented predators of native *Hyla squirella* tadpoles (Smith 2005). Cuban tree frogs will also invade bird nest boxes erected to benefit native wildlife. However, the prevalence of this behavior and its potential effect on use of nest boxes by native birds has not been studied to our knowledge. In addition, how Cuban tree frogs use natural tree cavities is unknown.

The close association of Cuban tree frogs with human-dominated landscapes and the frogs' propensity to seek tight, enclosed spaces during the day has led to negative economic impacts. Although poorly documented and in need of additional research, Cuban tree frogs have been responsible for short-circuiting electrical equipment. In one instance, a Cuban tree frog was deemed responsible for invading a switchgear box and causing a short circuit leading to a \$20,000 repair for the Lakeland Electric company (Johnson et al. 2010). An engineer with Lakeland Electric reported that Cuban tree frog invasion of other equipment has also led to power outages, but no estimates of monetary damages were given (S. Perkins, pers. comm.). Cuban tree frogs are also known to have caused damage to air conditioner compressor units and water pumps, which had to be repaired at cost to the homeowner (S.A. Johnson, pers. obs.). An additional economic burden, which has yet to be quantified, is the cost to

Floridians resulting from hospital visits by children and pets as a result of Cuban tree frog poisoning. When handled or harassed, the frogs secrete a sticky substance that is extremely irritating to mucous membranes (S.A. Johnson, pers. obs.). If the frog's secretion gets into a child's eyes, it causes an intense burning sensation, and we know of at least one instance when a young boy had to be taken to an emergency room for treatment resulting from the child's handling of a Cuban tree frog. Although we do not know of any deaths of pets, we have communicated with people who report their cat or small dog had health issues after encounters with Cuban tree frogs; significant costs were incurred for veterinarian care that resulted from such exposure. It seems probable that cases of Cuban tree frog poisoning in pets and children go unreported and undiagnosed.

Cuban tree frogs often inadvertently invade homes and become a serious nuisance to people. They do so by jumping through an open door or window, catching a ride on a potted plant brought inside, and often via plumbing vent stacks located on the roofs of homes (Johnson 2007). Once in the plumbing system, they can make their way to toilets and sinks. It is not uncommon for Florida residents to contact the University of Florida's (UF) Cooperative Extension Service with an image of a Cuban tree frog in a toilet requesting advice on identification and removal of the interloper. At night, Cuban tree frogs perch on windows and walls of homes and buildings to feed on insects attracted to lights. As a result, the frogs leave unsightly feces on the sides of people's homes.

Though nowhere near the magnitude of the problem caused by coqui frogs in Hawaii, an additional annoyance caused by Cuban tree frogs that has been consistently reported to UF Extension is the racket from their breeding choruses. The call of male Cuban tree frogs is a squeaking raspy sound and, compared to native species, does not sound very loud. Nonetheless, the density of these pests around homes, and the fact that they breed in ornamental ponds and poorly maintained swimming pools near bedroom windows, has resulted in people losing sleep (S.A. Johnson, unpublished data). However, we do not know of any studies that have measured the volume of their mating calls.

Historic and Current Management

There is no agency-led, statewide plan to manage Cuban tree frogs on public lands. Instead, most Cuban tree frog control efforts occur at local scales on private property and are conducted by citizens. These people most often initiate hand-removal of Cuban tree frogs after viewing educational materials or receiving guidance from the UF Cooperative Extension Service, including their website (<http://ufwildlife.ifas.ufl.edu>). Goals of these localized removal efforts are often twofold: (1) people remove frogs and take action on their property to help mitigate the nuisances caused by this pest, and (2) they seek to reduce the number of frogs with the hope that native frogs will benefit.

Hand-capture and removal of Cuban tree frogs via PVC pipes are the two methods recommended by the UF Cooperative Extension Service to people who wish to remove the frogs from their property (Johnson 2007). After capture, citizens are directed to apply liberally a benzocaine-containing ointment to the frogs until they are anesthetized and then secure the frogs in a plastic bag and place them in

the freezer for 24 hours (http://ufwildlife.ifas.ufl.edu/cuban_treefrog_inFL.shtml). Another humane method of euthanasia for Cuban tree frogs and other small ectotherms, including cane toads, is to place individual frogs in a standard refrigerator for several hours then transfer them to a freezer overnight to ensure death (Shine et al. 2015). Although the efficacy of PVC pipe refuges has been questioned (Wyatt and Forsy 2004) and there is bias among tree frog species in their propensity to shelter in PVC pipe “traps” (Hoffmann et al. 2009), Rice et al. (2011) found no evidence that Cuban tree frogs were behaviorally excluding native species from the pipes. Therefore, this passive sampling method remains an efficient means for Cuban tree frog removal. Additional strategies used as part of an integrated pest management plan for Cuban tree frogs on local scales include eliminating breeding opportunities (e.g., keep pools well chlorinated, dump out standing water, exclude frogs from rain barrels/cisterns), management of eggs and tadpoles (e.g., net egg masses from the surface of ponds, dump out containers with tadpoles), and excluding frogs from hiding places around homes.

The most common pathway for invasion of human dwellings by Cuban tree frogs is via plumbing vent pipes located on the roofs of buildings. Cuban tree frogs apparently enter the pipe seeking shelter from desiccation and eventually find their way to toilets and sinks. Commercially available covers can be placed on the vent pipes or hardware cloth can be cut and attached with cable ties to the pipes to exclude frogs. Homeowners can also purchase and apply a proven wildlife chemical deterrent that has been shown to be effective for dissuading Cuban tree frogs from enclosed spaces. In response to problems that Cuban tree frogs were causing for electric generating utilities, Johnson et al. (2010) tested the ability of the product “Sniff ‘n’ Stop” (ICORP-IFOAM Specialty Products Corporation, <https://sniffnstop.com>) to repel Cuban tree frogs. They tested several versions of the product (foam, gel, tape, epoxy) in controlled laboratory experiments. Although none of the applications of “Sniff ‘n’ Stop” were 100% effective at excluding frogs, they all deterred frogs from using treated hiding places.

CANE TOADS (*RHINELLA MARINA*)

History of the Introduction and Spread

Cane toads are native to Central and South America and extreme south Texas (Conant and Collins 1991). They are thought to be the most widespread amphibian in the world, and they are established in at least 40 countries (Lever 2001). Starting in the 1920s, cane toads were introduced to many areas to control pests in sugarcane plantations (Krakauer 1968). Internationally, they are established on islands throughout the Caribbean and Oceania. Cane toads were introduced to Puerto Rico in 1920 with a second group in 1923 (Schwartz and Henderson 1991). The introduction of the cane toad to Puerto Rico was deemed a success at controlling the white-grub on sugarcane (Anonymous 1934), but later its role in reducing the pest was questioned. However, in many ways, the damage was done once the Puerto Rico cane toad population was deemed successful, and they were quickly introduced elsewhere. By 1932, they were well established in Puerto Rico and introduced from there to Oahu. They established themselves quickly in Oahu, and were moved to the

other Hawaiian Islands (Easteal 1981). Cane toads were introduced to Guam in 1937 (Christy et al. 2007) and have also been introduced into the Northern Marianas and American Samoa in the Pacific, as well as in the U.S. Virgin Islands in the Caribbean (Lever 2001).

Initial releases in the 1930s and 1940s in Florida to control sugarcane pests were not thought to result in establishment. It appears that later accidental releases in the airport and by pet dealers, in the 1950s and 1960s, established the populations that continue to persist today (Krakauer 1968). Introductions to Louisiana were unsuccessful (Easteal 1981). Cane toads were introduced from Hawaii to Australia, where they are particularly problematic (Krakauer 1968). They are cold intolerant and therefore are unlikely to become widespread in most parts of the continental United States. However, recent research on cane toads in New South Wales, Australia, demonstrated that toads have the ability to acclimate rapidly to low temperatures (McCann et al. 2014). It has been noted that while their populations expand and increase quickly, they also experience precipitous drops in population size (Simberloff 2004). This was noticed in Puerto Rico and in Australia with no clear indication of why these population drops occurred; the populations in Puerto Rico never recovered (Freeland 1986).

Traits That Help Them Establish

Cane toads are large frogs, with lengths and sizes varying across populations, but reaching up to around 100–150 mm SVL in Florida (Marshall and Meshaka 2006) and 80 mm SVL in Hawaii (Beard and Pitt 2006). Their large size may help them avoid predation and outcompete other anurans. Their skin is resistant to desiccation, which helps them survive in arid conditions, such as the dry seasons of tropical environments (Duellman and Trueb 1986). Similar to the Cuban tree frog, they have minimal requirements for breeding other than presence of sufficient water (saline or fresh) for their eggs to hatch and mature, which can include small ditches (Ely 1944; De León and Castillo 2015). Salt water does not seem to deter cane toads, and adults are able to survive in salinities of up to 40% sea water (Liggins and Grigg 1985); they have been observed swimming in the sea and crossing 600 m of salt water between two islands (Lever 2001). Furthermore, Lever (2001) reports several observations of cane toads spawning in brackish water and calling on tidal mudflats.

Like most invasive species, cane toads are highly fecund, and females produce clutches of approximately 20,000 eggs (Hagman and Shine 2008). The time required for eggs to mature varies with climate, but they typically hatch within 48 hours, and it takes about 30 days for tadpoles to mature. Sexual maturity in cane toads can be reached within one year, depending on the environment (Shanmuganathan et al. 2010). They breed year round (Doody et al. 2014). Their generalist diet, which includes both vertebrates and invertebrates, has almost certainly helped them attain high population densities (over 2000 frogs/ha) in their introduced ranges (Freeland 1986). Finally, eggs, tadpoles, and adults are poisonous to many predators as they contain bufadienolides (alkaloid substances toxic to vertebrates), which make cane toad control via natural predators in the environment challenging (Shanmuganathan et al. 2010).

Habitat modeling in Australia has predicted that cane toads will greatly expand their current distribution of northern and eastern Australia because they can tolerate temperatures of less than 5°C (e.g., southeast Australia) and temperatures of greater than 37°C (e.g., parts of the Northern Territory) (Urban et al. 2007). Similar limits may exist in the United States. Cane toads also appear to favor open and human-disturbed habitats, such as roadside, urban, and suburban areas (Urban et al. 2007); diurnal shelters are important for maintaining body temperature and moisture year round but especially outside of the wet season (Seebacher and Alford 2002).

Scope of the Issues/Damage Caused by the Species

The cane toad can be devastating from an ecological perspective. The species has primarily been researched in Australia, where studies of its impacts have shed light on the invasion process in general. Because every part of their life cycle can be poisonous to predators, cane toads can have severe effects on potential predators and most specifically on native reptiles and mammals in Australia. They have been predicted to affect a large number of species in Australia (Phillips et al. 2003; Beckmann and Shine 2012); declines in snakes and crocodiles, in particular, as well as native mammals have been attributed to the cane toad invasion; however, impacts from cane toad invasions often show both population-level differences (Doody et al. 2009; Somaweera et al. 2013) and, in some cases, minimal impacts (Kamper et al. 2013).

Perhaps one of the most serious negative impacts of cane toads in Australia was their widespread, local extinction of a marsupial carnivore, the northern quoll (*Dasyurus hallucatus*); shortly after cane toads colonized natural areas containing the quolls, they went extinct (O'Donnell et al. 2010). Phillips et al. (2003) determined that many native Australian snakes die from consuming a single cane toad, and that approximately 30% of the populations of native snakes are threatened by cane toads. Boland (2004) discovered that cane toads significantly reduce fledging success of ground-nesting rainbow bee-eater birds (*Merops ornatus*) by usurping their burrows and consuming eggs and chicks. Some vertebrates, including at least seven native birds and three native rodents, can consume cane toads successfully either because they only eat the nontoxic parts of the toad or because they have developed some resistance to the toxicant (Covacevich and Archer 1975; Lever 2001).

Its impacts on native frogs are particularly equivocal as it might benefit them in areas where it reduces their predators (Shine 2014), although they do cause mass mortality of native frog larvae through direct consumption of the cane toad eggs (Crossland et al. 2008). There has been concern that cane toad egg and larvae presence alone would kill native organisms sharing the same water body, but data supporting this concern are lacking, and several native Australian frogs have been tested and survive in water bodies infected with cane toad toxicants (Hagman and Shine 2009b). Despite the findings that all native frogs consuming cane toad eggs die, mortality varies by species because not all native anurans' breeding coincides with that of cane toads (Crossland et al. 2008), and reductions in some native frog species may release others from competition and therefore increase their survival (Crossland 2000). Effects of cane toads on competitive interactions have also been demonstrated by Doody et al. (2015), where cane toad suppression of monitor lizards, which are

predators of native birds, resulted in 55%–81% increase in fledging success of a native finch.

Stomach content analyses reveal prey vulnerable to cane toad invasions. In their native range of Venezuela, 269 stomachs contained at least 18 invertebrate orders; beetles dominated on a mass basis (27%), followed by ants (13%), larvae of dragonflies/damselflies (8%), grasshoppers/crickets (4%), and butterflies/moths (3%) (Evans and Lampo 1996). In forested areas of northern Queensland, 81 stomachs contained spiders, cockroaches, earwigs, true bugs, flies, grasshoppers/crickets, centipedes, and millipedes (Heise-Pavlov and Longway 2011). In Papua New Guinea, snails, including the small *Subulina octina* and the large *Achatina fulica*, composed 42% of their diet in cacao plantations (Bailey 1976). Greenlees et al. (2006) used outdoor enclosure trials in northern Australia to determine cane toad effects on invertebrates. Their findings revealed that, although cane toads reduced invertebrate abundance and species richness, the level of reduction was equivalent to native frogs tested. Greenlees et al. (2006) point out that in the field, the massive amount of cane toad biomass relative to that of native frogs will result in a large nutrient sink in cane toads resulting from their feeding on invertebrates.

Whereas the impact of the cane toad in Australia is of great concern because of the naivety of the endemic fauna to this species; in Hawaii, where there are no native terrestrial reptiles or ground-dwelling mammals, its effect on potential predators has not been as well studied. In a study to determine if cane toads consume other nonnative frogs (*Eleutherodactylus* spp.) in wet forests in Hawaii, they were only found to consume roughly equal proportions of plants and invertebrates (36% snails, 23% millipedes, 17% beetles, and 10% butterflies/moths) (Beard and Pitt 2006). In Florida, in the same study referenced above where Cuban tree frogs were found to affect native frog larvae, cane toads were not found to affect larval growth or development of two native species (Smith 2005). There is valid concern for the native ecosystems of the United States where cane toads may establish because of the wide range of largely negative effects of these invaders in Australian ecosystem.

Similar to other frogs, cane toads carry and transmit diseases (Speare 1990). Large numbers of potentially pathogenic bacteria (e.g., *Aeromonas hydrophila*, *Mycobacterium* spp.), including *Salmonella* spp., fungi (*Fonsecaea pedrosoi* and *Candida* sp.), an amoeba, and helminths (*Spirametra mansoni* and *Rhabdias spherocéphala*), have been isolated from cane toads, but the level to which these cause disease is apparently small (Speare 1990; Drake et al. 2013). The extent to which these pathogens are transferred to native species or humans is not well known.

Most of the cost associated with cane toad management in Australia comes from control measures. Australia has spent about \$1 million per year supporting research and community-based control measures to reduce their impacts and developing a national plan (Shine et al. 2006; Shine 2010). While the United States has not focused any funds directly to control cane toads and no formal economic studies have covered their invasion in the United States, economic costs will range from losses in biodiversity to human and domestic animal health and safety (e.g., exposure to cane toad toxicants or carried pathogens). Given the wide biodiversity and human establishment along coastlines where cane toads are particularly common (Urban et al. 2007), the economic costs associated with cane toad invasion and spread could

be significant and will likely become more of a burden in the future with the potential for range expansion with global temperature changes.

From a societal perspective, the cane toad primarily is considered a pest because of the defensive secretions emitted from their parotoid as well as other glands that can cause illness to humans and death in domestic animals if ingested, and cause pain if it enters the eyes (Krakauer 1968). The poison is often released directly outside the gland, and while they cannot eject toxin at will, parotoid glands under pressure can squirt the toxin close to a meter (S. Johnson, pers. obs.). A review of 90 cases of cane toad intoxication in dogs conducted over 2.5 years in Brisbane showed that while most pet dogs became sick, survival rates were very high at 96% (Reeves 2004). In a similar study in southern Florida, Roberts et al. (2000) examined 94 cases of cane toad intoxication in dogs conducted over one year, and while in all dogs received some type of treatment, treatment varied considerably among patients and four dogs died as a result of toad exposure. Other societal impacts from cane toads include *Salmonella* contamination of water sources (including catchments), consumable vegetation, and dog food bowls (Drake et al. 2013).

Historic and Current Management

Traps, attractants, and barriers have been trialed in the past for cane toad control, mainly in Australia. Cage traps have been historically suggested as the most effective and least labor intensive of the current cane toad control techniques (Lampo and De Leo 1998), yet trapping cane toads using pit traps or cage traps, and manual removal of frogs in general, is difficult and only likely to be successful with small, isolated, incipient populations (Schwarzkopf and Alford 2007). However, use of attractants in combination with trapping can help increase trap effectiveness (Schwarzkopf and Alford 2007; Yeager et al. 2014). Existing cane toad trap designs in Australia use lights to lure insects to traps, and toads enter the traps to feed on the insects (Schwarzkopf and Alford 2007). Schwarzkopf and Alford (2007) used large pens and field trials to demonstrate that cane toads are attracted to conspecific mating vocalizations, and trap success increased threefold when playback vocalizations were present in traps compared to traps without playbacks. Furthermore, both male and female toads were attracted to quiet (47 dB at 1 m) playbacks, whereas only males responded to loud (67 dB at 1 m) playbacks (Schwarzkopf and Alford 2007). Yeager et al. (2014) demonstrated that using sound attractant inside a trap with ultraviolet light was particularly effective at capturing female cane toads. Schwarzkopf and Alford (2007) suggested that outfitting cage traps containing a light source with an inexpensive media player, speaker, and associated batteries would be about \$50.

Arranging trapping near water sources, particularly at the end of the dry season, in combination with other attractants, such as a light source and auditory attractant, has been a favorable method in Australia (Taylor and Edwards 2005). In theory, fencing could be used to keep cane toads out of a desired habitat, yet no trials investigating the minimum aperture size of the fencing mesh or the integrity of the fencing in gulches and water crossings have been carried out (Taylor and Edwards 2005). In Hawaii, the aperture size of fencing used to exclude invasive ungulates is too large to exclude cane toads (A.B. Shiels, pers. obs.). If logistically feasible, draining a breeding habitat may prevent breeding, but investigations of the efficacy of such

a control method have not occurred. Moist microsites for shelter and food may also limit cane toad establishment or densities. Heise-Pavlov and Longway (2011) found that restoration measures (e.g., providing rock piles or logs) appeared to benefit cane toad presence. Removal of moist microsites during the dry season may be particularly effective. Taking advantage of local dispersal pathways and favorable vegetation cover conditions may be another technique to improve effectiveness of cane toad control efforts. Road corridors and open landscapes that lack dense vegetation are areas of high cane toad activity and dispersal within Queensland, Australia (Brown et al. 2006).

The Australian government provided funds to support the National Cane Toad Taskforce, which also identified four approaches to long-term and widespread control of cane toads that seem trial-worthy in the future, and these were: (1) identification and release of a *Bufo*-specific pathogen, (2) development and release of a sterility agent or sterile males, (3) identification and use of a cane toad-specific toxicant, and (4) development of a genetically modified organism (GMO) that would interfere with the development of cane toads (as reviewed in Taylor and Edwards 2005). Although some of these approaches have ongoing research efforts (e.g., GMO), all require secured funding and commitment for at least five to ten years to conduct research trials (Taylor and Edwards 2005; Schwarzkopf and Alford 2007). For example, establishment of new toxicants or biocontrols would have to ensure minimal impacts to nontarget organisms, and in Australia, this would mean ensuring minimal risk for over 200 native frogs (Tyler and Knight 2009).

Unlike installing and using various types of barriers and trap designs, implementing biocontrol methods typically takes years or decades and often is unsuccessful (Yeager et al. 2014). There is no known pathogen that is specifically lethal to cane toads, which is why a GMO to serve this purpose has been explored (Shanmuganathan et al. 2010). Research on a virus (*Toddia* sp.) showed promise for controlling cane toads because all experimental infections caused cane toad death (Speare 1990). However, Shanmuganathan et al. (2010) reviewed the biocontrol efforts attempted over an eight-year period in Australia, and concluded that, so far, research efforts have failed to produce a tool for large-scale control of cane toad populations.

Chemical addition to water bodies may represent a future technique for suppressing the number and sizes of cane toads developing to the tadpole and adult stages (Crossland and Shine 2012). Recent research by Crossland and Shine (2012) has shown that cane toad eggs placed in water that already had a cohort of conspecific tadpoles had 45% greater mortality and 40% smaller tadpole body sizes than tadpoles grown in fresh water. Therefore, cane toad tadpoles produce waterborne chemical cues that suppress conspecific embryonic development (Crossland and Shine 2012). This apparent adaptation, to presumably reduce intraspecific competition or avoid development in predator-active environments (Hagman and Shine 2009a), may be applied as a management technique to reduce cane toads in water bodies where breeding occurs. Unlike the chemical cues exuded by tadpoles, many other chemical trials, such as adding scents of foods, native-range fish predators (cichlids—*Cichlasoma labiatum*), native-range axolotls predators (*Ambystoma mexicanum*), as well as thermal stimuli, did not illicit any response in cane toad tadpoles (Hagman and Shine 2008). Furthermore, examination of the negative effects of chemical cues

from cane toad tadpoles was tested against nine native frogs in Australia and was found to have no negative effects on the native frogs, which is encouraging for using these low-level cane toad alarm pheromones as a management technique to control this invasive species (Hagman and Shine 2009b).

Use of baits to attract cane toad predators or cause aversion to cane toads has also been trialed in Australia. Cat food bait was successfully used to recruit predatory ants (*Iridomyrmex reburrus*) to water edges where newly morphed cane toads had emerged (Ward-Fear et al. 2010). Additionally, taste aversion to cane toads has been trialed successfully in Australia and has potential as a management technique to benefit cane toad-threatened fauna. O'Donnell et al. (2010) successfully induced a taste aversion to live toads in juvenile quolls. The taste aversion (thiabendazole) was placed in dead toads to induce vomiting when eaten by quolls. From these results, O'Donnell et al. (2010) suggest that wildlife managers could aerially deploy taste aversion baits ahead of the invasion front of cane toads to benefit native wildlife that commonly consume cane toads. To our knowledge, such aerial application of bait to help avert native fauna from predation of cane toads on a landscape scale has not yet occurred. The breadth of management techniques that are being researched and implemented in Australia is impressive, and such techniques are certainly applicable to cane toad management in the United States.

In addition to future cane toad reduction approaches, biosecurity efforts to help prevent cane toad range expansion and otherwise prevent their colonization of new areas have been a priority for Australia but have been generally absent from the United States. Offshore islands are apparently colonized by cane toads from flood waters and cargo transport in Australia; significant educational campaigns have helped to inform the public about cane toad impacts and control efforts needed, and public involvement has been successful in some areas in northern and eastern Australia (e.g., community groups involved in “toad buster” or “tad round-up” activities; Schwarzkopf and Alford 2007).

FUTURE CHALLENGES

Preventing the introduction and establishment of nonnative species is the most efficient means of controlling their spread and negative impact. Most terrestrial, invasive amphibians are tropical or subtropical in origin, and as a result they are primarily establishing and spreading in tropical and subtropical U.S. states, such as Florida and Hawaii. Terrestrial breeders, such as the coqui and greenhouse frog, can invade with one egg mass (Peacock et al. 2009). For many of these species, the mode of transport has been via the horticulture trade (Kraus 2003, 2009). While an extremely important source of introduced amphibians is the pet trade (Kraus 2003, 2009), most amphibians introduced this way are aquatic (*Lithobates catebeiana*, *L. berlandieri*, and *Xenopus laevis*) (Herrel and van der Meijden 2014). The Cuban tree frog and cane toad are examples of invasive water-body breeders that were not introduced via the pet trade. These species are likely successful because they invade locations with plenty of water, do not have strict breeding requirements, breed year round, and produce a large number of offspring; therefore, in appropriate conditions, their populations grow quickly. While we focused on four terrestrial

species that are the most problematic invaders in the United States, there are several others that are probable candidates for invasion and negative impacts in the United States, and any potential introductions should be monitored closely: *Scinax ruber* (red-snouted treefrog), *Scinax x-signatus* (Venezuela snouted treefrog), and *Eleutherodactylus johnstonei* (Johnstone's Whistling Frog) (Global Invasive Species Database 2008a,b).

There are several areas of research and management in the United States that need to be addressed concerning the four species covered in this chapter. First, our knowledge of the location and spread of many of these species is still minimal. For example, we have not yet determined how widespread the greenhouse frog is on islands in Hawaii other than the Big Island (Olson et al. 2012a). Monitoring the potential spread of all these species is critical and citizen scientists can play a role. Second, there is great need for more research on the ecological impacts of all four of these species. As their ranges expand, these problematic species are likely to cause even more harm to wildlife, economies, and citizens. Third, we need greater educational campaigns and detailed risk assessments to curtail new invasions. Finally, development of more effective methods for population control of all four species is needed. Kalnicky et al. (2014) found that in the case of the coqui frog, there was a growing tolerance toward the species from people with greater exposure to them. If this is true for other nonnative amphibians, it suggests that managers may have a short window of public support for control. This may need to be kept in mind for all nonnative species.

REFERENCES

- Alix, D.M., C. Guyer, and C.J. Anderson. 2014. Expansion of the range of the introduced greenhouse frog, *Eleutherodactylus planirostris*, in Coastal Alabama. *Southeastern Naturalist* 13:N59–N62.
- Anonymous. 1934. Toads save sugar crop. *Nature* 134:877–877.
- Anonymous. 2010. Hawai'i's Coqui frog management, research and education plan. *State of Hawaii* 877–877.
- Austin, D.F., and A. Schwartz. 1975. Another exotic amphibian in Florida, *Eleutherodactylus coqui*. *Copeia* 1975:188.
- Bailey, P. 1976. Food of the marine toad, *Bufo marinus*, and six species of skink in cacao plantation in New Britain, Papua New Guinea. *Australian Wildlife Research* 3:185–188.
- Barbour, T. 1931. Another introduced frog in North America. *Copeia* 1931:140.
- Beachy, J.R., R. Neville, and C. Arnott. 2011. Successful control of an incipient invasive amphibian: *Eleutherodactylus coqui* on O'ahu, Hawai'i. In *Island Invasives: Eradication and Management. Proceedings of the International Conference on Island Invasives*, eds. C.R. Veitch, M.N. Clout, and D.R. Towns, pp. 140–147. Gland, Switzerland: IUCN.
- Beard, K.H. 2007. Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii. *Copeia* 2007:281–291.
- Beard, K.H., R. Al-Chokhachy, N.C. Tuttle, and E.M. O'Neill. 2008. Population density estimates and growth rates of *Eleutherodactylus coqui* in Hawaii. *Journal of Herpetology* 42:626–636.
- Beard, K.H., S. McCullough, and A.K. Eschtruth. 2003. Quantitative assessment of habitat preferences for the Puerto Rican terrestrial frog, *Eleutherodactylus coqui*. *Journal of Herpetology* 37:10–17.

- Beard, K.H., and E.M. O'Neill. 2005. Infection of an invasive frog *Eleutherodactylus coqui* by the chytrid fungus *Batrachochytrium dendrobatidis* in Hawaii. *Biological Conservation* 126:591–595.
- Beard, K.H., and W.C. Pitt. 2005. Potential consequences of the coqui frog invasion in Hawaii. *Diversity and Distributions* 11:427–433.
- Beard, K.H., and W.C. Pitt. 2006. Potential predators of an invasive frog (*Eleutherodactylus coqui*) in Hawaiian forests. *Journal of Tropical Ecology* 22:345–347.
- Beard, K.H., and W.C. Pitt. 2012. Chapter 26: Caribbean tree frog (*Eleutherodactylus coqui*). In *Handbook of Global Freshwater Invasive Species*, ed. R.A. Francis, pp. 311–319. London: Earthscan.
- Beard, K.H., E.A. Price, and W.C. Pitt. 2009. Biology and impacts of Pacific Island invasive species: *Eleutherodactylus coqui*, the Coqui frog (Anura: Leptodactylidae). *Pacific Science* 63:297–316.
- Beckmann, C., and R. Shine. 2012. How many of Australia's ground-nesting birds are likely to be at risk from the invasive Cane Toad (*Rhinella marina*)? *Emu* 112:83–89.
- Boland, C.R.J. 2004. Introduced cane toads *Bufo marinus* are active nest predators and competitors of rainbow bee-eaters *Merops ornatus*: Observational and experimental evidence. *Biological Conservation* 120:53–62.
- Briggs, C.J., V.T. Vredenburg, R.A. Knapp, and L.J. Rachowicz. 2005. Investigating the population-level effects of chytridiomycosis: An emerging infectious disease of amphibians. *Ecology* 86:3149–3159. doi: 10.1890/04–1428.
- Brown, G.P., B.L. Phillips, J.K. Webb, and R. Shine. 2006. Toad on the road: Use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation* 133:88–94.
- Campbell, E.W., and F. Kraus. 2002. Neotropical frogs in Hawaii: Status and management options for an unusual introduced pest. In *Proceeding of the 20th Vertebrate Pest Conference*, University of California Davis, eds R.M. Timm and R.H. Schmidt, pp. 316–318.
- Campbell, K.R., T.S. Campbell, and S.A. Johnson. 2010. The use of PVC pipe refugia to evaluate spatial and temporal distributions of native and introduced treefrogs. *Florida Scientist* 73:78–88.
- Campbell, T.S., P. Irvin, K.R. Campbell, K. Hoffmann, M.E. Dykes, A.J. Harding, and S.A. Johnson. 2009. Evaluation of a new technique for marking anurans. *Applied Herpetology* 6:247–256.
- Choi, R.T., and K.H. Beard. 2012. Coqui frog invasions change invertebrate communities in Hawaii. *Biological Invasions* 14:938–948.
- Christy, M.T., C.S. Clark, D.E. Gee, D. Vice, D.S. Vice, M.P. Warner, C.L. Tyrrell, et al. 2007. Recent records of alien anurans on the Pacific Island of Guam. *Pacific Science* 61:469–483.
- Conant, R., and J. Collins. 1991. *Reptiles and Amphibians: Eastern/Central North America*. New York: Houghton Mifflin Company.
- Covacevich, J., and M. Archer. 1975. The distribution of the cane toad, *Bufo marinus*, in Australia and its effects on indigenous vertebrates. *Memoirs of the Queensland Museum* 17:305–310.
- Crossland, M., and R. Shine. 2012. Embryonic exposure to conspecific chemicals suppress cane toad growth and survival. *Biology Letters* 8:226–229.
- Crossland, M.R. 2000. Direct and indirect effects of the introduced toad *Bufo marinus* (Anura: Bufonidae) on populations of native anuran larvae in Australia. *Ecography* 23:283–290.
- Crossland, M.R., G.P. Brown, M. Anstis, C.M. Shilton, and R. Shine. 2008. Mass mortality of native anuran tadpoles in tropical Australia due to the invasive cane toad (*Bufo marinus*). *Biological Conservation* 141:2387–2394.

- De León, L.F., and A. Castillo. 2015. *Rhinella marina* (Cane Toad). Salinity tolerance. *Herpetological Review* 46:237–238.
- Dodd, C.K., Jr. 2013. *Frogs of the United States and Canada*. Baltimore: Johns Hopkins University Press.
- Doody, J.S., B. Green, D. Rhind, C.M. Castellano, R. Sims, and T. Robinson. 2009. Population-level declines in Australian predators caused by an invasive species. *Animal Conservation* 12:46–53.
- Doody, J.S., P. Mayes, S. Clulow, D. Rhind, B. Green, C.M. Catellano, D. D'Amore et al. 2014. Impacts of the highly invasive cane toad on aquatic reptiles in a highly modified ecosystem: The importance of replicating impact studies. *Biological Invasions* 16:2303–2309.
- Doody, J.S., R. Soanes, C.M. Catellano, D. Rhind, B. Green, C.R. Mchenry, and S. Clulow. 2015. Invasive toads shift predator-prey densities in animal communities by removing top predators. *Ecology* 96:2544–2554.
- Drake, M., V. Amandi, U. Zieger, R. Johnson, and H. Hariharan. 2013. Prevalence of *Salmonella* spp. in cane toads (*Bufo marinus*) from Grenada, West Indies, and their antimicrobial susceptibility. *Zoonose and Public Health* 60:437–441.
- Duellman, W.E., and L. Trueb. 1986. *Biology of Amphibians*. New York: McGraw-Hill.
- Easteal, S. 1981. The history of introductions of *Bufo marinus* (Amphibia: Anura); a natural experiment in evolution. *Biological Journal of the Linnean Society* 16:93–113.
- Ely, C.A. 1944. Development of *Bufo marinus* larvae in dilute sea water. *Copeia* 56:256.
- Evans, M., and M. Lampo. 1996. Diet of *Bufo marinus* in Venezuela. *Journal of Herpetology* 30:73–76.
- Everman, E., and P. Klawinski. 2013. Human-facilitated jump dispersal of a non-native frog species on Hawai'i Island. *Journal of Biogeography* 40:1961–1970.
- Ferrerria, R.B., K.H. Beard, R.T. Choi, and W.C. Pitt. 2015. Diet of the non-native greenhouse frog in Maui. *Journal of Herpetology* 49:586–593.
- Freeland, W.J. 1986. Populations of cane toad, *Bufo marinus*, in relation to time since colonization. *Australian Wildlife Research* 13:321–329.
- Global Invasive Species Database, GISD. 2008a. *Scinax Ruber*. *Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission*. www.iucngisd.org. Accessed Retrieved June 29, 2015.
- Global Invasive Species Database, GISD. 2008b. *Scinax x-Signatus*. *Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission*. Accessed Retrieved June 29, 2015.
- Glorioso, B.M., J.H. Waddle, M.E. Crockett, K.G. Rice, and H.F. Percival. 2012. Diet of the invasive Cuban Treefrog (*Osteopilus septentrionalis*) in pine rockland and mangrove habitats in South Florida. *Caribbean Journal of Science* 46:346–355.
- 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. Vol. IV, Biological Science Series. Gainesville: University of Florida Press.
- Greenlees, M.J., G.P. Brown, J.K. Webb, B.L. Phillips, and R. Shine. 2006. Effects of an invasive anuran [the cane toad (*Bufo marinus*)] on the invertebrate fauna of a tropical Australian flood plain. *Animal Conservation* 9:431–438.
- Hagman, M., and R. Shine. 2008. Understanding the toad code: Behavioural responses of cane toad (*Chaunus marina*) larvae and metamorphs to chemical cues. *Austral Ecology* 33:37–44.
- Hagman, M., and R. Shine. 2009a. Factors influencing responses to alarm pheromone by larvae of invasive cane toads, *Bufo marinus*. *Journal of Chemical Ecology* 35:265–271.
- Hagman, M., and R. Shine. 2009b. Species-specific communication in an introduced toad compared with native frogs in Australia. *Aquatic Conservation: Marine and Freshwater Ecosystem* 19:724–728.

- 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. *International Journal of Pest Management* 56:255–263.
- Heinicke, M.P., L.M. Diaz, and S.B. Hedges. 2011. Origin of invasive Florida frogs traced to Cuba. *Biology Letters* on-line:1–5.
- Heise-Pavlov, S.R., and L.J. Longway. 2011. Diet and dietary selectivity of cane toads (*Rhinella marina*) in restoration sites: A case study in far north Queensland, Australia. *Ecological Management and Restoration* 12:230–233.
- Herrel, A., and A. van der Meijden. 2014. An analysis of the live reptile and amphibian trade in the USA compared to the global trade in endangered species. *Herpetological Journal* 24:103–110.
- Hoffmann, K.E., S.A. Johnson, and M.E. McGarrity. 2009. Intraspecific variation in use of polyvinyl chloride (PVC) refuges by hyloid treefrogs: A potential source of capture bias. *Herpetological Review* 40:423–426.
- Hölldobler, B., and E.O. Wilson. 1990. *The Ants*. Boston: Harvard University Press.
- Jensen, J.B. 2008. Greenhouse Frog (*Eleutherodactylus planirostris*). In *Amphibians and Reptiles of Georgia*, eds. J.B. Jensen, C.D. Camp, W. Gibbons, and M.J. Elliot, pp. 92–93. University of Georgia Press: Athens, Georgia.
- Johnson, S.A. 2007. *The Cuban treefrog in Florida*. Vol. Available from: <http://edis.ifas.ufl.edu/UW259>, Gainesville, FL: University of Florida Cooperative Extension Service. Available: <http://edis.ifas.ufl.edu/UW259> Accessed: October 20, 2015. Gainesville: University of Florida.
- Johnson, S.A., M.E. McGarrity, and C.L. Staudhammer. 2010. An effective chemical deterrent for invasive Cuban Treefrogs. *Human–Wildlife Interactions* 4:112–117.
- Kaiser, B., and K. Burnett. 2006. Economic impacts of *E. coqui* frogs in Hawaii. *Interdisciplinary Environmental Review* 8:1–11.
- Kalnicky, E.A., K.H. Beard, and M.W. Brunson. 2013. Community-level response to habitat structure manipulations: An experimental case study in a tropical ecosystem. *Forest Ecology and Management* 307:313–321.
- Kalnicky, E.A., M.W. Brunson, and K.H. Beard. 2014. A social–ecological systems approach to non-native species: Habituation and its effect on management of coqui frogs in Hawaii. *Biological Conservation* 180:187–195.
- Kamper, W., J.K. Webb, M.S. Crowther, M.J. Greenlees, and R. Shine. 2013. Behaviour and survivorship of a dasyurid predator (*Antechinus flavipes*) in response to encounters with the toxic and invasive cane toad (*Rhinella marina*). *Australian Mammalogy* 35:136–143.
- Klawinski, P.D., B. Dalton, and A.B. Shiels. 2014. Coqui frog populations are negatively affected by canopy opening but not detritus deposition following an experimental hurricane in a tropical rainforest. *Forest Ecology & Management* 332:118–123.
- Knight, C.M., M.J. Parris, and W.H.N. Gutzke. 2009. Influence of priority effects and pond location on invaded larval amphibian communities. *Biological Invasions* 11:1033–1044.
- Krakauer, T. 1968. The ecology of the neotropical toad, *Bufo marinus*, in south Florida. *Herpetologica* 214–221.
- Kraus, F. 2003. Invasion pathways for terrestrial vertebrates. In *Invasive Species: Vectors and Management Strategies*, eds. G.M. Ruiz, and J.T. Carlton, pp. 68–92. Washington, DC: Island Press.
- Kraus, F. 2009. *Alien Reptiles and Amphibians: A Scientific Compendium and Analysis Series, Invading Nature—Springer Series in Invasion Ecology*. Dordrecht: Springer.
- Kraus, F., and E.W. Campbell. 2002. Human-mediated escalation of a formerly eradicable problem: The invasion of Caribbean frogs in the Hawaiian Islands. *Biological Invasions* 4:327–332.

- Kraus, F., E.W. Campbell, A. Allison, and T. Pratt. 1999. *Eleutherodactylus* frog introductions to Hawaii. *Herpetological Review* 30:21–25.
- Krysko, K.L., K.M. Enge, and P.E. Moler. 2011. Atlas of amphibians and reptiles in Florida. In *Final Report, Project Agreement 08013, Florida Fish and Wildlife Conservation Commission*. Tallahassee, Florida, 524 pp.
- Lampo, M., and G. De Leo. 1998. The invasive ecology of the toad *Bufo marinus*: From South America to Australia. *Ecological Applications* 8:388–396.
- Lever, C. 2001. *The Cane Toad. The History and Ecology of a Successful Colonist*. Otley, UK: Westbury Academic and Scientific Publishing.
- Lever, C. 2003. *Naturalized Reptiles and Amphibians of the World*. Oxford, UK: Oxford University Press.
- Liggins, G.W., and G.C. Grigg. 1985. Osmoregulation of the cane toad *Bufo marinus* in salt water. *Comparative Biochemistry and Physiology* 82A:613–619.
- MacLean, W.P. 1982. *Reptiles and Amphibians of the Virgin Islands*. London, Basingstoke: Macmillan Caribbean.
- Mann, D.L., T. Mann, W. Lu, and N. Winstead. 2015. *Eleutherodactylus planirostris* (Greenhouse Frog). Geographic Distribution. *Herpetological Review* 46:377.
- Marr, S.R., S.A. Johnson, A.H. Hara, and M.E. McGarrity. 2010. Preliminary evaluation of the potential of the helminth parasite *Rhabdias elegans* as a biological control agent for invasive Puerto Rican coquis (*Eleutherodactylus coqui*) in Hawaii. *Biological Control* 54:69–74.
- Marshall, S.E., and W.E. Meshaka. 2006. An island of cane toads (*Bufo marinus*) in an ocean of xeric uplands in South-Central Florida. *Florida Scientist* 69:169–179.
- Mathies, T., W.C. Pitt, and J.A. Rabon. 2012. *Boiga irregularis* (Brown Treesnake) Diet. *Herpetological Review* 43:143–144.
- McCann, S., M.J. Greeless, D. Newell, and R. Shine. 2014. Rapid acclimation to cold allows the cane toad to invade montane areas within its Australian range. *Functional Ecology* 28:1166–1174.
- McGarrity, M.E., and S.A. Johnson. 2009. Geographic trend in sexual size dimorphism and body size of *Osteopilus septentrionalis*: Implications for invasion of the southeastern United States. *Biological Invasions* 11:1411–1420.
- McGarrity, M.E., and S.A. Johnson. 2010. A radio telemetry study of invasive Cuban treefrogs. *Florida Scientist* 73:225–235.
- Meshaka, W.E. Jr. 1996. Vagility and the Florida distribution of the Cuban treefrog (*Osteopilus septentrionalis*). *Herpetological Review* 27:37–39.
- Meshaka, W.E., Jr. 2001. *The Cuban Treefrog in Florida: Life History of a Successful Colonizing Species*. Gainesville, Florida: Univ. Press of Florida.
- Meshaka, W.E., B.P. Butterfield, and J. Brian Hauge. 2004. *The Exotic Amphibians and Reptiles of Florida*. Malabar: Krieger Publishing Company.
- Muths, E., P.S. Corn, A.P. Pessier, and D.E. Green. 2003. Evidence for disease-related amphibian decline in Colorado. *Biological Conservation* 110:357–365. doi: Pii s0006-3207(02)00239-2 10.1016/s0006-3207(02)00239-2.
- O'Donnell, S., J.K. Webb, and R. Shine. 2010. Conditioned taste aversion enhances the survival of an endangered predator imperilled by a toxic invader. *Journal of Applied Ecology* 47:558–568.
- Olson, C.A., and K.H. Beard. 2012. Diet of the invasive greenhouse frog in Hawaii. *Copeia* 2012:121–129.
- Olson, C.A., K.H. Beard, D.N. Koons, and W.C. Pitt. 2012a. Detection probabilities of two introduced frogs in Hawaii: Implications for assessing non-native species distributions. *Biological Invasions* 14:889–900.
- Olson, C.A., K.H. Beard, and W.C. Pitt. 2012b. Pacific Island invasive species: 8. *Eleutherodactylus planirostris*, the greenhouse frog (Anura: Leptodactylidae). *Pacific Science* 66:255–270.

- Olson, C.A., A. Diesmos, and K.H. Beard. 2014. Geographical distribution: *Eleutherodactylus planirostris* (greenhouse frog). *Herpetological Review* 45:652–653.
- Peacock, M.M., K.H. Beard, E.M. O'Neill, V.S. Kirchoff, and M.B. Peters. 2009. Strong founder effects and low genetic diversity in introduced populations of coqui frogs. *Molecular Ecology* 18:3603–3615.
- Phillips, B.L., G.P. Brown, and R. Shine. 2003. Assessing the potential impact of cane toads on Australian snakes. *Conservation Biology* 17:1738–1747.
- Pitt, W.C., K.H. Beard, and R.E. Doratt. 2012. Management of invasive coqui frog populations in Hawaii. *Outlooks on Pest Management* 23:166–169. doi: 10.1564/23aug05.
- Reeves, M.P. 2004. A retrospective report of 90 dogs with suspected cane toad (*Bufo marinus*) toxicity. *Australian Veterinary Journal* 82:608–611.
- Rice, K.G., J.H. Waddle, M.W. Miller, M.E. Crockett, F.J. Mazzotti, and H.F. Percival. 2011. Recovery of native treefrogs after removal of nonindigenous Cuban treefrogs *Osteopilus septentrionalis*. *Herpetologica* 67:105–117.
- Rivero, J.A. 1978. *Los Anfibios y Reptiles de Puerto Rico*, ed. Editorial Universitaria. San Juan, Puerto Rico: Universidad de Puerto Rico.
- Roberts, B.K., M.G. Aronsohn, B.L. Moses, R.L. Burk, J. Toll, and F.R. Weeren. 2000. *Bufo marinus* intoxication in dogs: 94 cases (1997–1998). *Journal of the American Veterinary Medical Association* 216:1941–1944.
- Rödter, 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.
- Rogelio Cedeno-Vazquez, J., J. Gonzalez-Vazquez, A. Martinez-Arce, and L. Canseco-Marquez. 2014. First record of the invasive greenhouse frog (*Eleutherodactylus planirostris*) in the Mexican Caribbean. *Revista Mexicana De Biodiversidad* 85:650–653. doi: 10.7550/rmb.43234.
- Schwartz, A., and R.W. Henderson. 1991. *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. Gainesville: University Press of Florida.
- Schwarzkopf, L., and R.A. Alford. 2007. Acoustic attractants enhance trapping success for cane toads. *Wildlife Research* 34:366–370.
- Seebacher, F., and R.A. Alford. 2002. Shelter microhabitats determine body temperature and dehydration rates of a terrestrial amphibian (*Bufo marinus*). *Journal of Herpetology* 36:69–75.
- Shanmuganathan, T., J. Pallister, S. Doody, H. McCallum, T. Robinson, A. Sheppard, C. Hardy et al. 2010. Biological control of the cane toad in Australia: A review. *Animal Conservation* 13:16–23.
- Shine, R. 2010. The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Quarterly Review of Biology* 85:253–291.
- Shine, R. 2014. A review of ecological interactions between native frogs and invasive cane toads in Australia. *Austral Ecology* 39:1–16.
- Shine, R., J. Amiel, A.J. Munn, M. Stewart, A.L. Vyssotski, and J.A. Lesku. 2015. Is “cooling then freezing” a humane way to kill amphibians and reptiles? *Biology Open* doi: 10.1242/bio.012179.
- Shine, R., G.P. Brown, B.L. Phillips, J.K. Webb, and M. Hagman. 2006. The biology, impact and control of cane toads: An overview of the University of Sydney's research program. In *Proceedings of the Cane Toad Workshop*. Canberra (Australia): University of Canberra, Invasive Animals Cooperative Research Centre.
- Simberloff, D. 2004. Now you see them, now you don't!—Population crashes of established introduced species. *Biological Invasions* 6:161–172.
- Simpson, S.E. 2013. Assessing critical thermal minima to determine the thermal limits of the invasive Cuban treefrog (*Osteopilus septentrionalis*). *MS thesis*, University of Florida.

- 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. *Biological Invasions* 10:335–345.
- Smith, K.G. 2005. Effects of nonindigenous tadpoles on native tadpoles in Florida: Evidence of competition. *Biological Conservation* 123:433–441.
- Smith, R.L. 2016. Invasive coqui frogs serve as novel prey for birds in Hawaii, and not as competitors. M.S. Thesis, Utah State University, Logan, Utah.
- Smith, R.L., K.H. Beard, and A.B. Shiels. 2017. Different prey resources suggest little competition between non-native frogs and insectivorous birds despite isotopic niche overlap. *Biological Invasions* 19:1001–1013.
- Somaweera, R., R. Shine, J. Webb, T. Dempster, and M. Letnic. 2013. Why does vulnerability to toxic invasive cane toads vary among populations of Australian freshwater crocodiles? *Animal Conservation* 16:86–96.
- Speare, R. 1990. A review of the diseases of the cane toad, *Bufo marinus*, with comments on biological control. *Australian Wildlife Research* 17:287–410.
- Stewart, M.M. 1977. “The role of introduced species in a Jamaican frog community.” *Actas del IV Simposium Internacional de Ecologica Tropical*, Panama City, pp. 113–146.
- Stewart, M.M., and F.H. Pough. 1983. Population density of tropical forest frogs: Relation to retreat sites. *Nature* 221:570–572.
- Storer, T.I. 1925. A synopsis of the amphibian of California. *University of California Publications in Zoology* 27:1–342.
- Taylor, R., and G. Edwards. 2005. A review of the impacts and control of cane toads in Australia with recommendations for future research and management approaches. The National Cane Toad Task Force Report.
- Townsend, D.S., and M.M. Stewart. 1985. Direct development in *Eleutherodactylus coqui* (Anura: Leptodactylidae): A staging table. *Copeia* 1985:423–436.
- Townsend, D.S., and M.M. Stewart. 1994. Reproductive ecology of the Puerto Rican Frog *Eleutherodactylus coqui*. *Journal of Herpetology* 28:34–40.
- 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.
- Tuberville, T.D., J.D. Willson, M.E. Dorcas, and J. Whitfield Gibbons. 2005. Herpetofaunal Species Richness of Southeastern National Parks. *Southeastern Naturalist* 4:537–569.
- Tuttle, N.C., K.H. Beard, and R. Al-Chokhachy. 2008. Aerially applied citric acid reduces an invasive frog. *Wildlife Research* 35:676–683.
- Tyler, M.J., and F. Knight. 2009. *Field guide to Australian Frogs*. Australia: CSIRO Publishing.
- Urban, M.C., B.L. Phillips, D.K. Skelly, and R. Shine. 2007. The cane toad’s (*Chaunus (Bufo) marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society B: Biological Sciences* 274:1413–1419.
- Waddle, J.H., R.M. Dorazio, S.C. Walls, K.G. Rice, J. Beauchamp, M.J. Schuman, and F.J. Mazzotti. 2010. A new parameterization for estimating co-occurrence of interaction species. *Ecological Applications* 20:1467–1475.
- Ward-Fear, G., G.P. Brown, and R. Shine. 2010. Using a native predator (the meat ant, *Iridomyrmex reburrus*) to reduce the abundance of an invasive species (the cane toad, *Bufo marinus*) in tropical Australia. *Journal of Applied Ecology* 47:273–280.
- Wilson, L.D., and L. Porras. 1983. *The Ecological Impact of Man on the South Florida Herpetofauna*, ed. University of Kansas Museum of Natural History, Special Publication No. 9. Lawrence: University of Kansas.
- Woolbright, L.L., A.H. Hara, C.M. Jacobsen, W.J. Mautz, and F.L. Benevides. 2006. Population densities of the Coqui, *Eleutherodactylus coqui* (Anura: Leptodactylidae) in newly invaded Hawaii and in native Puerto Rico. *Journal of Herpetology* 40:122–126.

- Woolbright, L.L., and M.M. Stewart. 1987. Foraging success of the tropical frog, *Eleutherodactylus coqui*: The cost of calling. *Copeia* 1987:6975.
- Wyatt, J.L., and F.A. Forsy. 2004. Conservation implications of predation by Cuban tree-frogs (*Osteopilus septentrionalis*) on native hylids in Florida. *Southeastern Naturalist* 3:695–700.
- Yeager, A., J. Commito, A. Wilson, D. Bower, and L. Schwarzkopf. 2014. Sex, light, and sound: Location and combination of multiple attractants affect probability of cane toad (*Rhinella marina*) capture. *Journal of Pest Science* 87:323–329.