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# Diet, Density, and Distribution of the Introduced Greenhouse Frog, *Eleutherodactylus planirostris*, on the Island of Hawaii

Christina A. Olson
*Utah State University*

# DIET, DENSITY, AND DISTRIBUTION OF THE INTRODUCED GREENHOUSE FROG, *ELEUTHERODACTYLUS PLANIROSTRIS*, ON THE ISLAND OF HAWAII

by

Christina A. Olson

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| _____ | _____ |
| Karen H. Beard<br>Major Professor | David N. Koons<br>Committee Member |
| _____ | _____ |
| Edward W. Evans<br>Committee Member | Byron R. Burnham<br>Dean of Graduate Studies |

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# ABSTRACT

Diet, Density, and Distribution of the Introduced Greenhouse Frog, *Eleutherodactylus planirostris*, on the Island of Hawaii

by

Christina A. Olson, Master of Science

Utah State University, 2011

Major Professor: Dr. Karen H. Beard
Department: Wildland Resouces

The greenhouse frog, *Eleutherodactylus planirostris,* native to Cuba and the Bahamas, was recently introduced to Hawaii. Studies from other invaded habitats suggest that it may impact Hawaiian ecosystems by consuming and potentially reducing endemic invertebrates. However, there have been no studies on the greenhouse frog in Hawaii. The first component of this study was to conduct a diet analysis. We conducted a stomach content analysis of 427 frogs from 10 study sites on the island of Hawaii. At each site, we also collected invertebrates using two different sampling methods: leaf litter collection and sticky traps to characterize available resources. Greenhouse frogs consumed predominantly leaf litter invertebrates. Dominant prey items consisted of Hymenoptera: Formicidae (32.4%), Acari (19.2%), and Collembola (17.4%). Greenhouse frogs consumed more Formicidae than was measured in the environment. At one study site, we estimated there were 12,500 frogs $ha^{-1}$ using mark-recapture methods and greenhouse frogs consumed 129,000 invertebrates $ha^{-1}$ $night^{-1}$ at this site. The

second component of this study was to determine the distribution of the greenhouse frog on the island of Hawaii, with a male breeding call presence/absence survey at 446 points along the major road network. The greenhouse frog was detected at 61 sites (14%), and found mostly in lowland areas, in habitats of native shrublands and forests, nonnative forests, agricultural lands, and pastures on the southwestern and eastern sides of the island. We determined detection probabilities of the greenhouse frog and the invasive coqui frog, *E. coqui*. Detection probability of the greenhouse frog was low on the first two surveys and improved by the third survey. Detection probability of the coqui was higher than the greenhouse frog, but overall site occupancy estimates were similar for both species. Because the greenhouse frog appears to be as widespread as the coqui, we recommend that research be conducted to investigate its impacts ecologically to determine whether control efforts should also be aimed at this species.

(129 pages)

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Christina A. Olson

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# BIOLOGY AND IMPACTS OF PACIFIC ISLAND INVASIVE SPECIES: *ELEUTHERODACTYLUS PLANIROSTRIS*, THE GREENHOUSE FROG (ANURA: ELEUTHERODACTYLIDAE)[1]

## BACKGROUND AND RESEARCH GOALS

The greenhouse frog, *Eleutherodactylus planirostris* (Cope 1862) is native to Cuba and has established on five Hawaiian Islands including Hawaii, Kauai, Lanai, Maui, and Oahu (Kraus et al. 1999). Due to the extreme isolation of the Hawaiian islands and lower diversity of native species, common vertebrate fauna, such as amphibians and reptiles, that are missing from the native assemblage of species, are successful and rapid invaders of Hawaiian habitats (Moulton and Pimm 1986, Kraus 2003). Native invertebrates are vulnerable to nonnative amphibians and reptiles because they have evolved without these types of predators (Kraus 2003). This is a critical concern in Hawaii because invertebrates comprise a large majority of the native fauna and are already at risk to threats of extinction (Eldredge and Miller 1995, Eldredge and Evenhuis 2002).

Despite reports that greenhouse frogs are widespread in Hawaii, there have been no studies examining their diet, density, or distribution. This research is the first assessment of the greenhouse frog invasion in Hawaii and will help determine if future studies are necessary to investigate its direct and indirect impacts to Hawaiian ecosystems.

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[1] This chapter is co-authored with Karen H. Beard and William C. Pitt. All sections except the Background and Research Goals section were written for an invited manuscript to be submitted to *Pacific Science*.

This study has two components and I conducted both aspects of the research on one island, the island of Hawaii:

1) *Diet and density study*: I conducted a diet study at sites across the island to determine which invertebrates the greenhouse frog consumes. I conducted a mark-recapture study to estimate greenhouse frog densities at one site to estimate the number of invertebrates greenhouse frogs consume per ha in Hawaii.
2) *Distribution study*: I conducted a presence/absence study across the island to determine greenhouse frog and the invasive coqui frog (*E. coqui*) distributions. Because of the cryptic nature of the greenhouse frog compared to the coqui, I used occupancy modeling to determine detection and occupancy probabilities of both species.

## LITERATURE REVIEW

### NAME

*Eleutherodactylus planirostris* (Cope, 1862)

Phylum Chordata, class Amphibia, order Anura, family Leptodactylidae

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

As the Latin meaning of the genus name implies, *Eleutherodactylus* (Dumeril & Bibron) frogs have individual (non-webbed) fingers and toes. The name *planirostris*, comes from the Latin "rostrum" (snout) and "planum" (level, flat), in reference to the frog's flattened snout. There are 185 species in the genus, distributed throughout the West Indies, the southern United States, Mexico, Belize, and Guatemala (Hedges et al. 2008). Recently, it has been suggested that *E. planirostris* should be classified in the subgenus *Euhyas* (Fitzinger), because of differences in liver shape, no external vocal sac, and more terrestrial behavior than the arboreal subgenus *Eleutherodactylus* (Hedges et al. 2008).

It is commonly known as the greenhouse frog because it is often found in plant nurseries, gardens, and greenhouses (Schwartz and Henderson 1991). Previously, the greenhouse frog was also commonly known as the Ricord's frog, cricket toad, Bahaman tree frog, and pink-snouted frog (Wright and Wright 1949).

## DESCRIPTION AND ACCOUNT OF VARIATION

### *Species Description*

A small species of *Eleutherodactylus* in its native Cuba, the greenhouse frog is sexually dimorphic with gravid females reaching a maximum snout-vent length (SVL) of 28 mm and reproductive males a maximum of 21 mm (Schwartz 1974). In Florida, size is somewhat smaller, with a maximum female SVL of 26.5 mm and a maximum male SVL of 17.5 mm (Meshaka et al. 2004). In Jamaica, the mean SVL (n = 83) measured from two different sites was 18 mm. Individuals measured from 10 study sites on the island of Hawaii (Chapter 2), were similar to Cuba, maximum female SVL was 27 mm

(mean = 22, n = 176) and maximum male SVL was 21 mm (mean = 17, n = 100), with females 30 to 40 % larger than males across sites.

The greenhouse frog has a flattened snout, long and slender toes, and truncated terminal disks (Conant and Collins 1991). There are two basic color phases, a mottled tan and brown phase, and a mottled tan and brown phase with two yellow dorso-lateral stripes extending from the eye along the length of the body (Lynn 1940). Dorsal coloring ranges from a spectrum of light tan to dark reddish brown (Goin 1947, Ashton and Ashton 1988) and the venter is an off-white to gray (Bartlett and Bartlett 2006).

The mottled pattern is recessive to the dominant striped pattern, and in Cuba, there is a 3:1 ratio of striped to mottled individuals (Goin 1947). A population from Gainesville, Florida (USA) exhibited a 1:1 ratio (Goin 1947). Goin (1947) hypothesized this could be a bottleneck effect from the initial founding population, but it may also be an example of extreme selective pressure depending on habitat type (Woolbright and Stewart 2008).

The dominant pattern observed in specimens collected in Hawaii (Chapter 2, Bishop Museum, Honolulu, Hawaii, USA) is mottled. All 427 individuals collected across 10 sites on the island of Hawaii were mottled (Chapter 2). The only records of striped individuals are from Oahu, with 12 (14%) striped individuals out of 85 specimens (0.16:1 ratio) from five localities (Fred Kraus, pers. comm.).

*Distinguishing Features*

The *Eleutherodactylus* genus comprises 90% of the native frog species in Cuba, with a total of 56 species (AmphibiaWeb 2010). The greenhouse frog was originally

identified as *E. ricordii* in its native range and was split when the two species were found syntopic in eastern Cuba (Schwartz 1974). *Eleutherodactylus ricordii* are larger than greenhouse frogs, with a maximum female SVL of 40 mm (Schwartz 1965). Both *E. goini* and *E. casparii* in the native range were at one time but are no longer considered subspecies of *E. planirostris* (Schwartz 1974). *Eleutherodactylus goini* is larger than greenhouse frogs (Schwartz 1974) and *E. casparii* is distinguished from greenhouse frogs by black bands on the sides of the body behind the front limbs and a greenish tint to the dorsal coloring (Díaz and Cádiz 2008). Other similar species in its native range include *E. tonyi* and *E. simulans*, which are almost identical to the greenhouse frog, but have very different male breeding calls (Díaz and Cádiz 2008).

Of the frogs that have been introduced to Hawaii, the greenhouse frog most resembles *E. coqui*, the Puerto Rican coqui frog. The distribution, ecology, and impacts of the coqui are better studied than that of the greenhouse frog both in its native range and Hawaii. Features that distinguish this species from the greenhouse frog are its light tan color, golden eyes, wider snout, and large toe pads (Beard et al. 2009). The coqui is also larger than the greenhouse frog with a maximum SVL for males of 39 mm and females 49 mm in Hawaii (Beard et al. 2009). Most notably, the male breeding call is different. The greenhouse frog produces short, irregular soft chirps (Schwartz 1974), which are often mistaken for a cricket or bird, while the coqui produces a loud, two note “ko” and a “kee” call that can reach decibels up to 80–90 dBA at 0.5 m (Beard and Pitt 2005).

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

(1) Size in Hawaii: SVL for reproductive males: 14.2 to 21.2 mm; gravid females: 17.2 to 27.3 mm (Chapter 2).

(2) Body color: venter is white to light gray and dorsal is tan-pink to dark reddish-brown (Ashton and Ashton 1988, Bartlett and Bartlett 2006). There is a dark band from top of tympanum to arm insertion (Wright and Wright 1949).

(3) Body shape: head as broad as body, snout truncated and extending slightly beyond the lower jaw (Wright and Wright 1949).

(4) Eye color: black with a red iris (Wright and Wright 1949).

(5) Foot features: toes are slender, lack webbing and with small, terminal disks (Wright and Wright 1949).

(6) Tympanum: White or coral red, approximately half the size of the eye (Wright and Wright 1949).

## ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACTS

### *Detrimental aspects*

Greenhouse frogs and their eggs frequently move unintentionally with plants or landscape materials, and therefore may affect industries involved with this movement. For example, the floriculture industry in Hawaii has been negatively impacted. Flowers and nursery product sales are the largest single agricultural commodity for the state and account for 15% of Hawaii's $621.6 million agricultural output (HASS 2005). Inter-island and international plant shipments are inspected and treated for frogs. This treatment increases shipment costs and may reduce trade. Plant shipments with infested frogs also may be refused port entry and destroyed (Raloff 2003). There is no

information available on the amount nursery owners spend to control greenhouse frogs, but the inability to distinguish between the coqui and the greenhouse frog may lead to costs to treat greenhouse frog infestations.

County, state, and federal government have also incurred costs to control coquis. Costs for public agencies exceeded $4 million in 2006, but have declined in recent years. For example, the State of Hawaii Legislature spent $2 million for frog control in 2006, but only $800,000 in 2007, $400,000 in 2008, and $100,000 in 2009 (Anonymous 2010). Funds have not specifically been allocated to target greenhouse frogs; however, populations are probably controlled at sites that are targeted for coqui eradication and control.

The only negative economic impacts not directly associated with *E. coqui* are the reports that large populations can be a nuisance. Several resorts in Hawaii attempt to manage greenhouse frogs because they are found in swimming pools and irrigation boxes (Will Pitt, unpubl. data).

*Beneficial aspects*

In general, there is little concern over the spread of greenhouse frogs (Kraus and Campbell 2002). Because of its quiet call, Hawaiian residents often do not consider the greenhouse frog a nuisance, and some have expressed preferences for the greenhouse frog over the coqui (Christina Olson, pers. comm.). Some residents find the frogs or their calls aesthetically pleasing and frogs have been intentionally moved to gardens or homes, although unintentional spread is much more common (Christy et al. 2007b). This ambivalence toward greenhouse frog infestations may lead to their further spread to new

areas. For example, both coqui and the greenhouse frog were introduced to Guam in 2003 (Christy et al. 2007b). The coqui was quickly eradicated but greenhouse frog populations became established and now have spread throughout the island with little alarm (David Vice, pers. comm.).

In addition, some individuals believe that all frogs are beneficial and can control harmful invertebrates, such as mosquitoes and termites (Fullington 2001, Singer 2001). However diet studies on both greenhouse frogs and coquis in Hawaii indicate that these invertebrates do not comprise a significant portion of their diet (Chapter 2, Beard 2007).

*Regulatory Aspects*

Most of the rules and regulations concerning frog movement around the Pacific basin stem from concerns over the spread of the coqui. In Hawaii, all frogs are listed as State Injurious Species and it is illegal to transport or release frogs into the wild. The requirements for treating plants prior to shipment are required primarily to combat coqui frogs but the presence of any frogs in the shipment would restrict their movement (Hawai‘i Department of Agriculture 150A-2, Hawai‘i Revised Statutes). Plant shipment to Guam, the continental United States, and other countries require a phytosanitary certificate that certify shipments are pest free but this often does little to prevent greenhouse frogs or their eggs because they can easily go undetected in shipments. The lack of restriction and the difficulty in detection may contribute to the continued spread of greenhouse frogs throughout the Pacific basin.

*Environmental Impacts*

Introduced Caribbean *Eleutherodactylus* species were identified as potential threats to Hawaiian ecosystems when their introduction and establishment was first recognized (Kraus et al. 1999). Because *Eleutherodactylus* are insectivores, it was hypothesized that the most likely impacts would be to invertebrate communities (Kraus et al. 1999).

Greenhouse frog diets were determined on the island of Hawaii, and they are estimated to be consuming 129,000 invertebrates $ha^{-1}$ $night^{-1}$ at some sites (Chapter 2). The greenhouse frog was found to predominantly consume leaf litter invertebrates (Chapter 2). Primary prey included ants, mites, and springtails, which comprised 32%, 19%, and 17% of the total prey consumed, respectively (Chapter 2). All ants are nonnative to Hawaii, but both mite and springtail groups contain endemic species. Stomach contents were not identified to species, and therefore it is unknown if greenhouse frogs are consuming mites and springtails native to Hawaii. They consume other groups of prey that contain native species in the following proportions: spiders (3%), beetles (2%), flies (2%), and booklice (2%) (Chapter 2).

Overall, 42% of the species identified in the diet were nonnative to Hawaii, including ants, isopods (8%) and amphipods (1%) (Chapter 2). There may be some positive environmental impacts as a result of the introduction. For example, species of ants identified in the diet included the big-headed ant (*Pheidole megacephala*), the Argentine ant (*Linepithema humile*), and the yellow crazy ant (*Anoplolepis gracilipes).* Because research indicates that these species have negative effects on native invertebrates

(Krushelnycky et al. 2005), greenhouse frogs may indirectly benefit invertebrates if they reduce ant populations.

It was also hypothesized that the invasive brown treesnake, *Boiga irregularis*, would prey on introduced greenhouse frogs on Guam (Hurley 2003). Since its introduction greenhouse frogs have been found in brown treesnake stomach contents (Shane Siers, pers. comm.). It is possible that greenhouse frogs bolster populations of the brown treesnake by providing an abundant food source. There is potential for future introductions of the brown treesnake to Hawaii (Rodda and Savidge 2007). If established, the brown treesnake may use *Eleutherodactylus* frogs as a prey source, thus bolstering populations of brown treesnake and facilitating its spread throughout the Hawaiian islands (Beard and Pitt 2005).

Other hypotheses regarding potential environmental impacts include *Eleutherodactylus* competing with other insectivores for prey, such as endemic birds or the endemic Hawaiian hoary bat (Kraus et al. 1999, Beard and Pitt 2005). However, no data has been collected to support or refute these hypotheses. In addition, it has been proposed that *Eleutherodactylus* may bolster introduced mammal populations, which are known bird predators. Beard and Pitt (2006) conducted diet analysis on mongoose and rat populations on the eastern side of the island of Hawaii, and found that *Eleutherodactylus* made up a small or negligible part of these small mammal diets.

Additional impacts may result from the indirect effects of predation. For example, many of the invertebrates that the greenhouse frog consumes play an important role in ecosystem processes such as herbivory and decomposition of plant material. In Hawaii, Sin et al. (2008) found that herbivory rates were lower and plant growth and leaf

litter decomposition rates were higher in sites with the nonnative *E. coqui* than without. These results also suggested that *E. coqui* has the potential to increase nutrient cycling rates in Hawaii, which may confer a competitive advantage to invasive plants in an ecosystem where native species have evolved under nutrient-poor conditions. Similar impacts may be possible at sites invaded by the greenhouse frog.

## GEOGRAPHIC DISTRIBUTION

Native to Cuba and the Bahamas, the greenhouse frog is found island-wide in Cuba, except in the highest elevations (Cuba maximum elevation = 1,100 m) with a maximum elevation of 720 m (Díaz and Cádiz 2008). In the Bahamas, it is found on Little Bahama Bank, South Bimini, New Providence, and possibly Eleuthera (Schwartz and Henderson 1991).

The first record in Florida was from the Florida Keys and isolated populations were later found in Miami (1899), Gainesville (1933), Tampa (1938), and Jacksonville (1943). These populations are thought to be established from other Florida populations, not from a Cuban source (Goin 1947). It was first noted that the greenhouse frog was becoming widespread and abundant in Florida by the 1920s (Barbour 1920) and at one point it was noted as the most common frog in the Florida Keys (Carr 1940). The founding population may have arrived from the West Indies through natural means on driftwood (Meshaka et al. 2004), but probably arrived through the cargo or nursery trade (Wilson and Porras 1983). The peninsular populations were initially first transported through the horticultural trade (Goin 1947), but later records indicate that they spread to

new areas, including undisturbed natural habitats, through natural spread from existing populations (Carr 1940).

The first record of the greenhouse frog in Louisiana was from a city park in New Orleans in 1975 and its range has expanded to 10 parishes (i.e. counties) in the southern part of the state (Meshaka et al. 2009). It was first recorded in Savannah, Georgia in 1998, and is now found in five southern counties (Jensen et al. 2008). Greenhouse frogs have been in Gulfport, Mississippi since 2003 (Dinsmore 2004) and in Baldwin County, Alabama since 1982 (Carey 1982). There is a report of a large, dense population in a tropical building at the Tulsa Zoo in Oklahoma, but it is thought that the species is confined indoors given the cold temperatures in winter (Somma 2010).

Greenhouse frogs were first reported in Jamaica in the 1930s, found around major ports of Montego Bay and Kingston (Stewart 1977), indicating a possible spread via the cargo industry. It is now found in all major regions of Jamaica except Hellshire Hills and the Portland Ridge Peninsula on the southern side of the island (Hedges 1999). There are also reports of introduced greenhouse frogs on Granada (Kraus et al. 1999), the Caicos Islands, and the Cayman Islands (Schwartz and Henderson 1991). According to Lever (2003), it is possible that the greenhouse frog is native to the Cayman Islands, however, it is found only on the islands of Grand Cayman and Cayman Brac (Seidel and Franz 1994). There is one report of the greenhouse frog from Veracruz, Mexico (Schwartz 1974).

The first record of the greenhouse frog to the Pacific basin is from the island of Hawaii in 1994. It is thought that the greenhouse frog arrived to Hawaii via nursery plants (Kraus et al. 1999) possibly from Florida. This is assumed because the greenhouse frog first appeared in nurseries in Hawaii, and it had relatively stable populations in

nurseries in Florida around the time of introduction. It was particularly abundant in nurseries raising *Dracaena* species (Kraus et al. 1999).

The current distribution of the greenhouse frog is relatively unknown in Hawaii. It is thought to be widespread on the island of Hawaii (Will Pitt, pers. comm.), Maui (Adam Radford, pers. comm.), Oahu (Katie Swift, pers. comm.) and Kauai (Keren Gunderson, pers. comm.), and there are records from Lanai as well (Figure 1.1). A systematic presence/absence study sampled every 2 km on the major network on the island of Hawaii in 2009 (Chapter 3) found males calling at 61 (14%) of the 446 points sampled. Occupancy modeling indicated that detection probabilities are low for the greenhouse frog, but by repeated visits to points, detection improved. Results from this survey are shown in Chapter 3 (Figure 3.1).

The greenhouse frog was introduced to Guam from Hawaii via the nursery trade in 2003 (Christy et al. 2007b). Frogs were first found in four localities: Tumon, Tamuning, Mangilao, and Manengon (Christy et al. 2007a), and have rapidly spread to the entire island (Elijah Wostl, pers. comm.).

It may be possible to determine genetically if the Pacific greenhouse frogs came from its native range or some area of its introduced range such as Florida, if the founder populations still exist. Color patterns have also been used to investigate the spread of the coqui frog species throughout the islands of Hawaii (O'Neill and Beard 2010), which may be possible with the greenhouse frog as well.

# HABITAT

## *Climatic requirements and limitations*

There have been few studies on the climatic requirements of the greenhouse frog. It has mostly invaded habitats that have similar overlap in annual mean temperature and maximum temperature in warmest month with its native range (Bomford et al. 2009, Rödder and Lötters 2010). However, it is found in areas with seasonal daily minimum temperatures as low as 4-8°C (Wray and Owen 1999, Tuberville et al. 2005) in the southeastern United States. One study suggests that in Hawaii, greenhouse frogs may be limited to areas with annual temperatures > 20°C; however, the results of this study may reflect its recent introduction, and the species may still be spreading to areas with cooler temperatures (Rödder and Lötters 2010).

The greenhouse frog is not found on the highest peaks in Cuba of 1,100 m (Díaz and Cádiz 2008) or in Jamaica (maximum elevation = 2,200 m) where greenhouse frogs are found only from sea level to 600 m (Stewart and Martin 1980). The USA continental range is limited to the southeastern coastal lowlands with an elevation < 200 m. In Hawaii, greenhouse frogs were detected at an elevation of 1,115 m in 2009 (maximum (Chapter 3). There are habitats in Hawaii above 1,115 m that may be suitable in terms of forest cover, although in addition to cooling temperatures, precipitation also starts to decline at higher elevations (Price 1983), so these habitats may not be suitable.

## *Ecosystem and community types invaded*

In its native range, the greenhouse frog is common and well adapted to a wide diversity of habitats, including wet and dry forests, coastal and mountainous areas, rivers

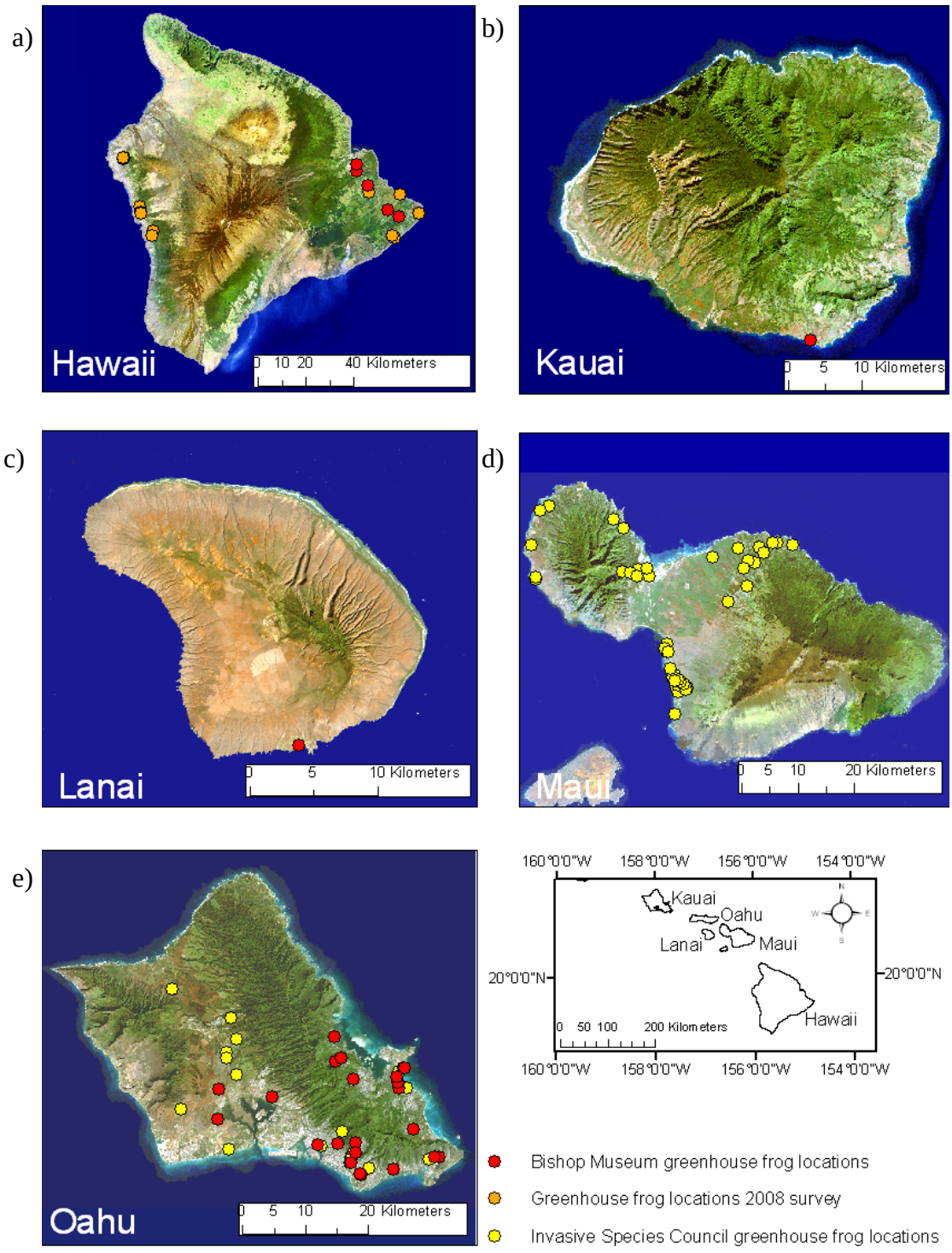


FIGURE 1.1. Map of recorded locations of *Eleutherodactylus planirostris* populations on the islands of a) Hawaii, b) Kauai, c) Lanai, d) Maui, and e) Oahu (Bishop Museum records, Maui Invasive Species Council, Oahu Invasive Species Council, Emily Kalnicky).

and stream beds, caves, rocky outcrops, gardens and interior houses (Garrido and Schwartz 1968, Díaz and Cádiz 2008). In Florida, the greenhouse frog is common in wet and dry forests, open grasslands, coastal areas, and scrub habitats (Enge 1997, Meshaka et al. 2004). In Jamaica, it is most often found in drier habitats such as open grasslands and scrub, as well as lawns, pastures, and roadsides (Stewart and Martin 1980).

Most populations in Hawaii are found in lowland (0–500 m) habitats. Populations have become established along roadsides, and in macadamia nut orchards, nurseries, pastures, residential gardens, resort areas, state forests, and state parks (Chapter 2, Chapter 3). Most of the invaded habitats, including the lowland state forests and parks, are dominated by nonnative plants, however, populations have also been found in native shrublands and forests that are dominated by the endemic O'hia tree, *Metrosideros polymorpha* (Chapter 3). In Guam, the greenhouse frog has invaded both urbanized and forested areas, including residential gardens and secondary scrub-forests (Bjorn Lardner, pers. comm.). Most of these habitats are also invaded by nonnative vegetation.

*Habitat resource requirements and limitations*

In its native range, the greenhouse frog is often found in the leaf litter, hidden under rocks, and in rock crevices at the mouth of caves (Garrido and Schwartz 1968). It is common in open grassy areas and will use coconut husk piles as daytime retreat sites in Jamaica (Stewart and Martin 1980). In Florida, it has been described as semi-fossorial, often burrowing into moist soil (Goin 1947, Meshaka et al. 2004) and found under rocks, fallen branches, and leaf litter (Goin 1947, Schwartz and Henderson 1991). It has also been found in low growing bromeliads in southern Florida (Neill 1951) and is an

inhabitant of gopher tortoise burrows (Lips 1991). It is predominantly terrestrial and fossorial in Hawaii, found in the leaf litter in natural areas and also commonly found under man-made objects (i.e. flower pots, water meters, and tarps), rocks, and inside lava tubes (Chapter 2).

Although there are numerous descriptions of its habitat, there have been no studies investigating factors that limit the greenhouse frog. The greenhouse frog is typically found on the forest floor (Chapter 2) and up to 2 m off of the ground (Duellman and Schwartz 1958, Stewart and Martin 1980). The use of daytime retreat sites on or below the forest floor has been documented in Hawaii, Florida, and Jamaica (Goin 1947, Stewart 1977, Chapter 2), which may indicate that similar to *E. coqui*, the greenhouse frog may be limited by the amount of available retreat sites (Stewart and Pough 1983, Woolbright 1996). However, this might not limit either species in Hawaii given its rocky terrain, and their use of rock crevices as retreat sites (Stewart and Woolbright 1996, Díaz and Cádiz 2008).

Because it has also mostly invaded areas with similar overlap of mean precipitation in the wettest month (Rödder and Lötters 2010), and overcast or rainy sky conditions are important factors in breeding call activity (Chapter 3), precipitation may be an important factor limiting the greenhouse frog distribution. Humidity is an important variable for egg development and hatching success (Goin 1947), although there is some indication that the greenhouse frog has a higher tolerance for drier conditions than other *Eleutherodactylus* species (Pough et al. 1977). Moisture and rainfall may also influence greenhouse frog behavior. In Cuba and in Florida, where there is a distinct wet

and dry season, frogs are much more active in terms of breeding during the wet season (Meshaka and Layne 2005, Díaz and Cádiz 2008).

## PHYSIOLOGY AND GROWTH

Based on a study of Florida greenhouse frogs, minimum body size for breeding males is 15.0 mm SVL and 19.5 mm SVL and reach sexual maturity after one year (Goin 1947). Eggs are laid individually in or under moist soil, or under fallen leaves or rocks and unlike other members of the *Eleutherodactylus* genus, there is no guarding of the eggs by either sex. Clutch size ranges from 3-26 eggs (n = 104 clutches), with a mean of 16 eggs per clutch (Goin 1947).

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

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

## REPRODUCTION AND POPULATION DYNAMICS

The breeding season in Cuba is April through January (Meshaka and Layne 2005). In Florida, breeding season is April to early September, with a peak during the mid-summer months (Goin 1947, Meshaka and Layne 2005), but there is some fluctuation that coincides with the onset of the rainy season. It is unclear if the greenhouse frog has a distinct breeding season in Hawaii but they call May through July on the island of Hawaii.

*Eleutherodactylus* species reach a calling peak at night between 1830-0500, but call frequency and duration vary by species (Drewry and Rand 1983). There is no specific information available on the calling times for the greenhouse frog in either its native or introduced habitats (Goin 1947). Meshaka and Layne (2005) found that calling at one site in central Florida most frequently took place when air temperature was

between 23-30°C and relative humidity ranged between 84-100 RH. Males will call from the ground or on vegetation under 1 m in height (Díaz and Cádiz 2008). In Hawaii, males call from under debris and stone fences, as well as from subterranean lava tubes (Chapter 2).

Greenhouse frog density was estimated in a macadamia nut orchard on the eastern side of the island of Hawaii in June, 2009 using mark-recapture techniques of adult frogs in a 50 x 50 m plot (Chapter 2). Over seven nights, 651 individuals were captured, with an equal initial capture and recapture rate of 0.12 (Chapter 2). Adult densities at this site were estimated at 4,500 frogs $ha^{-1}$ with a total population density of 12,500 frogs $ha^{-1}$ (Chapter 2).

In a removal study of coconut husk piles from four study sites in northern Jamaica of two native species and two introduced species, the highest density site was estimated to have 4,635 frogs $ha^{-1}$ of all four species of frogs (Stewart and Martin 1980). Overall abundance of the husk piles was higher in the dry season than the wet season for all species. Greenhouse frog abundance was lower in husk piles dominated by the native frog species, and higher in the coastal sites than the upland sites.

Meshaka and Layne (2005) conducted a long-term abundance study in two Florida fire-adapted, scrub habitats using mark-recapture techniques in 0.16 ha grid with pit-fall traps and drift fence arrays from 1984-1988 and 1994-1996. A total of 211 individuals were captured over the duration of the study. They found an increase in captures of adults and juveniles from September to December, possibly indicating a recruitment of juveniles. Survivorship of 17 unsexed individuals was mean of 1.9 ± 2.3 months (range: 0.03-6.6).

# RESPONSE TO MANAGEMENT

## *Chemical control*

Chemical control has been used in Hawaii to effectively control *Eleutherodactylus* frog populations over large areas (Tuttle et al. 2008). Most options have been developed to control coqui frog populations, but the chemicals used are equally effective against greenhouse frogs. Currently, only a citric acid solution can be used legally to control *Eleutherodactylus* frogs in Hawaii, although several other chemicals have been identified as effective frog toxicants (Campbell 2001, Pitt and Sin 2004b, Pitt and Doratt 2005). Hydrated lime was registered as a frog toxicant from 2005-2008 but the registration is no longer active. Citric acid is exempt from the requirements of FIFRA by regulation (40 CFR Section 152.25) because it is classified as a minimum risk pesticide. A 16% citric acid solution was 100% effective for greenhouse frogs in the laboratory, and lower concentrations were also found to be effective (Pitt and Sin 2004a).

Few control efforts have been directed exclusively at greenhouse frogs so field efficacy is uncommon. In 2003, we evaluated the ability to control greenhouse frogs at five Kauai resorts over a 5 month period (Will Pitt, unpubl. data) because resort guests were complaining about finding frogs in swimming pools. Greenhouse frogs are often found at resorts with arid landscapes in irrigation boxes used for landscaping watering. We evaluated the immediate and the long term effects of control on frog abundance in irrigation boxes. A 16% citric acid solution was applied bimonthly to irrigation boxes that were infested with greenhouse frogs. As expected, frogs reinvaded irrigation boxes because the citric acid application does not have long term residual effects on frogs (Pitt

and Sin 2004a). The number of irrigation boxes at each resort varied from 33−411 ($\bar{x}$ = 185). The application removed all frogs from 91% of irrigation boxes within 24 hours. After 5 months of treatments, 67% fewer irrigation boxes were infested with frogs.

*Mechanical Control*

Mechanical control techniques have been evaluated for coqui frogs. Most would likely have similar effects on greenhouse frogs. Mechanical control methods including hot water treatments, native habitat management, and hand capture are directed toward nursery operations, quarantine areas, or residential areas.

Hot water spray or vapor treatments are commonly used to treat plant shipments for a variety of pests. Hot water sprayed on plants at either 45 ºC for 1 minute or 39 ºC for 5 minutes was effective treatment against adult coqui frogs and similar results would be expected with greenhouse frogs, considering the two species have similar thermal tolerances (Pough et al. 1977, Hara et al. 2010). Native habitat management may be effective in reducing the abundance of frogs and reduce the likelihood that frogs will move into an area. Hand capture is effective when only a few adult frogs are present but would be ineffective for large populations (Beard et al. 2008). Traps and barriers developed for coqui frogs have not been tested to determine their effectiveness on greenhouse frogs, although barriers may be equally effective against both species.

## NATURAL ENEMIES

In its Caribbean range, three racer snakes (*Cubophis canterigerus* on Cuba, *C. caymanus* on Grand Cayman, and *C. vudii* in the Bahamas) and the Cuban treefrog

(*Osteopilus septentrionalis*) are predators of greenhouse frogs (Meshaka 1996, Henderson and Powell 2009). The ringneck snake (*Diadophis punctatus*), a small (8 – 38 cm) fossorial species found in humid and moist habitats, is also a predator of greenhouse frogs in Florida (Wilson and Porras 1983, Lazell 1989). In Guam the invasive brown tree snake, *Boiga irregularis*, is known to predate greenhouse frogs (Shane Siers, pers. comm.). Other predators of *Eleutherodactylus* species in the Caribbean include invertebrates, frogs, lizards, snakes, birds, and mammals (Henderson and Powell 1999). There are no records of Hawaiian species predating on greenhouse frogs.

Documented parasites in its native Cuba include nematodes, Spiruridae and *Oswaldocruzia lenteixeirai* (Henderson and Powell 2009). Two studies indicate that introduced amphibian and reptile species in Hawaii have lower parasite diversities in their introduced range versus their native range, the coqui (Marr et al. 2008) and the brown anole, *Anolis sagrei* (Goldberg and Bursey 2000). One parasite found in the Puerto Rican coqui population but not the Hawaiian coqui population, *Rhabdias elegans*, was found to reduce initial locomotory burst performance of the coqui (Marr et al. 2010).

## PROGNOSIS

Greenhouse frog populations are widespread in Hawaii and Guam. Because control efforts on Hawaii are targeted toward coqui eradication, and there have been no efforts to control the frog on Guam, it is unlikely they will be controlled with current methods and available monetary resources. The best method to control greenhouse frog is to reduce the spread of frogs to new areas with good management techniques, such as

inspecting and treating cargo and plant materials, using barriers, and not transporting material that is known to be infested.

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# CHAPTER 2

## DIET OF THE INTRODUCED GREENHOUSE FROG IN HAWAII[2]

## ABSTRACT

This research is motivated by the recent introduction of the Cuban terrestrial greenhouse frog, *Eleutherodactylus planirostris*, to Hawaii. Studies from other invaded habitats suggest that greenhouse frogs may impact Hawaiian ecosystems by consuming and potentially reducing Hawaiian endemic invertebrates. However, until now, there has been no research investigating its diet in Hawaii. To determine its potential impacts on native invertebrates, we conducted a stomach content analysis of 427 frogs from 10 study sites on the island of Hawaii. At each site, we also collected invertebrates with two sampling methods, leaf litter collection and sticky traps, to determine if diets were representative of the available resources. Dominant prey items consisted of Hymenoptera: Formicidae (32.4%), Acari (19.2%), and Collembola (17.4%). Nonnative invertebrate orders comprised 43.2% of their diet (Amphipoda, Isopoda, and Hymenoptera: Formicidae). Invertebrate orders containing endemic species most threatened by the invasion include Acari (mites), Araneae (spiders), Collembola (springtails), and Psocoptera (booklice), which each comprised greater than 2% of their diet. Greenhouse frogs consumed predominantly leaf litter invertebrates and selected more Formicidae than was available in the environment. A total population of 12,500 frogs $ha^{-1}$ was estimated at a single study site. With these high densities and number of prey consumed, the greenhouse frog may consume 129,000 invertebrates $ha^{-1}$ $night^{-1}$ at some sites. This research highlights the

[2] This chapter is co-authored with Karen H. Beard and written for the journal *Copeia*.

need for an understanding of the indirect effects of greenhouse frog predation on invertebrates in Hawaii.

## INTRODUCTION

The greenhouse frog (*Eleutherodactylus planirostris*) is a nocturnal, terrestrial species native to Cuba and the Bahamas that has invaded areas of the southeastern United States, Jamaica, and Guam, and five Hawaiian Islands: Hawaii, Kauai, Lanai. Maui, and Oahu (Kraus et al., 1999; Christy et al., 2007). It was first recorded in Hawaii in 1994, arriving through the nursery trade (Kraus et al., 1999), and it is thought to have spread rapidly between and across the islands through the sale and movement of infested nursery plants, in part because it has direct development (Kraus and Campbell, 2002). In general, the invasion is not well studied, possibly because the species is not observed often in invaded habitats, due to its small size [maximum snout-vent-length (SVL) in Cuba of 27 mm (Schwartz, 1974)] and inconspicuous breeding call (Kraus and Campbell, 2002).

However, the greenhouse frog is thought to be widespread in Hawaii, including in natural areas (Campbell and Kraus, 2002), and amassing large undetected populations (Raloff, 2003). Because the greenhouse frog is an insectivore (Goin, 1947; Stewart, 1977), the most obvious potential impact of the invasion on Hawaiian ecosystems is the consumption and possible reduction of invertebrates. Because it is a predominantly terrestrial and semi-fossorial species (Meshaka et al., 2004), we expect that the greenhouse frog primarily forages in the leaf litter. Previous research in other areas where it has been introduced suggests it consumes Coleoptera, Hymenoptera (mainly Formicidae), Blattodea, and Arachnida (mainly Araneae) (Goin, 1947; Stewart, 1977).

However, these findings may reflect prey availability and not preferences. Thus, it is difficult to extrapolate these findings to Hawaii, where prey availability, foraging location, and microhabitat usage may be different.

The impact of greenhouse frogs on invertebrates is likely to be greater where they attain high densities, and we might expect this to be the case in Hawaii because there are few amphibian predators (Woolbright et al., 2006). For example, the nonnative, Puerto Rican coqui (*E. coqui*) can attain densities three times higher in Hawaii than in its native range (Woolbright et al., 2006; Beard et al., 2008). It can also consume an estimated 690,000 invertebrates $ha^{-1}$ in one night (Beard, 2007; Beard et al., 2008), and has been documented to reduce invertebrate abundances (Sin et al., 2008, Choi, unpubl. data). Even though both the greenhouse frog and coqui have been documented to have arrived around the same time to Hawaii, the coqui has received a disproportionate amount of attention in terms of management, control, and research because of its loud mating calls (Kraus and Campbell, 2002; Beard and Pitt, 2005).

The objectives of this study were three-fold: 1) to conduct a stomach content analysis to determine dominant prey taxa, 2) to determine primary foraging microhabitat, prey preferences, and microhabitat usage, and 3) to develop an estimate of greenhouse frog abundance so that consumption rate of invertebrates could be estimated.

## MATERIALS AND METHODS

***Study sites***.–Study sites were 10, 100 m x 100 m areas on the island of Hawaii, USA (Fig. 2.1, Table 2.1) located in an agricultural research station (WR), macadamia nut orchards (KM, PP), natural areas (KL, PH, MS, WF), outdoor plant nurseries (KP,

PN), and a resort (ML). Sites were selected that had relatively large greenhouse frog populations and a sufficiently large area to sample. They were selected also to maximize habitat diversity across sites. Dominant overstory across the sites included *Casuarina equisetifolia* (KL and MS), *Macadamia integrifolia* (KM and PP), *Metrosideros polymorpha* (WF), and *Psidium cattleianum* (PH). There was little overstory at KP, ML, PN, and WR. Dominant understory included *Clidemia hirta* (WF), *Dicranopteris linearis* (WF), *Lapranthus* sp. (ML), *Nephrolepis* sp. (KL, PH, MS), *Pennisetum clandestinum* (KL, PH, MS), *Sphagneticola trilobata* (PH, WR), and *Stenotaphrum secundatum* (KP, PN, and WR). Percent canopy cover closure (Table 2.1) was measured using a convex spherical densiometer (Ben Meadows Company Inc., Janesville, WI, USA) along five 20 m transects every 20 m, for a total of 20 measurements per site. Percent ground cover (Table 2.1, eight categories: concrete, flower pot, grass, herbaceous, leaf litter, other, soil, and rock) was measured at each site using 20, 1 m x 1 m quadrats located every 20 m along five, 100-m transects, separated by 20 m.

***Frog sampling***.–From 19 May to 19 July 2009, frogs were collected from each site between 1900–2330 h over 1-3 days; except at PN, where because access was limited, frogs were collected from 1000–1400 h. At each site, two to three researchers walked the entire area and hand-captured all frogs encountered. To locate frogs, researchers visually scanned the ground and vegetation while turning over dead logs, debris, rocks, and man-made items. Most often, frogs were first observed jumping away from the researchers. If 25 frogs were not collected, researchers returned the following day and re-surveyed the site until a minimum of 25 frogs was collected. For each frog collected, microhabitat structure and height from the forest floor where the frog was first observed were.

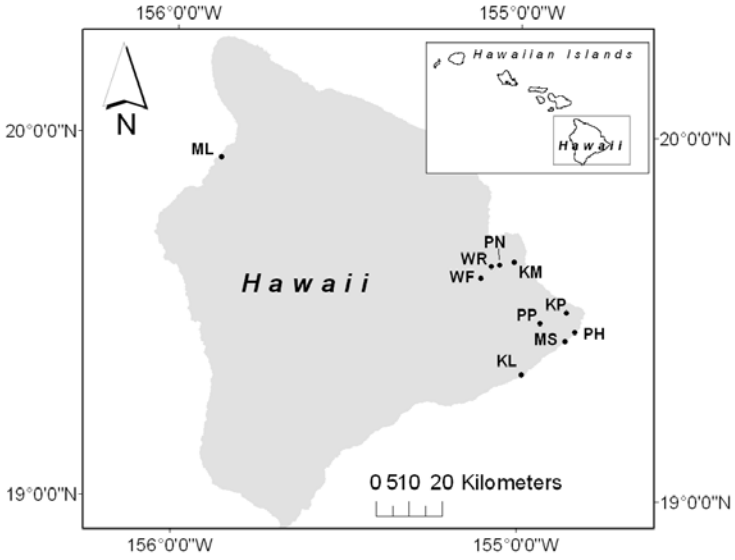


**Fig. 2.1.** Location of the 10 collection sites of *Eleutherodactylus planirostris*, island of Hawaii, USA. (Study site abbreviations: KP = Kalapana, KM = Keaau Macadamia Orchard, KP = Kapoho Nursery, ML = Mauna Lani Resort, MS = MacKenzie State Park, PH = Pohoiki, PN = Panaewa Nursery, PP = Pahoa Plantation, WF = Waiakea Forest Reserve, WR = Waiakea Research Station).

recorded, and frogs were retained in individual bags until they were euthanized with $CO_2$ at the end of the night.

In the laboratory, snout-vent-length (SVL) of each frog was measured with dial calipers to the nearest 0.1 mm. Frogs were dissected and assigned a stage class based on examination of gonads (preadult, male, or female). Stomachs were removed, punctured, and stored in 70% ethanol until further analysis. Stomach contents were identified to the lowest recognizable taxonomic unit (RTU), typically order. Order Hemiptera was identified to sub-order, and the family Formicidae was sorted as a separate category from order Hymenoptera. For each item, maximum length and width were measured to 0.01 mm (Magnusson et al., 2003) using a 10-mm reticle **(**Thermo Fisher Scientific Inc., Waltham, MA, USA). Volume for each prey item was calculated using the formula: v =

**Table 2.1.** Site name, elevation, dominant groundcover, percent (%) canopy cover, and number of frogs collected of *Eleutherodactylus planirostris* by site for the island of Hawaii, USA.

| Site name | Elevation (m) | Dominant groundcover | Canopy cover (%) | Sample size |
|---|---|---|---|---|
| Kalapana | 22 | leaf litter, herbaceous | 94.28 | 53 |
| Keaau Macadamia Orchard | 150 | leaf litter, rock | 88.98 | 49 |
| Kapoho Nursery | 83 | other (tarp), grass | 62.46 | 29 |
| Mauna Lani Resort | 44 | herbaceous, grass | 47.84 | 47 |
| MacKenzie State Recreation Area | 35 | leaf litter, herbaceous | 94.96 | 50 |
| Pohoiki | 20 | herbaceous, leaf litter | 98.34 | 49 |
| Panaewa Nursery | 118 | rock, concrete, herbaceous | 43.11 | 34 |
| Pahoa Plantation | 223 | soil, leaf litter, rock | 75.40 | 35 |
| Waiakea Forest Reserve | 418 | grass, soil, herbaceous | 83.31 | 48 |
| Waiakea Research Station | 209 | soil, grass, rock | 13.47 | 32 |

$4/3\ \pi \times l/2 \times (w/2)^2$, where $l$ = prey length and $w$ = prey width (Beard, 2007; Vitt et al., 2008). Prey importance was determined for each prey category using the following formula: I = ($F$% + $N$% + $V$ %), where $F$% = occurrence percentage, $N$% = numeric percentage, and $V$ % = volumetric percentage (Beard, 2007; Bonansea and Vaira, 2007).

***Invertebrate sampling***.–During frog collections, invertebrates in the environment were also collected. For sites requiring one day to collect frogs, invertebrates were collected that day. For sites requiring more than one day, invertebrates were collected the day that 50% or more of the frogs were collected. To collect leaf litter invertebrates, leaf litter was collected at night following frog collection from four 0.25 m x 0.25 m subplots (Beard, 2007) located randomly within the 100 m x 100 m area, a minimum of 10 m apart. Invertebrates were extracted from the litter using Berlese-Tullgren funnels and stored in 70% ethanol until identification. Flying and phytophagous invertebrates were

collected by randomly placing eight 10 cm x 18 cm sticky traps (Seabright Laboratories, Emeryville, CA, USA) on stakes within the 100 m x 100 m area, a minimum of 10 m apart, with the bottom of the sticky trap located 10 cm above the forest floor, for 24 h. Sticky trap samples were stored in a freezer until invertebrates were identified. All invertebrates were counted and sorted to order and lowest RTU.

***Frog population census***.–To obtain a density estimate, mark-recapture methods were used over seven nights, 24 June–1 July 2009, in one 50 m x 50 m plot at study site KM. Because there have been no previous mark-recapture studies conducted on greenhouse frogs , methods used for other *Eleutherodactylus* species (Funk et al., 2003; Woolbright, 2005) were modified and employed.

Each night beginning at 1915 h, three researchers walked each of 10 adjoining 5 m × 50 m subplots for 20 min, for a total search time of 200 min for the plot, not including handling time. Surveys began the first night in the first subplots, moving to adjoining subplots, and alternated between starting in the first or last subplots each subsequent night. Frogs were hand-captured and SVL was measured to the nearest 0.1 mm using dial calipers. Frogs with ova in any stage of development visible through their semi-transparent body wall were recorded as breeding females. To be conservative, sex for all other individuals was considered undeterminable. Frogs were marked by clipping a total of 1–4 toes (one clip per foot) in unique combinations. The smallest male from the diet study population was 14.2 mm; therefore, only frogs >14.0 mm were considered adults and marked. Frogs < 14.0 mm, hereafter preadults, were considered too small for clipping (as in Woolbright, 2005). The number of preadults observed was counted each night and recorded (as in Woolbright, 2005).

***Statistical analysis***.–Four different ANOVAs were used to assess diet differences. A one-way factorial ANOVA was used in a completely randomized design to examine the effect of site (10 levels) on total prey items and total prey diversity (i.e. number of prey categories consumed). As with most count data, the data were not normally distributed, and a model with a negative binomial distribution was used. The effect of stage class (male, female, preadults) was not included in this statistical model because our main interest was in site differences, and there was a strong interaction between stage class and site ($F_{16,350} = 3.9$, $P < 0.0001$, $F_{16,350} = 3.7$, $P < 0.0001$). However, we were interested in stage class and site differences for the total number of main prey categories (comprising >1% of the frog diet). For this test, a two-way factorial ANOVA was used in a completely randomized design to examine the effect of stage class (3 levels) and site (10 levels) on total number of items for prey categories that comprised > 1% of the greenhouse frog diet.

For total volume consumed and the volume of individual prey items consumed, a two-way factorial ANCOVA was used in a completely randomized design to examine the effect of stage class (3 levels) and site (10 levels). The covariate SVL was included in these statistical tests because SVL varied by stage class ($F_{2,424} = 621.3$, $P < 0.0001$) and SVL was positively related (Fig. A-1) to total prey volume ($R^2 = 0.20$, $F_{1,423} = 103.7$, $P < 0.0001$). A Spearman's rank correlation procedure was used to determine if there was a correlation between the number of items consumed and volume of each item consumed. Finally, a two-way factorial ANOVA was used to examine the effect of stage class (3 levels) and site (10 levels) on total volume consumed of each prey category that comprised > 1% of total diet. To meet assumptions of normality and homogeneity of

variance, volume data were log transformed. All means comparison tests were conducted using the Tukey-Kramer procedure. Because no preadults were collected at WF, this site was excluded from analysis when there was a significant interaction between stage class and site.

A Bray-Curtis dissimilarity index was used to calculate a dissimilarity matrix of invertebrate communities for each site and sample type (stomach samples, leaf litter samples, and sticky trap samples). Nonmetric multidimensional scaling (NMDS) of the Bray-Curtis index was then used to compare stomach contents to invertebrate communities (leaf litter and sticky trap invertebrates) at each site to determine foraging location. Weighted average scores (wascores) were determined for dominant invertebrate categories for NMDS configuration and categories with mean weight > 0.05 are presented. Analysis of Similarity (ANOSIM) was used to calculate Global R, a statistic that tests for differences in community composition (Clarke, 1993), to determine if stomach samples were more similar across sites, or more similar to the available invertebrates in either foraging location (leaf litter or flying/phytophagous communities).

Prey selection for each site was determined using the Jacobs' prey electivity formula (Jacobs, 1974): $e_i = ( p_i - p_k) / (( p_i + p_k) - (2\ p_i\ p_k))$, where $p_i$ is the proportion of each prey taxon in stomachs, and $p_k$ is the proportion of each prey category in the environment (Toft, 1981; Tuttle et al., 2009). Electivity values range from -1 to +1, where negative values indicate avoidance of a prey category, and positive values indicate preference. Mean $e_i$ values < -0.70 and > 0.70, indicating strong preference for invertebrate taxa that represented > 2% of the diet or environmental samples are

presented (Tuttle et al., 2009). A Pearson's chi-square exact test was then used to compare greenhouse frog microhabitat use by site of dominant microhabitat categories.

All statistical analyses, except NMDS and ANOSIM, were conducted using SAS v.9.1.3 for Windows (SAS Institute, Cary, North Carolina). The NMDS and ANOSIM were conducted using R 2.8.1 (R Development Core Team, 2004). *P*-values < 0.05 were considered significant for all tests. Means ± 1 SE are presented, and were first calculated within sites, and then across the 10 study sites.

Huggins closed capture models in Program MARK were used to estimate abundance (White and Burnham, 1999). Individual encounter histories were used to estimate initial capture probability (*p*), probability that a previously-marked frog is recaptured (recapture probability, *c*), and population abundance ($\hat{N}$). Captured frogs were divided into two groups, breeding females and other adults. Models examined allowed capture probabilities to vary for time (t) and examine covariates of stage class, SVL, and number of toes removed. We used a model selection index, the Bayes Information Criterion, which is similar to Akaike Information Criterion but more conservative in selecting less complex models (Link and Barker, 2006). For each model, we used the 95% confidence intervals of the beta estimates (i.e., slope) to measure statistical significance for each parameter, and consider differences among parameter estimates significant when confidence intervals did not overlap (Beard et al., 2008).

To obtain an estimate of total abundance and density (individuals / ha ± 1 SE), preadult numbers were estimated in the plot as the product of the adult estimate and the ratio of maximum preadult to adult counts, assuming that preadult and adult probabilities of encounter by observers are similar (as in Woolbright, 2005; Woolbright et al., 2006)

## RESULTS

***Diet descriptions***.–A total of 427 *E. planirostris* were collected from the 10 sites (151 preadults, 100 males, and 176 females). Mean SVL across all individuals was 16.7 mm ± 0.9. For preadults, mean SVL was 9.9 mm ± 1.3 mm (min: 2.8 mm, max: 19.2 mm), 16.5 mm ± 0.31 mm (max: 21.2 mm) for adult males, and 21.8 mm ± 0.29 mm (max: 26.6 mm) for adult females. Females were between 30% and 40% larger than males at all sites.

In total, 7,442 invertebrates in 32 prey categories were identified from stomach contents (Table 2.2). The most important prey items, in descending order of importance, were Formicidae, Acari, Collembola, Isopoda, and Araneae. All other prey categories were identified in < 50% of stomachs examined. Twelve frogs (3.0%) collected had empty stomachs: four preadults (2.6%), five adult males (5.0%), and three adult females (1.7%).

Frogs consumed a mean of 16.9 ± 2.9 items. The maximum number of prey items consumed by one frog was 134 (121 Acari, four Formicidae, three Pseudoscorpiones, three Psocoptera, two Collembola, and one Araneae; adult male at MS). Number of prey items consumed varied across sites ($F_{9,415} = 17.1$, $P < 0.0001$) and ranged from 7.3 to 33.6. Mean prey diversity per stomach was 4.4 ± 0.3 prey categories, and maximum prey diversity was 12 prey categories. Mean prey diversity varied across sites ($F_{9,415} = 11.9$, $P < 0.0001$) and ranged from 2.7 to 6.0.

Mean prey volume was 31.3 $mm^3$ ± 6.8, with a maximum of 402.3 $mm^3$ (15 Formicidae, three Collembola, three Heteroptera (order Hemiptera), and one Psocoptera,

**Table 2.2.** Frequency of prey items (%), total number of prey items consumed (%), volume of prey items ($mm^3$) (%), and importance (I) of each item in *Eleutherodactylus planirostris* diet of 427 stomachs collected from 10 sites on the island of Hawaii.

| Prey category | Frequency (%) | Number (%) | Volume (%) | I |
|---|---|---|---|---|
| Anura | | | | |
| Tissue | 3 (0.71) | 2 (0.03) | 10.66 (0.10) | 0.83 |
| Eggs | 2 (0.47) | 2 (0.03) | 0.32 (0.00) | 0.50 |
| Arachnida | | | | |
| Acari | 275 (64.71) | 1513 (19.17) | 202.09 (1.81) | 85.69 |
| Araneae | 148 (34.82) | 245 (3.10) | 227.4 (2.04) | 39.97 |
| Pseudoscopiones | 46 (10.82) | 75 (0.95) | 121.85 (1.09) | 12.87 |
| Chilopoda | 65 (15.29) | 80 (1.01) | 622.37 (5.58) | 21.89 |
| Diplopoda | 22 (5.18) | 27 (0.34) | 116.6 (1.05) | 6.56 |
| Pauropoda | 10 (2.35) | 17 (0.22) | 31.45 (0.28) | 2.85 |
| Gastropoda | 4 (0.94) | 8 (0.10) | 13.18 (0.12) | 1.16 |
| Insecta | | | | |
| Coleoptera | | | | |
| Adult | 72 (16.94) | 148 (1.87) | 1008.69 (9.05) | 27.87 |
| Larvae | 6 (1.41) | 6 (0.08) | 33.96 (0.30) | 1.79 |
| Collembola | 270 (63.53) | 1375 (17.42) | 485 (4.35) | 85.30 |
| Dermaptera | 26 (6.12) | 37 (0.47) | 662.89 (5.95) | 12.53 |
| Diptera | | | | |
| Adult | 84 (19.76) | 141 (1.79) | 720.24 (6.46) | 28.01 |
| Larvae | 6 (1.41) | 8 (0.10) | 2.77 (0.02) | 1.54 |
| Egg mass | 21 (4.94) | 28 (0.35) | 4.97 (0.04) | 5.34 |
| Hemiptera | | | | |
| Auchenorrhyncha | 20 (4.71) | 23 (0.29) | 40.54 (0.36) | 5.36 |
| Heteroptera | 70 (16.47) | 112 (1.42) | 1074.84 (9.64) | 27.53 |
| Sternorrhyncha | 44 (10.35) | 73 (0.92) | 20.33 (0.18) | 11.46 |
| Hymenoptera | 24 (5.65) | 30 (0.38) | 55.55 (0.50) | 6.53 |
| Formicidae | 291 (68.47) | 2555 (32.37) | 2798.54 (25.11) | 125.95 |
| Lepidoptera larvae | 21 (4.94) | 24 (0.30) | 345.98 (3.10) | 8.35 |
| Neuroptera | 3 (0.71) | 3 (0.04) | 0.94 (0.01) | 0.75 |
| Orthoptera | 1 (0.24) | 3 (0.04) | 116.21 (1.04) | 1.32 |
| Other larvae | 17 (4.00) | 24 (0.30) | 33.91 (0.30) | 4.61 |
| Psocoptera | 65 (15.29) | 178 (2.25) | 125.96 (1.13) | 18.68 |
| Pupa | 2 (0.47) | 2 (0.03) | 0.36 (0.00) | 0.50 |
| Thysanoptera | 15 (3.53) | 17 (0.22) | 1.41 (0.01) | 3.76 |
| Malacotraca | | | | |
| Amphipoda | 48 (11.29) | 85 (1.08) | 727.61 (6.53) | 18.90 |
| Isopoda | 190 (44.71) | 600 (7.60) | 600.28 (5.39) | 57.69 |
| Oligochaeta | 2 (0.47) | 1 (0.01) | 23.37 (0.21) | 0.69 |
| Unidentified | 46 (10.82) | 56 (0.71) | 77.18 (0.69) | 12.23 |
| Man-made object | 9 (2.11) | - | 4.05 (0.04) | 0.04 |
| Rock | 116 (27.20) | - | 87.38 (0.78) | 0.78 |
| Vegetation | 150 (35.10) | - | 745.88 (6.69) | 6.69 |
| Total | - | 7498 | 11144.8 | - |

adult female at MS). After controlling for SVL, volume of prey consumed did not differ among the three stage classes, and only for adult females did prey volume differ across sites ($F_{2,349} = 2.7$, $P = 0.0004$).

Volume of each item consumed was 1.4 mm $^3 \pm$ 2.4. After controlling for SVL, volume did not vary by stage class ($F_{2,397} = 2.4$, $P = 0.0903$), but did vary by site ($F_{9,397} = 3.3$, $P = 0.0006$) and ranged from 0.7 to 3.9 $mm^3$. Sites where the most number of items were consumed (ML: 33.6 $\pm$ 2.2, PH: 31.9 $\pm$ 4.2) were also sites where frogs consumed some of the smallest prey items (ML: 0.9 $\pm$ 0.1, PH: 0.9 $\pm$ 0.2). Total number of items consumed was not correlated with the size of items consumed across all sites ($r_{425} = -0.03$, $p = 0.5665$) and only at site PH was the total number of items consumed negatively related with the size of items consumed (PH: $r_{425} = -0.58$, $p < 0.0001$).

Of the main prey taxa consumed, preadults consumed more Acari and Collembola than adult males and adult females ($P < 0.05$) and adult males consumed more Acari than adult females ($P < 0.05$). Adult females consumed more Coleoptera and Heteroptera than both adult males and preadults ($P < 0.05$). Variation in stage class consumption of Formicidae ($F_{15,350} = 3.2$, $P < 0.0001$) and Isopoda ($F_{15,350} = 1.8$, $P = 0.0054$) was influenced by site differences.

Formicidae was the dominant prey item consumed at six of ten sites, Collembola was the dominant prey item at three sites, and Acari was the dominant prey item consumed at one site (Fig. 2.2). Amounts of Acari, Collembola, Formicidae, Heteroptera, Isopoda, and Psocoptera consumed (Table A-1) all varied by site ($P < 0.05$). Total volume consumed of Amphipoda, Coleoptera, Diptera, Lepidoptera larvae, and Pseudoscorpiones (Table A-2) also varied by site ($P < 0.05$).

***Foraging location***.–A total of 21,758 invertebrates was identified from environmental samples (Table 2.3). The NMDS of invertebrate community composition by site and sample type (stomach, leaf litter, and sticky traps) yielded a stress coefficient of 0.113 for the two dimensions, indicating that the resulting ordination plot may be confidently interpreted (Clarke, 1993). The first dimension of the NMDS separated the sticky trap samples from the stomach and leaf litter samples (Fig. 2.3). The second dimension separated the stomach samples from the leaf litter samples. Wascores indicate that the prey categories that contribute to the position of the sticky trap sample points on the NMDS plot were Diptera, Thysanoptera, and Hymenoptera; Acari was the prey category contributing to the position of the leaf litter sample points; and Formicidae was the prey category contributing to the position of the stomach sample points. ANOSIM showed that invertebrate composition among sample types was different (global $R$ = 0.868, $P < 0.001$) but that sample types did not differ across sites (global $R$ = -0.224, $P$ = 0.994).

***Prey preferences***.–Because the results of the NMDS indicated that flying/phytophagous invertebrates were not represented in the stomach samples, prey preferences from only the leaf litter samples were analyzed with the Jacobs' electivity formula. Of the leaf litter invertebrate categories only Formicidae (0.7455) was a preferred prey item (Table A-3), and no invertebrate categories were specifically avoided.

***Microhabitat use***.–All but one frog collected was first observed on the ground (0 m from the forest floor). Across sites, 14.8% of frogs were collected underneath objects: 29 preadults, 23 adult males, and 11 adult females. Frogs were mostly (96.8%) collected under man-made objects (i.e. flower pots, water meters, and tarps) but one was also

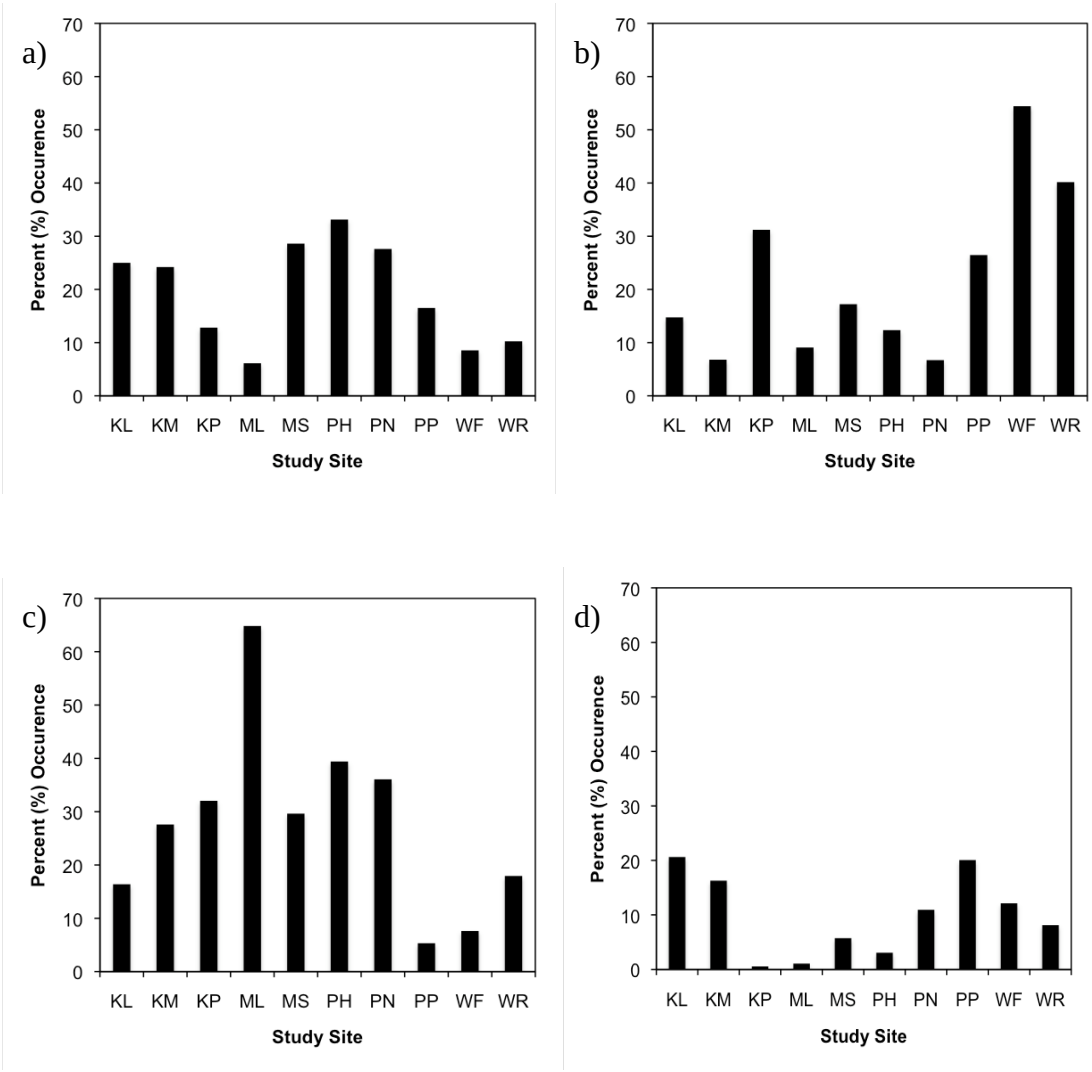


**Fig. 2.2.** Percent occurrence of the dominant invertebrate categories (> 5% of stomach contents) that varied by site ($p < 0.05$) found in *Eleutherodactylus planirostris* for a) Acari, b) Collembola, c) Formicidae, d) and Isopoda, on the island of Hawaii, USA, 2009 (KL: n=53, KM: n = 49, KP: n = 29, ML: n = 49, MS: n = 50, PH: n = 49, PN: n = 34, PP: n =35, WF: n= 48, WR: n = 35; site abbreviations in Fig. 2.1).

**Table 2.3.** Mean number of invertebrates collected (± SE) in environmental samples from 10 study sites on island of Hawaii (n=10).

| Prey Category | Leaf Litter Sample | Sticky Trap Sample |
|---|---|---|
| Arachnida | | |
| Acari | 233.20 (65.84) | 0.78 (0.24) |
| Araneae | 2.48 (0.59) | 0.21 (0.09) |
| Pseudoscopiones | 0.08 (0.05) | 0.00 (0.00) |
| Chilopoda | 0.03 (0.02) | 0.00 (0.00) |
| Diplopoda | 0.18 (0.11) | 0.00 (0.00) |
| Pauropoda | 1.73 (1.13) | 0.00 (0.00) |
| Gastropoda | 0.80 (0.36) | 0.00 (0.00) |
| Insecta | | |
| Blattodea | 0.10 (0.06) | 0.00 (0.00) |
| Coleoptera | | |
| Adult | 2.58 (0.83) | 0.39 (0.12) |
| Larvae | 0.25 (0.15) | 0.00 (0.00) |
| Collembola | 63.13 (18.98) | 3.80 (0.89) |
| Dermaptera | 0.23 (0.14) | 0.00 (0.00) |
| Diptera | | |
| Adult | 0.18 (0.08) | 13.09 (4.25) |
| Larvae | 0.13 (0.10) | 0.03 (0.02) |
| Hemiptera | | |
| Auchenorrhyncha | 0.40 (0.19) | 1.14 (0.43) |
| Heteroptera | 0.90 (0.60) | 2.35 (1.07) |
| Sternorrhyncha | 61.58 (60.30) | 0.05 (0.03) |
| Hymenoptera | 0.08 (0.04) | 7.03 (2.17) |
| Formicidae | 19.65 (15.31) | 0.44 (0.22) |
| Lepidoptera | | |
| Adult | 0.00 (0.00) | 0.05 (0.03) |
| Larvae | 0.25 (0.12) | 0.00 (0.00) |
| Neuroptera | 0.05 (0.05) | 0.05 (0.04) |
| Orthoptera | 0.03 (0.02) | 0.20 (0.11) |
| Other larvae | 3.73 (1.30) | 0.00 (0.00) |
| Psocoptera | 2.08 (1.00) | 0.93 (0.26) |
| Pupa | 0.15 (0.11) | 0.00 (0.00) |
| Thysanoptera | 1.73 (0.48) | 17.85 (8.04) |
| Malacotraca | | |
| Amphipoda | 3.43 (2.25) | 0.00 (0.00) |
| Isopoda | 20.95 (4.86) | 0.00 (0.00) |
| Oligochaeta | 0.65 (0.36) | 0.00 (0.00) |
| Unidentified | 0.10 (0.04) | 0.80 (0.19) |

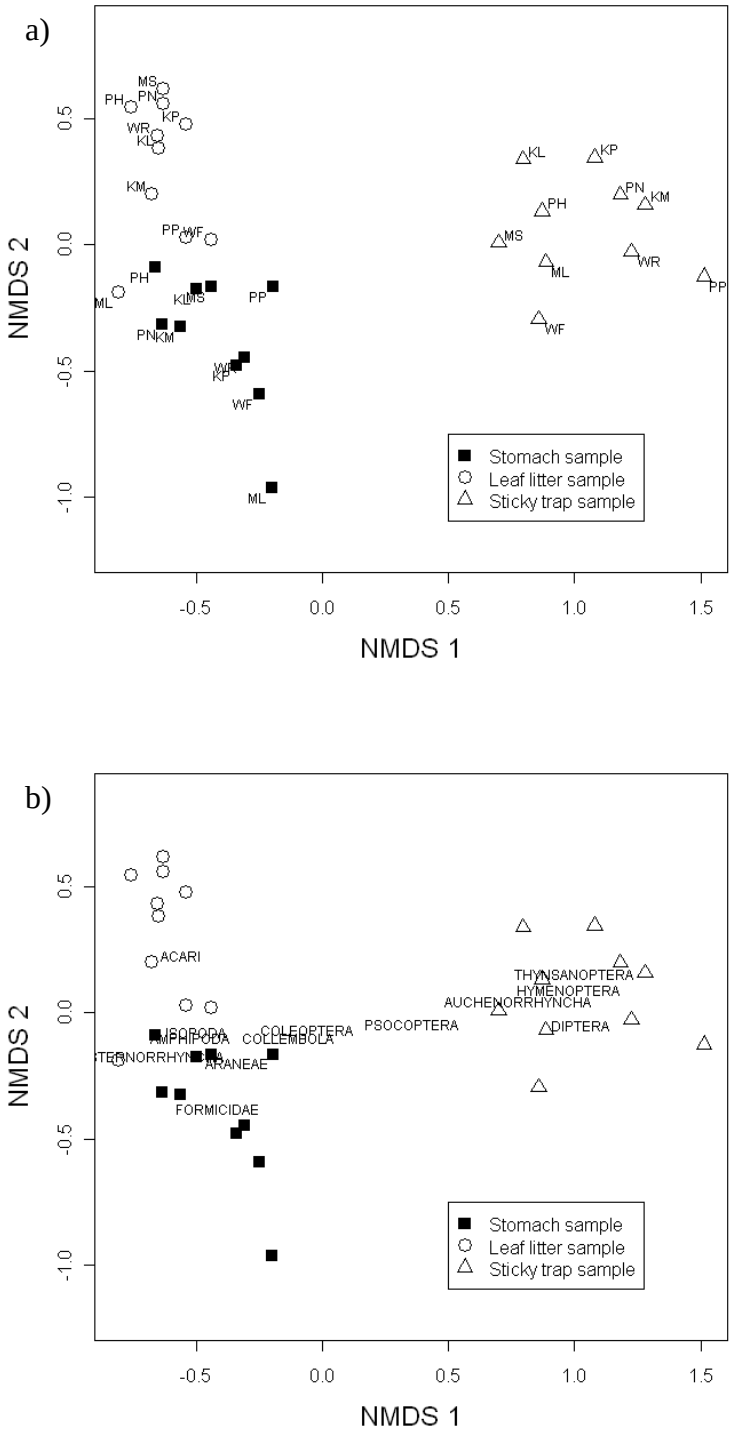


**Fig. 2.3.** Nonmetric multidimensional scaling (NMDS) of invertebrate categories found in *Eleutherodactylus planirostris* stomachs, leaf litter samples, and sticky trap samples (stress = 0.113) from 10 study sites on the island of Hawaii, USA with a) site names and b) wascores of important prey categories (>0.05% of the diet).

collected under a rock (1.6%) and one under a fallen branch (1.6%). All 32 frogs collected at the diurnal capture site, PN, were found underneath objects.

Microhabitat use by the greenhouse frog varied across sites ( $\chi^2$ = 739.66, df = 63, $P < 0.0001$). Leaf litter was the dominant microhabitat (Fig 2.4) used in most natural areas and the macadamia orchard sites (KL, KM, MS, PH, and PP). At the high elevation natural area (WF) and at the two plant nurseries (KP and PN), frogs were observed most often on soil. Herbaceous plant stems and grass were the dominant microhabitat used at the resort (ML) and concrete at the agricultural research station (WR).

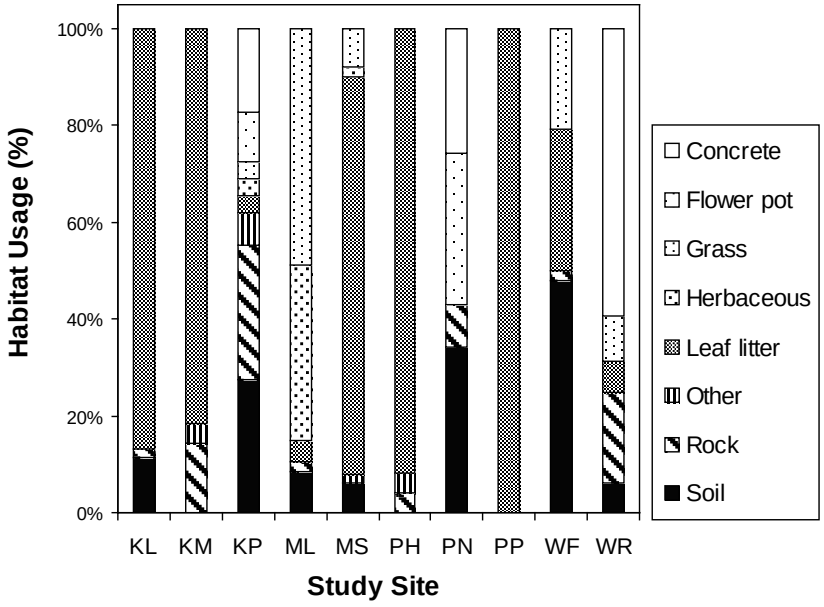


**Fig. 2.4.** Use of microhabitat structures (%) by *Eleutherodactylus planirostris* from 10 study sites on the island of Hawaii, USA, 2009.

***Population estimates***.–A total of 651 adult frogs were marked over seven nights at KM; 518 were males/non-breeding females, and 133 were breeding females. Frogs

captured on the final night of the survey included 56% recaptures. The top model indicated no temporal variation in capture rates, but they did vary with SVL (Table A-4). Initial capture (*p*) rates were equal to recapture (*c*) rates ($0.12 \pm 0.01$).

Adult densities were estimated to be 4,564 frogs $ha^{-1}$ (Table 2.4). The maximum number of preadults observed from one night was 204, with a preadult to adult ratio of 1.7 (Table A-5). Multiplying this ratio by the adult population estimate (as in Woolbright et al., 2006; Beard et al., 2008), we estimated the number of preadults to be 7,958 frogs $ha^{-1}$. Combined with the total adult estimates, the greenhouse frog population estimate at site KM was 12,522 frogs $ha^{-1}$.

Because number of prey items consumed by stage class did vary at this site ($F_{2,396} = 11.5$, $P < 0.0001$), the mean number of invertebrates consumed by each subclass (preadults < 14.0 mm, adults > 14.0 mm, and breeding adult females) was multiplied by their abundance estimates (as in Beard, 2008). Preadults were estimated to consume 98,039.4 invertebrates $ha^{-1}$ $night^{-1}$, and adults were estimated to consume 31,090.2 invertebrates $ha^{-1}$ $night^{-1}$. In total, greenhouse frogs were estimated to consume 129,129.6 invertebrates $ha^{-1}$ $night^{-1}$ at this site.

**Table 2.4.** *Eleutherodactylus planirostris* adult male/non-breeding female, adult breeding female, and preadult population estimates (± SE) $ha^{-1}$, the mean number of items consumed (± SE), and total invertebrates consumed (± SE) $ha^{-1}$, from study site Keaau Macadamia Orchard (KM).

| | Population estimate | Number of items consumed | Invertebrates consumed |
|---|---|---|---|
| Adult males and non breeding females | 3,608 (3,433 - 3,783) | 7.85 (2.25) | 28,309 (396) |
| Adult breeding females | 956 (889 - 1,022) | 2.91 (0.55) | 2,781 (74) |
| Preadults | 7,958 | 12.32 (1.30) | 98,039 |

# DISCUSSION

***Diet***.–We found that Acari (19%), Collembola (17%), and Formicidae (32%) were the dominant prey categories in greenhouse frog stomachs by number of individuals consumed, across the island of Hawaii, comprising 68% of their diet. These groups appear the most likely to be impacted by the greenhouse frog introduction. All Formicidae in Hawaii are nonnative, but both Acari and Collembola contain native species. Although these three groups were the dominant prey, we identified a total of 32 different prey categories (23 invertebrate orders) in the diet. Thus, the greenhouse frog will consume a wide diversity of prey in Hawaii.

Collembola and Acari may be dominant prey items because they were abundant in invaded sites. For example, sites with the highest availability of Collembola were the sites where the most Collembola were consumed. This finding was different from studies in other parts of their introduced range where these two groups were found to comprise < 2% of their diet (Goin, 1947; Stewart, 1977). By volume, these prey categories were not very important food sources, Collembola (4% of total volume) and Acari (2%), whereas Formicidae was the dominant prey item consumed and was also 25% of total volume.

Other prey categories with native species that were important in the diet included Araneae (3%), Coleoptera (2%), Diptera (2%), and Psocoptera (2%). Of particular concern are native Araneae, such as species in the *Tetragnatha* genus, due to their endemism in Hawaii and high extinction rates (Gillespie and Reimer, 1993). Araneae was identified in the diet at all 10 study sites, ranging from 2 to 6% of the total items consumed. However, most native species of Araneae are limited to high elevation

habitats (Gillespie et al., 1998) and not likely to be a major component of the greenhouse frog diet with their present distribution (Chapter 3).

Gastropoda, particularly small terrestrial snails, and Orthoptera (Hadfield et al., 1993; LaPolla et al., 2000) are two more prey categories with similar concerns but were negligible in the greenhouse frog diet (< 1%). Gastropoda consumed were mostly small snails (< 3 mm in length), but only identified in the stomach contents at four study sites. Orthoptera was only identified in the stomach contents of one frog at one site. Both Gastropoda and Orthoptera were not common in the environmental samples (< 1%), indicating that high abundances of these groups were not at risk of predation by the greenhouse frog.

Formicidae appears to be an important component of the greenhouse frog diet across its introduced and native range. It comprised 41% of the prey items in Florida (Goin, 1947), 63% in Jamaica (Stewart, 1977) and 100% in Cuba, but only three stomachs were evaluated in Cuba (Goin, 1947). Results were similar to studies of other nonnative *Eleutherodactylus* species from the Caribbean islands (Stewart, 1977; Ovaska, 1991) and to that of the coqui in Hawaii (Beard, 2007). However, the results contrast with studies that suggest most *Eleutherodactylus* species avoid ants (Toft, 1981; Simon and Toft, 1991). Ovaska (1991) suggests that *Eleutherodactylus* may consume more Formicidae in some areas because of its availability, however, in this study, Formicidae was consumed in greater proportion than its measured availability. Because research indicates that Formicidae identified in the stomachs, including the big-headed ant (*Pheidole megacephala*), the Argentine ant (*Linepithema humile*), and the yellow crazy

ant (*Anoplolepis gracilipes*), have negative effects on native invertebrates (Krushelnycky et al., 2005), greenhouse frogs may indirectly benefit these invertebrates.

In addition to Formicidae, all Isopoda (8% of total number of items consumed) and Amphipoda (1% of total items consumed) identified in the stomach contents were also nonnative. Therefore, at least 45% of the greenhouse frog diet at these study sites consisted of nonnative species. Isopoda were consumed at all sites (1 - 21%), Amphipoda was not a dominant prey category, but it was consumed at eight of the 10 sites (1 - 6%). While we found that the greenhouse frog had a preference for Formicidae, we did not find that the greenhouse frog had a strong preference for these other nonnative groups. The number of Amphipoda and Isopoda found in the stomachs is likely influenced by availability at the sites. This contrasts with the coqui, where Amphipoda was a higher percentage of the diet (21%) and was over-represented in the stomachs compared to what was available in the measured environment (Beard, 2007). However, the percent occurrence of total number of Formicidae and Isopoda consumed were similar for both the coqui and the greenhouse frog.

One order commonly found in the greenhouse frog diet (8% of the total) in Florida (Goin, 1947), which was not found in stomachs in Hawaii, is Blattodea (cockroaches). This may be because Blattodea was not common in the environmental samples (< 1%), and only collected at three of the 10 study sites. In addition, only one small (maximum: 8 mm) Blattodea species was identified in the Florida diet, which has not been documented in Hawaii, where there are no native Blattodea species, and only large species (> 25 mm) have been introduced (Nishida, 2002).

Although the goal of the study was to select sample sites from a variety of habitat types, there were sites of unrepresented habitat types that were not included. In particular, sites that had lower densities of frogs and where the minimum number of frogs needed for analysis (n=25) could not be collected were deliberately excluded from the study. These sites may have different types of prey; therefore our study might not be representative of the greenhouse frog diet across all invaded sites on the island of Hawaii.

The mean number of items found in stomachs of greenhouse frogs across sites ranged from 7 to 34. The mean number of prey items consumed across all sites, 17 items per individual frog, was more than the mean number of 8 prey items in Jamaica (Stewart, 1977) and 6 prey items in Florida (Goin, 1947). Results also suggest that individual greenhouse frogs consume more items than individual coquis (mean of 8 prey items) in Hawaii (Beard, 2007), and more than native and nonnative *Eleutherodactylus* (1 to 8) in the Caribbean (Toft, 1981; Ovaska, 1991; Stewart and Woolbright, 1996).

Our results suggest that, similar to coquis, greenhouse frogs may consume more prey items in Hawaii than in their Caribbean range (Stewart and Woolbright, 1996; Beard, 2007). This may be because available prey is smaller in Hawaii than in the Caribbean. Alternatively, because small frogs typically consume more prey than larger frogs (Whitfield and Donnelly, 2006), the greenhouse frog may be smaller in Hawaii than in its Caribbean range. There is evidence that this is the case for coqui in Hawaii (O'Neill and Beard, 2010). Only the Jamaica study included SVL measurements in their diet study, and mean SVL was smaller in Hawaii (16.7 mm) than in Jamaica [18.1 mm (Stewart, 1977).

There was an ontogenetic shift in prey category consumed, similar to studies of other terrestrial anurans including *Eleutherodactylus* (Whitfield and Donnelly, 2006). Preadults consumed more small prey categories (i.e. Acari and Collembola) than adult males and females. Adult females consumed more of the larger prey categories such as Coleoptera and Heteroptera. Several studies suggest that in addition to consuming smaller prey items, preadults consume more items than adults (Whitfield and Donnelly, 2006; Beard, 2007); however, we did not see differences in the overall total number of prey consumed between stage classes across all 10 study sites. If we had equal sample sizes of each stage class at each site, perhaps we would have seen a more distinct difference in number of items consumed. We did observe this trend at five (50%) of our sites where sample size was more evenly distributed among stage classes.

***Foraging location and microhabitat use***.–Multivariate analysis suggests that stomach contents were more similar to invertebrates collected in leaf litter than invertebrates collected on sticky traps, and supports the hypothesis that the greenhouse frog primarily forages in leaf litter (Goin, 1947). The most dominant invertebrate categories found in the leaf litter, Acari and Collembola, were also dominant items found in the stomachs. In contrast, the dominant invertebrates collected on the sticky traps, Thysanoptera (36%), Diptera (27%) and Psocoptera (14%) made up a small percentage of the diet (> 1%, 2%, 2%, respectively).

Multivariate analysis also suggests that diets were more similar across sites than to the environmental samples at each site. There was also less variability in the stomach contents than in the leaf litter samples across sites. This suggests that while greenhouse frogs consume many different prey items and proportions of invertebrate orders vary with

what is available at each site, their overall diet is generally consistent across sites. More specifically, results appear to reflect that Formicidae was the dominant category in the stomach contents, while Acari was the dominant category in the leaf litter.

The greenhouse frog was observed in structures that provide cover, such as leaf litter in natural areas and man-made structures in nurseries. This is similar to results of other studies in microhabitat use, using especially leaf litter, debris piles, and man-made structures (Goin, 1947; Stewart and Martin, 1980). These microhabitat structures may provide refuge from desiccation (Goin, 1947) or provide good forage habitat. At all sites, almost all frogs were first observed on the ground. In addition, the observed use of subterranean lava tubes seem to suggest that they are somewhat fossorial in Hawaii as described in the species' native and introduced ranges (Schwartz and Henderson, 1991; Meshaka et al., 2004).

***Population estimates***.–Our mark-recapture techniques for this species yielded high percentages of recaptured frogs on the seventh night of the survey, but low initial capture and recapture probabilities. These numbers were similar to rates obtained for the coqui in Hawaii (Woolbright et al., 2006; Beard et al., 2008; Tuttle et al., 2008). The total density estimate of 12,521 frogs $ha^{-1}$ was higher than estimates from Jamaica (4,635 frogs $ha^{-1}$), which combined densities of greenhouse frogs with three other species of *Eleutherodactylus* (Stewart and Martin, 1980). Our results estimate adult greenhouse frog densities to be as high as some coqui population estimates in Hawaii (Beard et al., 2008; Tuttle et al., 2008), however, because we only conducted the mark-recapture at one site, we do not know if this estimate is representative of populations across the island.

Based on the consumption rate at this site, we estimate that greenhouse frogs can consume up to 129,129 invertebrates $ha^{-1}$ $night^{-1}$, particularly Acari, Collembola, and Formicidae. We recommend additional studies to investigate if the greenhouse frog, given their densities and the number of items consumed, reduce invertebrate populations and alter invertebrate community composition across its range of invaded habitats in Hawaii.

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# CHAPTER 3

# DETECTION PROBABILITIES OF TWO INTRODUCED FROGS IN HAWAII: IMPLICATIONS FOR ASSESSING INVASIVE SPECIES DISTRIBTUIONS[3]

## Abstract

Two nonnative Caribbean frogs, the Puerto Rican coqui and the Cuban greenhouse frog, recently invaded Hawaii. Because the coqui has a louder breeding call, management and control efforts have focused on the coqui, while very little has been done to address the greenhouse frog. Although the greenhouse frog is more cryptic, it may be just as widespread and have similar ecological impacts to the coqui. In addition, the loud call of the coqui may block our ability to detect the greenhouse frog. The goal of this research was to determine the distribution of both species on the island of Hawaii, use single-season occupancy models to determine the detection probability of each species, and assess whether the presence of one species affected the detection of the other. We conducted a presence/absence surveys at 446 sites (25-m radius) every 2 km along major road networks using breeding calls. We re-surveyed 135 systematically selected sites twice to determine detection and occupancy probabilities. The coqui was detected at 91 of the 446 sites and mostly found in lowland native and nonnative forests, and agricultural lands on the eastern side of the island. The greenhouse frog was detected at 61 sites, and found mostly in lowland areas, and in native shrublands and forests, nonnative forests, agricultural lands, and pastures on the southeastern and western sides of the island. Overall site occupancy estimates for the coqui and greenhouse frog were

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0.31 ± 0.03 and 0.35 ± 0.05. Detection probabilities of the greenhouse frog were lower than those of the coqui (0.58 ± 0.07, 0.73 ± 0.08, 0.50 ± 0.08) and increased with repeated visits (0.24 ± 0.05, 0.29 ± 0.06, 0.48 ± 0.07) while those of the coqui did not (0.58 ± 0.07, 0.73 ± 0.08, 0.50 ± 0.08). Detection probabilities of the greenhouse frog were lower in the presence of calling coqui for the first two surveys (0.12 ± 0.06, 0.14 ± 0.048) than in sites with greenhouse frogs alone (0.41 ± 0.06). The presence of calling greenhouse frog had no effect on the detection of the coqui. Results suggest multiple visits to a site may be required to detect the greenhouse frog audibly. Because the greenhouse frog is as widespread as the coqui, we recommend that research be conducted to investigate its impacts ecologically to determine whether control efforts should also be aimed at this species.

**Introduction**

Evaluating the ability to detect species is critical in the assessment of species distribution (MacKenzie 2005; Mazerolle et al. 2007). In the case of invasive species, the ability to detect species is particularly important because it influences our ability to monitor populations, which, as a result, influences our understanding of the degree of invasiveness and our ability to manage species (Christy et al. 2010). For example, by definition, a cryptic invader is less likely to be noticed than an invader that is obvious to observers. This presents several specific problems: (1) cryptic invaders are likely to be more widespread than appreciated; (2) because early detection is one of the most important components in successfully controlling invasive species, cryptic invaders are more likely to become widespread and, therefore, unmanageable; and (3) because they

are more difficult to detect, they are more difficult to control, because populations may easily be missed (Bomford and Obrien 1995; Pitt and Witmer 2006). Therefore, it is critical that we understand the detectability of invasives so that we conduct the appropriate level of monitoring for each species.

The greenhouse frog (*Eleutherodactylus planirostris*) invasion into Hawaii is an example of an invasive species that is likely widespread in the invaded range, but is difficult to detect because of its semi-fossorial, nocturnal habits, and relatively quiet breeding call (Chapter 1, Kraus and Campbell 2002; Raloff 2003). On the other hand, the coqui frog (*Eleutherodactylus coqui*), which invaded Hawaii around the same time as the greenhouse frog (Kraus and Campbell 2002) provides an interesting contrast, because while it uses similar habitat, the coqui has a loud breeding call (up to 80-90 db at 0.5 m) that has made its invasion history and patterns relatively easy to monitor (Beard and Pitt 2005). The coqui is widespread on the island of Hawaii, attains extremely high densities (up to 90,000 frogs $ha^{-1}$), and reduces native invertebrates (Beard et al. 2009, R. Choi, prelim. data). In addition, the coqui frog has been the target of a massive control effort (Hawaii Invasive Species Council 2007). In contrast, the invasion of the greenhouse frog has been largely ignored in terms of control and determining its ecological impacts. Because the greenhouse frog is a more cryptic invader, there is a need to determine its distribution in Hawaii as well as its detectability.

Because both species have audible breeding calls, it is possible to conduct a presence/absence survey to determine their distribution patterns and detection probabilities. Because the coqui is considered to be a bigger nuisance than the greenhouse frog as a result of its louder call (Raloff 2003), we hypothesized that detection

probabilities would be high for the coqui and low for the greenhouse frog, but that overall site occupancy would be similar, given their same approximate time of introduction and pathway to the island (Kraus and Campbell 2002). Because of the loudness of the coqui call, we hypothesized that the ability to detect the greenhouse frog would be lower in the presence of calling coqui, and that the ability to detect the coqui would not be affected by the presence of calling greenhouse frogs. Although we expected that occupancy rates would be similar, we also hypothesized that the species are more likely to occur independently than at the same sites, as individuals are randomly introduced to new sites by either accidental or intentional means (Kraus and Campbell 2002; Peacock et al. 2009).

Because both the coqui and greenhouse frog increase breeding activity in warmer and wetter conditions (Goin 1947; Meshaka and Layne 2005; Pough et al. 1983; Townsend and Stewart 1994), we expected that higher air temperatures and relative humidity, lower wind speeds, and increased sky cover (i.e. from clear skies to rain) would increase the likelihood of call activity and detection. Finally, we expected that because the introduction and spread of both species is through human-mediated means (Kraus and Campbell 2002) and because the coqui continues to spread to new areas (Hawaii Invasive Species Council 2007), the likelihood of these species occupying a site would be greater in lower elevation sites than higher elevation sites. We included these covariates in our detection probability models to account for variability among sites. The objectives of this study were three-fold: 1) to conduct an exploratory analysis with single-species occupancy models to determine the detection probability and occupancy rate of the greenhouse frog and the coqui independently across the island of Hawaii, 2) to determine

if the ability to detect either species is influenced by the presence of the other species using both a single-species occupancy model and a two-species occupancy model, and 3) to determine if the greenhouse and coqui frog co-occur in the same sites more often than is expected by random chance alone.

**Methods**

Sampling design

The sampling design was created by selecting every other pixel of a 1 km grid overlaid on the island of Hawaii (19° 41' 1" N, 155° 23' 35" W at its center location), intersecting with the road network (as in Bisrat 2010). The road layer was obtained from the Hawaii Data Clearinghouse website (http://hawaii.wr.usgs.gov/hawaii/). This method was chosen because the design 1) increased the likelihood of sampling areas that are invaded, because frogs in Hawaii are known to spread via vehicular traffic (Peacock et al. 2009), 2) increased our ability to sample many points over a short period of time, and thus increase sample size, and 3) avoided spatial autocorrelation by creating a distance of more than 1 km between points. However, because data were collected along the road network, evergreen forest and bare land cover types were underrepresented while grasslands, scrub/shrub, and cultivated land cover types were well represented (Bisrat 2010). The design generated 464 points across the island but only 446 points were sampled due to limited access at some sites (Fig. 3.1). A Garmin eTrex Legend GPS handheld receiver (Garmin International, Inc, Olathe, KS) was used to geolocate sample points.

Non-detection of a species during a presence/absence survey does not necessarily

mean that the species is not there and "false" absences can be minimized with multiple visits to a site over a short time (MacKenzie et al. 2002). This is necessary for herpetological surveys where extrinsic factors affect the detection of the species, such as the probability of a male frog calling, as well as the observer's ability to detect species that are often cryptic or have quieter calls (Mazerolle et al. 2007; Weir et al. 2005). Breeding call surveys have been successful in determining amphibian species distributions when detection probabilities were high (Brown 2007; Mazerolle et al. 2005; Pellet and Schmidt 2005). Therefore, a subset of the original sample points was re-sampled over two additional survey periods. An ArcGIS extension (Hawth's Analysis Tools for ArcGIS; http://www.spatialecology.com/htools/) was used to draw a random selection of 45 points from each of the following three subgroups: 1) greenhouse frog presence only, 2) coqui presence only, and 3) neither species present. This generated a stratified sample set of 135 points. Repeated surveys were at the same GPS point and followed the same protocol as the first survey.

Coqui breeding activity increases during the rainy season in its native range (Townsend and Stewart 1994) and the greenhouse frog only breeds during the rainy season in its native range in Cuba and its introduced range in Florida (Meshaka and Layne 2005; Schwartz and Henderson 1991). Rainfall occurs year-round on the eastern side of the island (Chu and Chen 2005), but the eastern side of the island experiences its maximum rainfall May to October (Kolivras and Comrie 2007). Because we were interested in sampling the entire island, surveys took place from May to July. The first survey occurred 02 -15 May 2009, the second survey 06 - 10 July 2009, and the third survey 13 - 17 July 2009, beginning at 1900 hr and ending at 0200, the peak calling hours

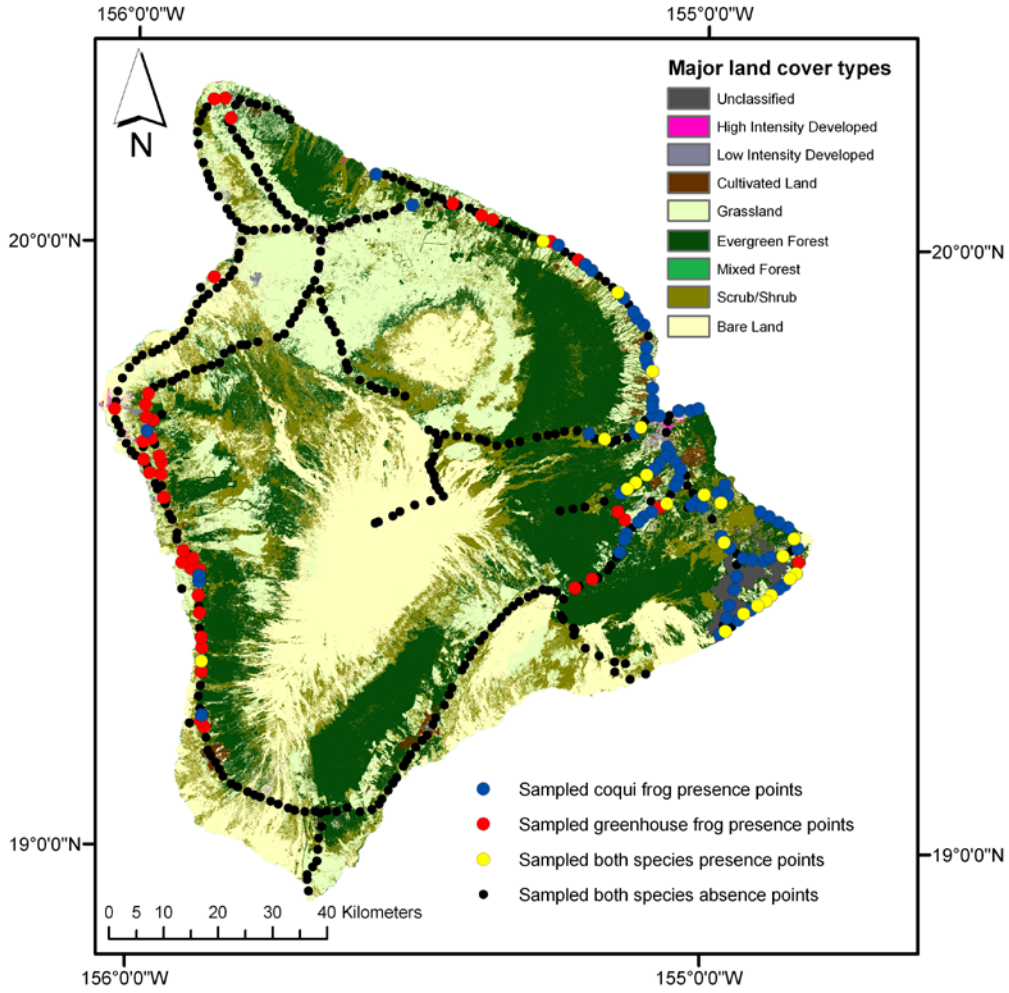


**Fig. 3.1** Sampled *Eleutherodactylus coqui* and *E. planirostris* presence/absence points from the island of Hawaii, USA, 2009 with major land cover type, over all three combined surveys. Blue circles indicate sites where coqui was detected, red circles indicate sites where greenhouse frog was detected, yellow circles indicate sites where both species were detected, and black circles indicate sites where neither species were detected. All detections were within a 50m diameter of sample point. (Source: Land Cover Analysis - http://www.csc.noaa.gov/crs/lca/hawaii.html).

for both species in their native range (Goin 1947; Woolbright 1985).

At each point, the observer walked 25 m off of the road, listened for 5 minutes and considered a site occupied by the greenhouse frog or the coqui frog by the detection of the male breeding call of either species. To avoid observer bias, presence was determined by the same researcher for each survey point. Even though coqui calls can be heard over 100 m, but because the greenhouse frog is only audible from a distance of 25 m (Olson, unpublished data), coqui presence was only documented if heard within a radius of 25 m from observer point, which was confirmed by walking to the calling frog. We measured air temperature, relative humidity, and wind speed (maximum) using a portable weather device ( Kestrel 3000, Kestrel Meters, MI), and estimated sky conditions using a continuous classification code (0-clear skies, 1-broken/sky few clouds, 2-partly cloudy, 3-overcast, 4-drizzle, 5-rain).

Single-season, single species model

We used a single-season, single species model to conduct an exploratory analysis and estimate occupancy and detection probabilities for each frog species. Analysis was conducted in program Presence to estimate $\psi$, the probability of species occurrence at a site and *p*, the probability of detecting the species at that site, using maximum likelihood estimates, where $\psi_i = \frac{Occ_{naive}}{p_i}$, and $Occ_{naive}$ = proportion of total sites occupied by a species, or the naïve occupancy rate. Elevation (ELEV) in Hawaii (Fig. 3.1) was included as a site-specific covariate in determining $\psi$, to account for site variability.

We then developed models in a step-wise manner to account for factors that might lead to variation in detection probabilities (Tables C-1 and C-2). Model selection was

based on the corrected Akaike's Information Criteria ($AIC_c$) and if overdispersion was detected in the most parameterized model ($\hat{c} > 1$), then the small-sized quasi-AIC ($QAIC_c$) was used. High estimates of $p$ (> 0.7) were used to substantiate the ability to detect a species at that site (Brown 2007).

We identified three factors that might lead to these variations including 1) time, 2) environmental variables, and 3) detection of co-species.

1) Time. We considered detection probabilities to be constant (.) or varying between the three surveys (t). Due to the duration of the surveys (e.g. two weeks for the first survey), we also considered temporal variation in detection probability by including linear (T) and quadratic ($T^2$) time trends, coinciding with the first day of the survey, 02 May 2009, delineated as Day 1.

2) Environmental variables. We explored the effect of four environmental covariates, air temperature (TEMP), relative humidity (RH), wind gust (WIND), and sky cover (SKY). To avoid problems with multicollinearity, we first determined that variables were independent and not correlated ($r_{spearman} < 0.5$) using SAS v.9.1.3 for Windows (SAS Institute, Cary, North Carolina). We explored additive models with all possible combinations of the four variables for a total of 15 possible models. If eliminating a covariate led to a reduction in $AIC_c$ we discarded the higher order model from our model set, until no additional covariates could be eliminated without leading to an increase in $AIC_c$ (as in Pagano and Arnold 2009). Complex models with one additional covariate and $\Delta AIC_c < 2$ were considered to have uninformative parameters and removed from the model set.

3) Detection of other species. Because we hypothesized that calling coqui frogs may

influence our ability to detect greenhouse frogs, but not vice versa, we explored the effect of the detection of the co-species on the top model (GHF for coquis, COQUI for greenhouse frogs). If the new model had a lower $AIC_c$, all models were then evaluated with the co-species covariate (an additional 14 models). Models with the co-species covariate that did not have a lower $\Delta AIC_c > 2$ were discarded from the model set.

Two species single-season model

We used a single season, two-species model to estimate occupancy and detection probabilities for both frog species and to evaluate whether the coqui call influenced the detection of the greenhouse frog. Analysis was also conducted in program Presence to estimate the following parameters: $\psi^m$, the probability a site is occupied by species *m* regardless of occupancy status of the other species, $\rho_j^m$, the probability of detecting species *m*, on the *j*th survey, given only species *m* is present at the site, and $r_j^m$, the probability of detecting species *m* during the *j*th survey, given both species are present.

One of the benefits of using the two species model is the ability to explore species interactions using empirical model selection approaches with two additional species interaction parameters (or species interaction factors, SIF): $\varphi$, the ratio of how likely the species are to co-occur at a site compared to what would be expected under a hypothesis of independence, and $\delta$, an interaction factor for detection probabilities given co-occurrence. In our study, the occupancy interaction is expressed as $\varphi = \frac{\psi^{GrCo}}{\psi^{Gr}\psi^{Co}}$, where $\psi^{GrCo}$ is the probability that the site is occupied by both greenhouse and coqui frogs. If $\varphi$ is > 1, then the species tended to co-occur more often then expected than if they were

distributed independently. Similarly, $\delta = \frac{r^{GrCo}}{r^{Gr} r^{Co}}$, where $r^{GrCo}$ is the probability of detecting both species during a survey at a site where both species occur. If $\delta$ is < 1, then it is likely that observers were less likely to detect one species if the other species was heard during the same survey.

We first modeled the occupancy parameters as a function of elevation (ELEV), and detection parameters as a function of the covariates found in the single species model that were most significant (from the top model results) for greenhouse frogs (SKY) and for coquis (RH and WIND), removing covariates in a stepwise process as in the single-species model method. We then examined if detection parameters varied by time with the top covariate model.

To explore our hypotheses about detection probabilities, the model was evaluated for $\rho = r$ and $\rho \neq r$ for both frog species. First, because the coqui has a louder call, we expected the coqui to have higher detection probabilities than the greenhouse frog ($\rho^{Co} > \rho^{Gr}$). Second, we expected that given the presence of the coqui, detection probabilities of the greenhouse frog would be lower in sites without the coqui ($r^{Gr} < \rho^{Gr}$). Finally to examine species interactions, models with and without $\varphi$ and $\delta$ were evaluated, for a total of 28 models included in the analysis. Due to the number of parameters in two-species modeling, complex models may be over-parameterized, (MacKenzie et al. 2006), and were removed from model results. The model with the lowest $AIC_c$ was considered the top or best model of the models examined.

## Results

### Study sites

The elevation of study sites ranged from 13 m to 3386 m. Temperatures during data collection ranged from 4.9 to 29.5°C, with a mean of 21.8 ± 0.5 across all sites for all three surveys. Variation was greater between sites (SD ± 3.0) than between survey period at each site (mean SD of 1.4 ± 0.06). Humidity values ranged from 5.7 to 100 with a mean of 88.2 ± 1.6, and variation was also greater between sites (SD ± 9.5) than between survey periods (8.0 ± 0.7). Wind gusts ranged from 0 to 54.9 kph, with a mean of 6.4 ± 0.8, and variation was greater between sites (SD ± 3.0) than between survey periods (2.0 ± 0.1). Mean sky conditions was 1.9 ± 0.1, and variation was greater between surveys at each site (1.3 ± 0.1) than between sites (SD ± 0.9).

### Single-season, single species model

We detected coqui frogs at 91 of the study sites (0.20), with 22 sites (24%) co-occupied with the greenhouse frog. Estimated occupancy probability was 0.31 ± 0.04 (Table 3.1). On the first survey, 83 sites (91.2% of total coqui sites) were positively identified with coqui frogs, six new sites (6.6% of total coqui sites) were identified on the second survey, and zero new sites were positively identified with coqui frogs on the third survey. Sites were mostly in lowland nonnative and native forests and agricultural lands on the eastern and southeastern sides of the island of Hawaii (see Fig. 3.1). The highest elevation coquis were detected was 737 m.

Model selection results indicate that there is a time (t) effect in detection probability of the coqui (Table 3.2). Detection probabilities were highest for the second

survey, and lowest for the third survey (Table 3.1), and ranged across all study sites from 0.0001 ± 0.0002 to 0.92 ± 0.04 for the first survey, 0.0001 ± 0.0003 to 0.97 ± 0.02 for the second survey, and 0.0001 ± 0.0001 to 0.87 ± 0.05 for the third survey. Detection probabilities > 0.7 were more frequent on the eastern side of the island (see Fig. 3.2).

All of the top models supported the inclusion of WIND as a covariate (Table 3.2). The probability of detection of coqui frogs decreased with higher wind speeds, increased slightly with higher relative humidity, and decreased with elevation (Table 3.3). Variations in temperature, sky cover, and the detection of the greenhouse frog had little effect on coqui detection probabilities.

We detected the greenhouse frog at 61 of the sites (0.14), with coquis detected at 22 of the greenhouse frog sites (36%). Estimated occupancy probability was 0.39 ± 0.08 (Table 3.1). On the first survey, 46 sites (75.4% of total greenhouse frog sites) were positively identified with greenhouse frogs, four new sites (6.5% of total greenhouse frog sites) were identified on the second survey, and 12 new sites (19.6% of total greenhouse frog sites) were identified on the third survey. Sites were mostly in lowland native shrublands and forests, nonnative forests, agricultural lands, and pasture lands on the southwestern and eastern sides of the island of Hawaii (Fig. 3.1). The highest elevation greenhouse frogs were detected was 1115 m.

Model selection results indicate that detection probability increased over time (Tables 3.1 and 3.2). Detection probabilities across all study sites ranged from 0.15 ± 0.04 to 0.60 ± 0.12 for the first survey, 0.18 ± 0.05 to 0.66 ± 0.11 for the second survey, and 0.34 ± 0.07 to 0.81 ± 0.08 for the third survey. Detection probabilities > 0.7

**Table 3.1** Mean individual covariate parameter estimates (± SE) and 95% confidence intervals from the top model for the single-season, single species models for the two *Eleutherodactylus* species, on the island of Hawaii, USA, 2009.

| Parameter | *E. coqui* | 95% confidence interval | *E. planirostris* | 95% confidence interval |
|---|---|---|---|---|
| Model | Model: $\Psi$(ELEV),*p*(t+RH+WIND) | | Model: $\Psi$(ELEV),*p*(t+SKY) | |
| Survey 1 *p* | 0.58 (0.07) | 0.44,0.72 | 0.24 (0.05) | 0.15,0.36 |
| Survey 2 *p* | 0.73 (0.08) | 0.56,0.89 | 0.29 (0.06) | 0.18,0.42 |
| Survey 3 *p* | 0.50 (0.08) | 0.34,0.66 | 0.48 (0.07) | 0.33,0.62 |
| $\psi$ | 0.31 (0.04) | 0.23,0.39 | 0.39 (0.08) | 0.24,0.54 |

**Table 3.2** Set of top ten competing single-season single species models with selection and fit statistics for the two *Eleutherodactylus* species on the island of Hawaii, USA, 2009. Model selection was based on AIC for *E. coqui* and $QAIC_c$ for *E. planirostris* ($\hat{c}$ = 1.13). Models with lowest $\Delta AIC_c$ are considered the best. ($AIC_c$ = small-sample size Akaike Information Criterion, $w_i$ = model weights, K = number of parameters).

| Model | $AIC_c$/ $QAIC_c$ | $\Delta AIC_c$ | $w_i$ | Model likelihood | K | -2log (likelihood) |
|---|---|---|---|---|---|---|
| *E. coqui* | | | | | | |
| $\Psi$(ELEV),*p*(t+RH+WIND) | 464.17 | 0.00 | 0.60 | 1.00 | 7 | 449.91 |
| $\Psi$(ELEV),*p*(t+WIND) | 466.55 | 2.38 | 0.18 | 0.30 | 6 | 454.36 |
| $\Psi$(ELEV),*p*(t+TEMP+WIND+SKY) | 467.33 | 3.16 | 0.12 | 0.21 | 8 | 451.00 |
| $\Psi$(ELEV),*p*(t+TEMP+WIND) | 467.88 | 3.71 | 0.09 | 0.16 | 7 | 453.62 |
| $\Psi$(ELEV),*p*(t+TEMP+RH+SKY) | 487.10 | 22.93 | 0.00 | 0.00 | 8 | 470.77 |
| $\Psi$(ELEV),*p*(t+TEMP+RH) | 489.59 | 25.42 | 0.00 | 0.00 | 7 | 475.33 |
| $\Psi$(ELEV),*p*(t+RH+SKY) | 491.14 | 26.97 | 0.00 | 0.00 | 7 | 476.88 |
| $\Psi$(ELEV),*p*(t+SKY) | 491.98 | 27.81 | 0.00 | 0.00 | 6 | 479.79 |
| $\Psi$(ELEV),*p*(t+TEMP+SKY) | 493.25 | 29.08 | 0.00 | 0.00 | 4 | 485.16 |
| $\Psi$(ELEV),*p*(t+TEMP) | 493.69 | 29.52 | 0.00 | 0.00 | 6 | 481.50 |
| *E. planirostris* | | | | | | |
| $\Psi$(ELEV),*p*(t+SKY) | 452.84 | 0.00 | 0.59 | 1.00 | 6 | 497.93 |
| $\Psi$(ELEV),*p*(t+RH+SKY) | 454.88 | 2.04 | 0.21 | 0.36 | 7 | 497.91 |
| $\Psi$(ELEV),*p*(t+TEMP+WIND+SKY) | 456.85 | 4.01 | 0.08 | 0.13 | 8 | 497.79 |
| $\Psi$(ELEV),*p*(t+RH+WIND+SKY) | 456.95 | 4.11 | 0.08 | 0.13 | 8 | 497.90 |
| $\Psi$(ELEV),*p*(t+TEMP+RH+WIND+SKY) | 458.93 | 6.09 | 0.03 | 0.05 | 9 | 497.79 |
| $\Psi$(ELEV),*p*(t) | 462.43 | 9.59 | 0.00 | 0.01 | 5 | 511.09 |
| $\Psi$(ELEV),*p*(t+RH) | 463.66 | 10.82 | 0.00 | 0.00 | 6 | 510.16 |
| $\Psi$(ELEV),*p*(t+ WIND) | 464.07 | 11.23 | 0.00 | 0.00 | 6 | 510.62 |
| $\Psi$(ELEV),*p*(t+TEMP) | 464.42 | 11.58 | 0.00 | 0.00 | 6 | 511.02 |
| $\Psi$(ELEV),*p*(t+RH+WIND) | 465.41 | 12.57 | 0.00 | 0.00 | 7 | 509.81 |

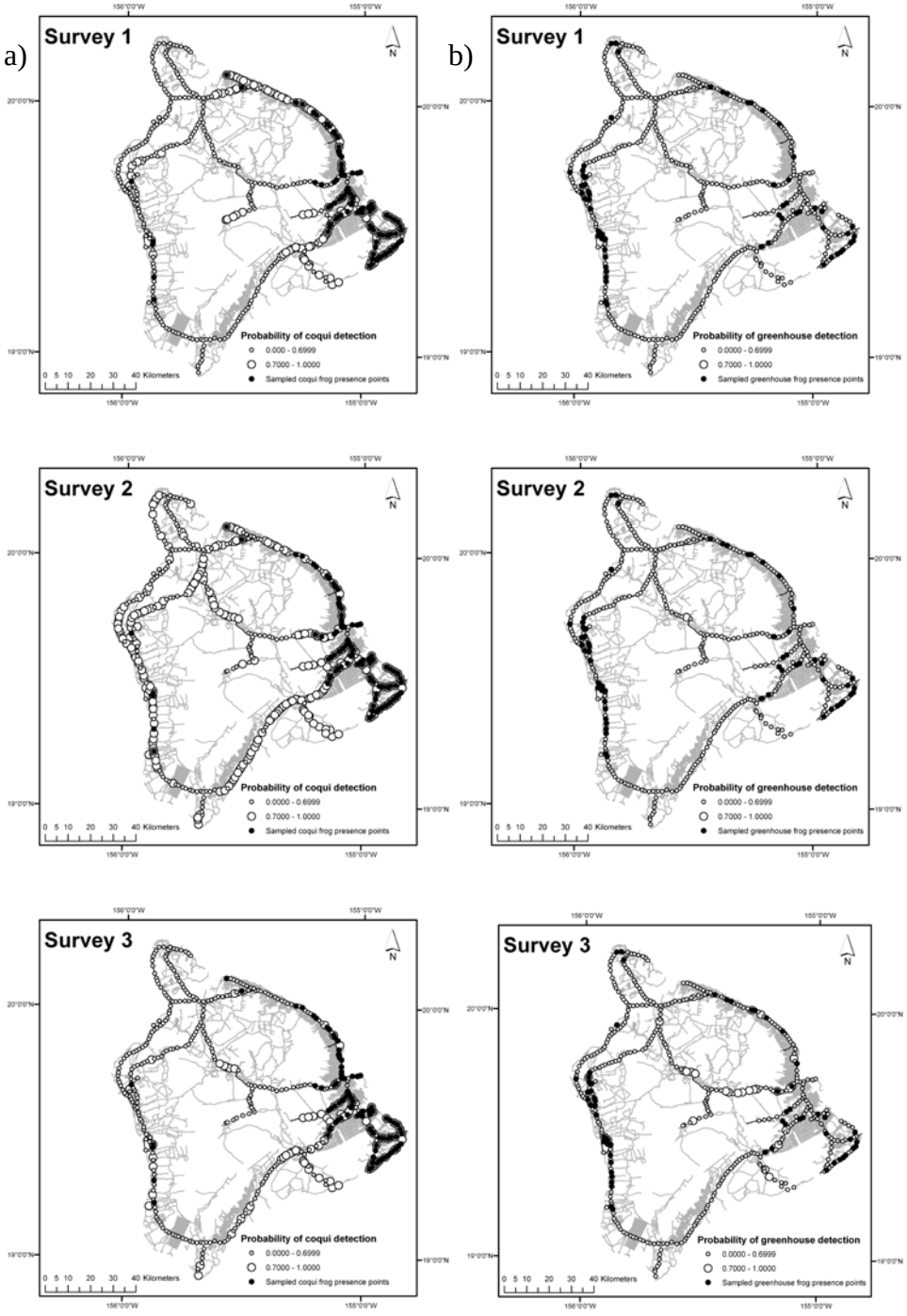


**Fig**. **3.2** Detection probabilities for each sample point for a) *Eleutherodactylus coqui* and b) *E. planirostris* for the three surveys on the island of Hawaii, USA, 2009. Small white circles indicate a detection probability < 0.7, large white circles indicate a detection probability ≥ 0.7. Black circles indicate that the species was detected as present at sampled point.

**Table 3.3** Untransformed parameter estimates and 95% confidence intervals for explanatory variables from the two highest ranked (lowest $\Delta AIC_c$/$QAIC_c$) single-season, single species models for the two *Eleutherodactylus* species, on the island of Hawaii, USA, 2009.

| Covariate | Estimate | 95% confidence interval | Estimate | 95% confidence interval |
|---|---|---|---|---|
| *E. coqui* | Model: $\Psi$(ELEV),*p*(t+RH+WIND) | | Model: $\Psi$(ELEV),*p*(t+WIND) | |
| Occupancy probability | | | | |
| Intercept ($\Psi$) | 0.73 | 0.14,1.33 | 0.59 | 0.05,1.12 |
| ELEV | -1.48 | -1.96,-1.00 | -1.38 | -1.83,-0.93 |
| Detection probability | | | | |
| *p*1 | -1.41 | -4.84,2.01 | 1.82 | 1.03,2.60 |
| *p*2 | -0.43 | -4.18,3.32 | 2.92 | 1.85,3.99 |
| *p*3 | -1.89 | -5.41,1.64 | 1.55 | 0.83,2.27 |
| RH | 0.04 | 0.00,0.08 | - | - |
| WIND | -0.33 | -0.46,-0.20 | -0.34 | -0.46,-0.21 |
| *E. planirostris* | Model: $\Psi$(ELEV),*p*(t+SKY) | | Model: $\Psi$(ELEV),*p*(t+RH+SKY) | |
| Occupancy probability | | | | |
| Intercept ($\Psi$) | 0.43 | -0.40,1.27 | 0.43 | -0.41,1.27 |
| ELEV | -0.64 | -1.04,-0.23 | -0.64 | -1.04,-0.24 |
| Detection probability | | | | |
| *p*1 | -1.75 | -2.42,-1.08 | -1.86 | -2.80,-0.93 |
| *p*2 | -1.50 | -2.17,-0.82 | -1.61 | -2.61,-0.61 |
| *p*3 | -0.68 | -1.32,0.04 | -0.79 | -1.76,0.17 |
| RH | - | - | 0.00 | -0.01,0.01 |
| SKY | 0.44 | 0.19,0.68 | 0.43 | 0.18,0.68 |

only occurred at 37 sites for the greenhouse frog (Fig. 3.2).

The top 15 models all included the SKY covariate (Table 3.2). The probability of detection of greenhouse frogs increased with rainy conditions and decreased with elevation (Table 3.3). Models with the covariate for coqui detection did not have a $\Delta AIC_c < 2$. Variations in relative humidity, temperature, and wind speeds had little effect on detection of the greenhouse frog.

Single-season two species model

Models that included a covariate ELEV for $\psi^{Co}$ and $\psi^{Gr}$ and the covariate RH for $p^{Co}$ and $r^{Co}$ were overparmeterized and removed from the model set. Models that included SKY for $p^{Gr}$ and $r^{Gr}$ and WIND for $p^{Co}$ and $r^{Co}$ were ranked higher than models without weather covariates (Table 3.4). Model selection results indicate that coquis and greenhouse frogs do not occur independently (Table 3.4), and indicate that the species are more likely to co-occur at a study site than would be expected by random chance (Table 3.5). In addition, estimated occupancy rates for the greenhouse frog ($0.35 \pm 0.05$) are not significantly different than estimated occupancy rates for the coqui ($0.31 \pm 0.03$) (Table 3.5). Model results also indicate that the species are more likely to be detected together than independently (Table 3.4).

There was no time effect on the detection of the coqui in the two species model, and the probability of detecting the coqui when only the coqui is calling is equal to the probability of detecting the coqui when the greenhouse frog is calling ($p^{Co} = r^{Co}$, Table 3.5). For the first two surveys, the probability of detecting the greenhouse frog is higher in sites where only the greenhouse frog is present than in sites where the coqui is first

**Table 3.4** Set of top ten competing single-season two species models with selection and fit statistics for the two *Eleutherodactylus* species on the island of Hawaii, USA, 2009. The best models are ranked top of the list. Absence of φ and δ implies no interaction in occupancy or detection probability (e.g., φ = 1 and/or δ = 1). Model selection was based on AIC. Models with lowest $\Delta AIC_c$ are considered the best. (Co = *E. coqui*, Gr = *E. planirostris*, $AIC_c$ = small-sample size Akaike Information Criterion, $w_i$ = model weights, K = number of parameters).

| Model | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | Model likelihood | K | -2log (likelihood) |
|---|---|---|---|---|---|---|
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$(SKY), $p^{Co}$(WIND)=$r^{Co}$(WIND),$r^{Gr}$(t+SKY),δ | 1052.29 | 0.00 | 0.43 | 1.00 | 12 | 1027.57 |
| $\psi^{Gr}, \psi^{Co}, p^{Gr}$(t+SKY), $p^{Co}$(WIND)=$r^{Co}$(WIND),$r^{Gr}$(t+SKY),δ | 1052.71 | 0.42 | 0.35 | 0.81 | 11 | 1030.10 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$(SKY), $p^{Co}$(WIND)=$r^{Co}$(WIND),$r^{Gr}$(t+SKY) | 1054.17 | 1.88 | 0.17 | 0.39 | 11 | 1031.56 |
| $\psi^{Gr}, \psi^{Co}, p^{Gr}$(t+SKY), $p^{Co}$(WIND)=$r^{Co}$(WIND),$r^{Gr}$(t+SKY),δ(t) | 1056.56 | 4.27 | 0.05 | 0.12 | 14 | 1027.59 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$(t+SKY)=$r^{Gr}$(t+SKY), $p^{Co}$(WIND)=$r^{Co}$(WIND),δ | 1065.69 | 13.40 | 0.00 | 0.00 | 10 | 1045.18 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$(SKY)=$r^{Gr}$(SKY), $p^{Co}$(WIND)=$r^{Co}$(WIND),δ | 1073.86 | 21.57 | 0.00 | 0.00 | 8 | 1057.53 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$(SKY), $p^{Co}$(WIND), $r^{Gr}$(SKY),$r^{Co}$(WIND),δ | 1075.35 | 23.06 | 0.00 | 0.00 | 12 | 1050.63 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$(t+SKY), $p^{Co}$(WIND), $r^{Gr}$ (SKY),$r^{Co}$(WIND),δ | 1079.31 | 27.02 | 0.00 | 0.00 | 14 | 1050.34 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$, $p^{Co}$(WIND),$r^{Gr}$(SKY), $r^{Co}$(WIND),δ | 1084.55 | 32.26 | 0.00 | 0.00 | 11 | 1061.94 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$(SKY)=$p^{Co}$(WIND)= $r^{Co}$(WIND),$r^{Gr}$ (t+SKY), δ | 1094.55 | 42.26 | 0.00 | 0.00 | 11 | 1071.94 |
| $\psi^{Gr}, \psi^{Co}, \varphi, p^{Gr}$, $p^{Co}$,$r^{Co}$,$r^{Gr}$,δ | 1107.14 | 54.85 | 0.00 | 0.00 | 8 | 1090.81 |

**Table 3.5** Mean individual covariate parameter estimates (± SE) and 95% confidence intervals from the top model for the single-season, two species model for the two *Eleutherodactylus* species on the island of Hawaii, USA, 2009.

| Model: | $\psi^{Gr},\psi^{Co},\varphi,p^{Gr}(SKY),p^{Co}(WIND)=r^{Co}(WIND),r^{Gr}(t+SKY),\delta$ | |
|---|---|---|
| Parameter | Estimate | 95% confidence interval |
| $\psi^{Gr}$ | 0.35 (0.05) | 0.26,0.46 |
| $\psi^{Co}$ | 0.31 (0.03) | 0.24,0.38 |
| $\varphi$ | 1.36 (0.24) | 1.28,2.57 |
| $p^{Gr}$ | 0.41 (0.06) | 0.29,0.53 |
| $p^{Co}$ | 0.69 (0.05) | 0.59,0.79 |
| $r^{Gr}1$ | 0.12 (0.06) | 0.01,0.23 |
| $r^{Gr}2$ | 0.14 (0.08) | 0.04,0.38 |
| $r^{Gr}3$ | 0.67 (0.15) | 0.38,0.96 |
| $r^{Co}$ | 0.69 (0.05) | 0.59,0.79 |
| $\delta$ | 1.12 (0.06) | 1.11,1.37 |

**Table 3.6** Untransformed parameter estimates and 95% confidence intervals for explanatory variables from the two highest ranked (lowest $\Delta AIC_c$) single-season, two species models for the two *Eleutherodactylus* species, on the island of Hawaii, USA, 2009.

| Model: | $\psi^{Gr},\psi^{Co},\varphi,p^{Gr}(SKY),$ $p^{Co}(WIND)=r^{Co}(WIND),r^{Gr}(t+SKY),\delta$ | | $\psi^{Gr},\psi^{Co},p^{Gr}(SKY),p^{Co}(WIND)$ $=r^{Co}(WIND),r^{Gr}(t+SKY),\delta$ | |
|---|---|---|---|---|
| Parameter | Estimate | 95% confidence interval | Estimate | 95% confidence interval |
| Occupancy probability | | | | |
| $\psi^{Gr}$ | -0.62 | -1.06,-0.17 | -0.60 | -1.06,-0.15 |
| $\psi^{Co}$ | -0.81 | -1.13,-0.49 | -0.78 | -1.11,-0.46 |
| $\varphi$ | 0.31 | -0.04,0.66 | - | - |
| Detection probability | | | | |
| $p^{Gr}$ | -1.15 | -1.81,-0.49 | -1.30 | -1.93,-0.67 |
| $p^{Co}$ | 1.80 | 1.19,2.42 | 1.78 | 1.19,2.38 |
| $r^{Gr}1$ | -2.21 | -3.42,-1.01 | -1.92 | -3.09,-0.74 |
| $r^{Gr}2$ | -1.84 | -3.21,-0.47 | -1.66 | -3.01,-0.32 |
| $r^{Gr}3$ | 0.48 | -1.08,2.03 | 0.81 | -0.73,2.35 |
| $\delta$ | 0.11 | 0.01,0.22 | 0.11 | 0.00,0.22 |
| $p^{Gr}$ CLOUD | 0.55 | 0.21,0.88 | 0.55 | 0.23,0.87 |
| $r^{Gr}$ CLOUD | 0.18 | -0.26,0.61 | 0.15 | -0.30,0.59 |
| $p^{Co}$ WIND | -0.31 | -0.44,-0.19 | -0.32 | -0.44,-0.20 |

detected ($p^{Gr} > r^{Gr}$, Table 3.5). By the third survey, 95% confidence intervals indicate that there is an overlap in the detection probability of the greenhouse frog whether or not the coqui is detected. Detection probabilities for the two species were considerably different, with a high and constant detection probability for the coqui, and a more variable, and overall lower detection probability of the greenhouse frog.

Overall, both the single-species and two-species models estimated occupancy probabilities slightly higher for the greenhouse frog than the coqui, and there is a greater discrepancy between naïve occupancy rates and estimated occupancy probabilities for the greenhouse frog than for the coqui. Lower detection probabilities of the greenhouse frog may contribute to this discrepancy (Bailey et al. 2009).

**Discussion**

We determined that detection probabilities from a breeding call survey differed between the two introduced *Eleutherodactylus* species on the island of Hawaii. As expected, detection probabilities for the quieter greenhouse frog were low for the initial surveys and improved over time. Although coqui detection probabilities were higher than those for the greenhouse frog, probabilities varied amongst the three surveys, and were lower than expected on the first and third survey. The ability to detect greenhouse frogs was lower in the presence of calling coqui while calling greenhouse frog had no effect on the ability to detect the coqui. Contrary to our predictions that the two species distributions would be independent, we found that the two species were more likely to co-occur at our sampled sites.

In the single-species model, detection of the coqui was highest on the second

survey (0.73) and lowest on the third survey (0.50) which suggests that the detection probability of the coqui did not increase over the three surveys, but was affected by individual site covariates during each survey. More specifically, sites with the lowest detection probabilities were also sites that had the highest wind speeds and lowest relative humidity. Interestingly, sites with low detection probabilities on the second survey were in areas with the lowest predicted distribution potential of the coqui (Bisrat 2010). We suggest we found low detection rates in areas that are less likely to be invaded by coqui because these areas have weather conditions that do not encourage coqui calling.

Other studies support that coquis reduce calling in lower humidity and higher wind speeds (Pough et al. 1983), but that calling is not influenced by temperature and cloud cover (Townsend and Stewart 1986). Coquis are highly susceptible to water loss and decreased cutaneous respiration (Rogowitz et al. 1999) and, because they call from mid-to-upper level forest canopies, are more exposed to dry conditions from increased wind speeds and low humidity than species that call from the forest floor (Pough et al. 1983). It should be noted that the two-species model was over-parameterized when we included a covariate for relative humidity on the detection of the coqui. It is possible that the variation in coqui detection probability due to differences in relative humidity was not captured in the two-species model due to the complexity of the two-species model and the small effects this parameter had on coqui detection probability (MacKenzie et al. 2004).

Detectability of the greenhouse frog was especially low during the first and second surveys and improved significantly by the third survey. Thus, unlike the coqui, detection

improved by repeated visits to sites and this suggests multiple visits to sites are needed to determine if a site is occupied (MacKenzie et al. 2002). As expected, detection probabilities were lower for the greenhouse frog than for the coqui, although not significantly by the third survey. This difference for the first two surveys may be due to the loud call of the coqui. Alternatively, differences in detection probabilities may result if populations of greenhouse frogs are smaller than coqui populations at the sample sites. Higher abundances are more likely to result in higher detection probabilities, particularly when sampled populations are small (e.g. $< 10$) (MacKenzie et al. 2006), and density estimates of the coqui range from 2,200 – 91,000 frogs $ha^{-1}$ (Beard et al. 2008; Woolbright et al. 2006), while greenhouse frogs have been estimated at 12,500 frogs $ha^{-1}$ at one site (Chapter 2).

Increased detection of the greenhouse frog on the third survey may be a result of different local weather conditions for each site and survey. For example, higher wind speeds and increased cloud cover on the third survey may have increased the number of sites where greenhouse frogs were calling and decreased the number of sites where the coquis were calling, allowing the observer to better detect greenhouse frogs. Results were consistent with other studies suggesting that greenhouse frogs increase calling activity during overcast skies and after recent rain (Goin 1947; Meshaka and Layne 2005).

The single and two-species models differed in the inclusion of the effect of coqui on greenhouse frog detectability. The presence of calling coqui on the detectability of the greenhouse frog was only slightly supported in the single-species model. This may be because in the single-species model, the covariate for presence of calling coqui does not account for false absences. In the two single species models, greenhouse frog detection

was lower in the presence of calling coqui. This was not unexpected because the coqui's louder call was thought to potentially mask the greenhouse frog's call. Results support our hypothesis that the presence of the greenhouse frog did not have an effect on the detection of the coqui.

In our two species model, the interaction factor for detection probabilities suggests that we were more likely to detect both species at sites where they both occur than to not detect a species if the other was present (MacKenzie et al. 2004). In their native ranges, there are often multiple *Eleutherodactylus* species calling at breeding sites. Frequency and temporal partitioning of calls is used to distinguish species in multi-species assemblages (Bourne and York 2001; Drewry and Rand 1983). Given the difference in call type (the two note call of the coqui versus the trill of the greenhouse frog), the coqui and the greenhouse frog may not competing for audio exposure and, their calls may be easily distinguished by the females of each species.

The estimated occupancy probabilities for both species overlap and, thus, are not significantly different between the two species. In other words, the total number of sites occupied by the greenhouse frog and by the coqui on the island of Hawaii appears similar. Our occupancy probabilities are only based on audio detection, and the survey method may be biased towards one species. In addition our data are from only one breeding season, and different factors may affect both species in other years. Although we attempted to account for possible variables that would influence the ability to detect the species, there may be other factors influencing whether frogs were calling at the time of our visit to a study site. We cannot account for this, and as a result, these occupancy estimates are conservative and may be biased towards one species.

Elevation had a similar effect on the likelihood of sites being occupied by both species, which was expected given that both species were introduced to lowland sites and are likely to be limited by climatic conditions at high elevations (Kraus and Campbell 2002). Coquis have been found up to 1,200 m (Hawaii Invasive Species Council 2007), higher than our maximum elevation record for this study (740 m), and close to the maximum elevation of detected greenhouse frogs in this study (1,100 m). It is unknown if the frogs may be limited to areas < 1,200 m or if they have not yet spread to higher elevation sites (Bisrat 2010; Rödder and Lötters 2010).

The two-species model suggests that the coqui and greenhouse frog were more likely to be found at the same sites than different sites (MacKenzie et al. 2004). This contradicted our expectation that the distributions of these species would be independent, given that individuals of both species are randomly introduced to new sites (Kraus and Campbell 2002; Peacock et al. 2009). One possible explanation is their similar mode of spread across the island through the sale and transport of nursery plants and via vehicular traffic (Kraus and Campbell 2002; Peacock et al. 2009). In addition, initial introductions may have been to the same areas: nurseries, plant retailers, and surrounding areas as well as roadsides, residential areas, and resorts. Finally, it is possible that both the coqui and the greenhouse frog are now spreading to new sites via natural means, and that because there is some overlap in their preferred habitat, including human altered areas (Beard et al. 2009, Chapter 1), they are more likely to occur in the same locations.

Our study supports the possibility that the perception of the coqui being more widespread than the greenhouse frog may be due to the ease in detecting the coqui. One of the most important impacts of the coqui invasion is the noise nuisance (Raloff 2003)

and the resulting economic losses to home owners (Kaiser and Burnett 2006). This impact is not realized for the quieter greenhouse frog. Other invasive species like the greenhouse frog initially may be overlooked until the number of infested habitats and population densities are too high to begin feasible population control measures (Bomford and Obrien 1995). Our results emphasize the need for early detection methods of invasive species using surveys appropriate for detecting that species.

Because detection of both species was < 1, our study suggests that occupancy modeling is necessary to determine the distribution of both the coqui and the greenhouse frog, using a form of replicated sampling with population closure (MacKenzie 2005). Multiple visits to sites improved the detection probability of the greenhouse frog. Thus, either multiple surveys to sites or additional methods of species detection such as visual encounter surveys or trapping is necessary to determine if a site is occupied, although these methods are more labor-intensive. Because the greenhouse frog appears to be as widespread as the coqui, we recommend that research be conducted to investigate its impacts ecologically to determine whether control efforts should also be aimed at this species.

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# CHAPTER 4

# CONCLUSIONS

*Major conclusions*

This study was the first to examine the ecology and distribution of the greenhouse frog in Hawaii. We found that its diet predominantly consisted of leaf litter invertebrates and that the frog predominantly foraged in the leaf litter. Invertebrate orders with native species most at risk of predation include Acari, Araneae, Collembola, Coleoptera, Diptera, and Psocoptera. Only Formicidae was found in a greater proportion in the stomach contents than what was available in the environment. A total population estimate of 12,500 frogs $ha^{-1}$ was determined at one study site. With these high densities and large number of prey consumed, the greenhouse frog may consume up to 129,000 invertebrates $ha^{-1}$ $night^{-1}$.

Distribution results suggest that the greenhouse frog is found mostly in lowland areas, including native shrublands and forests, nonnative forests, agricultural lands, and pasture lands on the southwestern and eastern sides of the island of Hawaii. Detection probabilities were low on the first two surveys and improved by the third survey. Our study suggests that occupancy modeling is necessary to determine the distribution of the greenhouse frog on the island of Hawaii.

*Future studies*

A systematic distribution study on the other islands would be important to determine the extent of the greenhouse frog invasion in Hawaii. There were more recorded locations of the greenhouse frog on Kauai, Maui, and Oahu (Chapter 1) than on

Hawaii prior to our distribution study of the greenhouse frog. Because the coqui has mostly been eradicated on the other islands (Kraus and Duffy 2010), greenhouse frog detection probabilities may be higher on the other islands. The greenhouse frog may also have a wider distribution on these islands given the greater extent of low and high intensity developed areas (Chapter 1).

Because our research was focused only on the island of Hawaii, we are unable to extrapolate our results to other islands of the Hawaiian archipelago. Diets may be different if the greenhouse frog is found in different habitats or if available prey is different on other islands. Additional studies on its diets and densities on the islands of Kauai, Maui, and Oahu are recommended to fully characterize the ecology of the greenhouse frog in Hawaii.

In addition, this study only included a density estimate from one site on the island of Hawaii. As population studies of other *Eleutherodactylus* in Hawaii have shown, densities can vary greatly among sites (Woolbright et al. 2006, Beard et al. 2008). It is possible that at higher densities, greenhouse frogs may consume more invertebrates, or densities may be limited by available prey. Further studies into the population dynamics of greenhouse frogs would provide many insights into the invasion of this species.

Because there is little information available on the diet and densities from Cuba, we are unable to compare our results in Hawaii to their native range. We do know that *E. coqui*, can consume more prey items per ha (Stewart and Woolbright 1996) and can have higher densities (Woolbright 2005, Woolbright et al. 2006) in Hawaii than in its native Puerto Rico (Woolbright et al. 2006, Beard 2007, Beard et al. 2008), which may also be true for the greenhouse frog. Comparative studies with its native range would provide

important information on the adaptability of the greenhouse frog and its niche breadth, and may provide insight into its ability to successfully establish populations in areas outside of its native range.

One problem with our study is that we do not know our site conditions prior to the greenhouse frog invasion. Diets might reflect what they are consuming now, but not what they were consuming when they first invaded a site. There already may have been reductions in primary prey prior to greenhouse frog introduction. In addition, many of the invertebrates found in the diet play an important role in ecosystem processes such as herbivory and decomposition of plant material. In Hawaii, Sin et al. (2008) used a small-scale enclosure experiment to test the effects of nonnative coqui on plant growth and leaf litter decomposition rates. They found that plant growth and leaf litter decomposition rates were higher in enclosures with the nonnative coqui than without, mostly by consuming invertebrates and increasing the amount of available nutrients through excrement and not by reducing populations of herbivore and detritivore invertebrates. An experiment investigating invertebrates and ecosystem processes on both sides of the invasion front could address these questions.

Finally, our results from the distribution study indicate that there are sites where the greenhouse frog and coqui co-occur, and there may be complex species interactions between the species. The greenhouse frog is predominantly terrestrial in Hawaii (Chapter 2), while the coqui is also terrestrial but is much more frequently observed on vegetation (Beard 2007). Although both species are in the genus *Eleutherodactylus*, the greenhouse has recently been classified in the subgenus *Euhyas* while the coqui has been classified in the subgenus *Eleutherodactylus* (Hedges et al. 2008). These classifications are based on

geographical divisions, with *Euhyas* from the Western Caribbean (i.e. Cuba) having smaller toe pads and more terrestrial behaviors than *Eleutherodactylus* from the Eastern Caribbean (i.e. Puerto Rico) (Hedges et al. 2008). Future studies should investigate if the two species use different niches in their invaded habitats and are not in competition for prey, nesting sites, or daytime retreat sites. It is also possible that the two species compete for prey where they co-occur, and that in the presence of greenhouse frogs, the coqui is able to exploit more herbaceous and or flying invertebrates like it does in its native Puerto Rico (Stewart and Woolbright 1996). Alternatively, densities of either species may be lower where they do co-occur because of competition for resources. Studies comparing diet and densities in sites where they co-occur with only one invaded species would provide insight on how similar species adapt to and impact invaded ecosystems.

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# APPENDICES

# Appendix A

## Chapter 2 Supplemental Tables and Figures

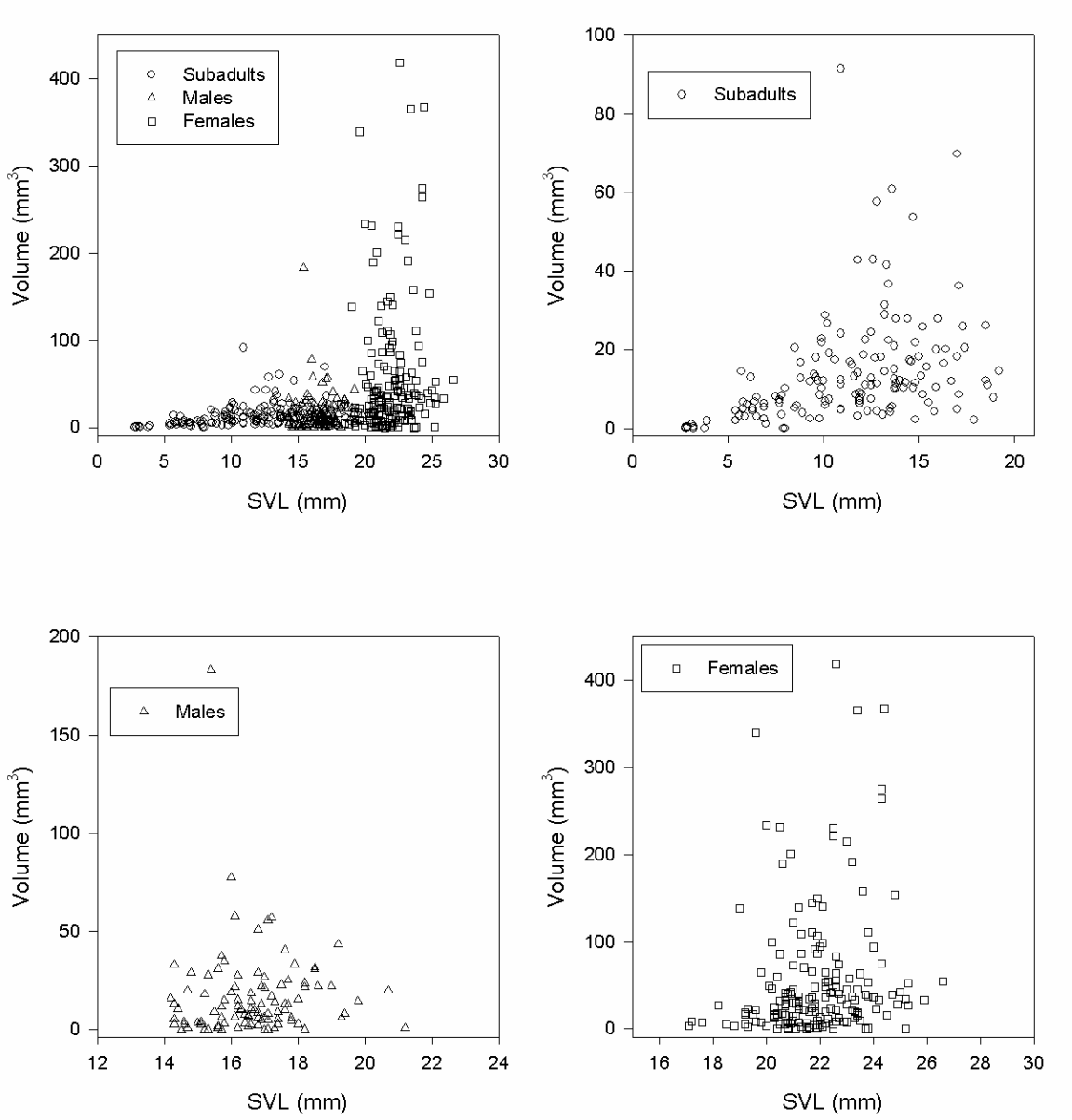


Fig. A-1. Total prey volume consumed by snout-vent-length (SVL) for a) total population (n=427) b) preadults (n=151) c) males (n=100), and d) females (n=176) for *Eleutherodactylus planirostris* collected from 10 study sites on the island of Hawaii, USA, 2009 ($R^2 = 0.20$, $F_{1,423} = 103.7$, $P < 0.0001$, $\hat{Y} = 1.34 + (1.04)X_i$ ).

Table A-1. Percent of items consumed, by site, by *Eleutherodactylus planirostris*, collected from 10 sites on the island of Hawaii. *Mean values with same lower case letter are not significantly different when comparing across sites (Tukey-Kramer comparisons of means, $P < 0.05$).

| Prey category | KL (n=53) | KM (n=49) | KP (n=29) | ML (n=49) | MS (n=50) | PH (n=49) | PN (n=34) | PP (n=34) | WF (n=48) | WR (n=32) |
|---|---|---|---|---|---|---|---|---|---|---|
| Anura | | | | | | | | | | |
| Tissue | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.06$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.43$^{a}$ |
| Eggs | 0.14$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.18$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Arachnida | | | | | | | | | | |
| Acari | 25.00$^{a}$ | 24.21$^{ab}$ | 12.81$^{b}$ | 6.12$^{ab}$ | 28.62$^{ab}$ | 33.14$^{a}$ | 27.61$^{a}$ | 16.52$^{a}$ | 8.55$^{a}$ | 10.26$^{ab}$ |
| Araneae | 6.28$^{ab}$ | 5.20$^{ab}$ | 5.85$^{a}$ | 2.46$^{ab}$ | 1.74$^{ab}$ | 1.54$^{b}$ | 5.72$^{ab}$ | 3.91$^{ab}$ | 2.80$^{ab}$ | 5.13$^{ab}$ |
| Pseudoscopiones | 3.69$^{a}$ | 1.13$^{a}$ | 2.23$^{a}$ | 0.00$^{a}$ | 1.23$^{a}$ | 1.22$^{a}$ | 1.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Chilopoda | 0.55$^{ab}$ | 1.81$^{a}$ | 1.11$^{ab}$ | 0.13$^{b}$ | 1.33$^{ab}$ | 1.09$^{ab}$ | 2.24$^{ab}$ | 1.60$^{ab}$ | 1.56$^{ab}$ | 1.71$^{ab}$ |
| Diplopoda | 0.68$^{a}$ | 0.90$^{a}$ | 0.28$^{a}$ | 0.00$^{a}$ | 0.51$^{a}$ | 0.38$^{a}$ | 0.00$^{a}$ | 0.53$^{a}$ | 0.16$^{a}$ | 0.85$^{a}$ |
| Pauropoda | 0.00$^{a}$ | 0.00$^{a}$ | 0.56$^{a}$ | 0.00$^{a}$ | 0.51$^{a}$ | 0.00$^{a}$ | 0.25$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Gastropoda | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.38$^{a}$ | 0.10$^{a}$ | 0.06$^{a}$ | 0.25$^{a}$ | 1.42$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Insecta | | | | | | | | | | |
| Coleoptera | | | | | | | | | | |
| Adult | 2.05$^{ab}$ | 3.17$^{a}$ | 1.67$^{ab}$ | 1.26$^{ab}$ | 0.51$^{ab}$ | 1.28$^{ab}$ | 2.49$^{ab}$ | 6.75$^{a}$ | 1.40$^{b}$ | 1.28$^{ab}$ |
| Larvae | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.06$^{a}$ | 0.10$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.36$^{a}$ | 0.16$^{a}$ | 0.43$^{a}$ |
| Collembola | 14.75$^{bcd}$ | 6.79$^{cd}$ | 31.20$^{abc}$ | 9.09$^{bcd}$ | 17.23$^{bc}$ | 12.35$^{bcd}$ | 6.72$^{d}$ | 26.47$^{ab}$ | 54.43$^{a}$ | 40.17$^{ab}$ |
| Dermaptera | 0.55$^{a}$ | 0.68$^{a}$ | 1.11$^{a}$ | 0.32$^{a}$ | 0.10$^{a}$ | 0.26$^{a}$ | 0.50$^{a}$ | 2.49$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Diptera | | | | | | | | | | |
| Adult | 1.50$^{a}$ | 2.71$^{a}$ | 2.23$^{a}$ | 1.77$^{a}$ | 3.08$^{a}$ | 0.58$^{a}$ | 1.74$^{a}$ | 5.68$^{a}$ | 0.93$^{a}$ | 2.14$^{a}$ |
| Larvae | 0.68$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.06$^{a}$ | 0.00$^{a}$ | 0.36$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Egg mass | 0.41$^{a}$ | 0.23$^{a}$ | 0.84$^{a}$ | 0.13$^{a}$ | 0.21$^{a}$ | 0.83$^{a}$ | 0.00$^{a}$ | 0.18$^{a}$ | 0.16$^{a}$ | 0.85$^{a}$ |
| Hemiptera | | | | | | | | | | |
| Auchenorrhyncha | 0.82`$^{a}$ | 0.23$^{a}$ | 0.00$^{a}$ | 0.25$^{a}$ | 0.10$^{a}$ | 0.32$^{a}$ | 0.00$^{a}$ | 0.53$^{a}$ | 0.47$^{a}$ | 0.00$^{a}$ |
| Heteroptera | 1.91$^{ab}$ | 0.23$^{c}$ | 0.28$^{bc}$ | 1.52$^{abc}$ | 3.28$^{ab}$ | 0.58$^{abc}$ | 1.99$^{ab}$ | 1.24$^{abc}$ | 0.78$^{c}$ | 4.70$^{a}$ |
| Sternorrhyncha | 0.27$^{a}$ | 0.45$^{a}$ | 2.79$^{a}$ | 2.15$^{a}$ | 0.10$^{a}$ | 1.09$^{a}$ | 0.25$^{a}$ | 0.36$^{a}$ | 0.31$^{a}$ | 0.85$^{a}$ |
| Hymenoptera | 0.55$^{a}$ | 1.13$^{a}$ | 0.84$^{a}$ | 0.32$^{a}$ | 0.72$^{a}$ | 0.19$^{a}$ | 0.50$^{a}$ | 0.18$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Formicidae | 16.39$^{b}$ | 27.60$^{ab}$ | 32.03$^{ab}$ | 64.84$^{a}$ | 29.64$^{ab}$ | 39.41$^{a}$ | 36.07$^{ab}$ | 5.33$^{c}$ | 7.62$^{c}$ | 17.95$^{bc}$ |
| Lepidoptera larvae | 0.27$^{a}$ | 0.00$^{a}$ | 0.28$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.06$^{a}$ | 0.00$^{a}$ | 1.78$^{a}$ | 1.24$^{a}$ | 0.85$^{a}$ |
| Neuroptera | 0.27$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.06$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Orthoptera | 0.00$^{a}$ | 0.45$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.18$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Other larvae | 0.41$^{a}$ | 0.00$^{a}$ | 0.28$^{a}$ | 0.06$^{a}$ | 0.21$^{a}$ | 0.45$^{a}$ | 1.24$^{a}$ | 0.36$^{a}$ | 0.31$^{a}$ | 0.43$^{a}$ |
| Psocoptera | 0.82$^{ab}$ | 0.00$^{ab}$ | 0.84$^{ab}$ | 6.94$^{a}$ | 3.90$^{a}$ | 0.96$^{ab}$ | 0.00$^{ab}$ | 0.36$^{b}$ | 0.47$^{b}$ | 0.43$^{ab}$ |
| Pupa | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.06$^{a}$ | 0.25$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Thysanoptera | 0.14$^{a}$ | 0.23$^{a}$ | 0.56$^{a}$ | 0.25$^{a}$ | 0.10$^{a}$ | 0.26$^{a}$ | 0.00$^{a}$ | 0.53$^{a}$ | 0.00$^{a}$ | 0.43$^{a}$ |
| Malacotraca | | | | | | | | | | |
| Amphipoda | 0.00$^{b}$ | 4.52$^{a}$ | 1.11$^{ab}$ | 0.63$^{ab}$ | 0.31$^{ab}$ | 0.19$^{b}$ | 0.25$^{ab}$ | 0.00$^{b}$ | 5.75$^{ab}$ | 2.99$^{ab}$ |
| Isopoda | 20.63$^{a}$ | 16.29$^{a}$ | 0.56$^{d}$ | 1.07$^{cd}$ | 5.74$^{ab}$ | 3.07$^{bc}$ | 10.95$^{ab}$ | 20.07$^{a}$ | 12.13$^{a}$ | 8.12$^{ab}$ |
| Oligochaeta | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.18$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |

Table A-2. Mean volume consumed, by site, by *Eleutherodactylus planirostris*, collected from 10 study sites on the island of Hawaii. *Mean values with same lower case letter are not significantly different when comparing across sites (Tukey-Kramer comparisons of means, P<0.05).

| Prey category | KL (n=53) | KM (n=49) | KP (n=29) | ML (n=49) | MS (n=50) | PH (n=49) | PN (n=34) | PP (n=34) | WF (n=48) | WR (n=32) |
|---|---|---|---|---|---|---|---|---|---|---|
| Anura | | | | | | | | | | |
| Tissue | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 5.87$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 4.79$^{a}$ |
| Eggs | 0.07$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ | 0.25$^{a}$ | 0.00$^{a}$ | 0.00$^{a}$ |
| Arachnida | | | | | | | | | | |
| Acari | 24.0$^{bcd}$ | 15.3$^{cde}$ | 5.2$^{de}$ | 10.6$^{cde}$ | 31.0$^{bc}$ | 59.9$^{a}$ | 11.1$^{cde}$ | 28.6$^{ab}$ | 13.0$^{bcd}$ | 3.4$^{e}$ |
| Araneae | 22.4$^{a}$ | 16.9$^{a}$ | 14.6$^{a}$ | 65.4$^{a}$ | 9.0$^{a}$ | 20.1$^{a}$ | 31.8$^{a}$ | 14.9$^{a}$ | 20.3$^{a}$ | 12.0$^{a}$ |
| Pseudoscopiones | 32.2$^{ab}$ | 15.2$^{bc}$ | 7.2$^{abc}$ | 0.0$^{c}$ | 22.1$^{abc}$ | 43.0$^{a}$ | 2.2$^{bc}$ | 0.0$^{c}$ | 0.0$^{c}$ | 0.0$^{c}$ |
| Chilopoda | 61.8$^{ab}$ | 16.2$^{ab}$ | 8.4$^{ab}$ | 3.4$^{b}$ | 129.6$^{ab}$ | 141.0$^{a}$ | 35.4$^{ab}$ | 163.4$^{ab}$ | 41.4$^{ab}$ | 21.9$^{ab}$ |
| Diplopoda | 79.1$^{a}$ | 2.4$^{ab}$ | 3.4$^{ab}$ | 0.0$^{b}$ | 12.0$^{ab}$ | 8.6$^{ab}$ | 0.0$^{ab}$ | 4.5$^{ab}$ | 5.2$^{ab}$ | 1.6$^{ab}$ |
| Pauropoda | 0.0$^{a}$ | 0.0$^{a}$ | 1.1$^{a}$ | 0.0$^{a}$ | 11.3$^{a}$ | 0.0$^{a}$ | 0.8$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |
| Gastropoda | 0.0$^{ab}$ | 0.0$^{ab}$ | 0.0$^{ab}$ | 15.6$^{ab}$ | 3.8$^{ab}$ | 0.2$^{ab}$ | 0.6$^{ab}$ | 11.3$^{a}$ | 0.0$^{b}$ | 0.0$^{ab}$ |
| Insecta | | | | | | | | | | |
| Coleoptera | | | | | | | | | | |
| Adult | 123.9$^{bc}$ | 37.4$^{bc}$ | 13.1$^{bc}$ | 180.4$^{ab}$ | 9.2$^{bc}$ | 31.3$^{bc}$ | 40.7$^{bc}$ | 239.6$^{a}$ | 11.3$^{c}$ | 33.5$^{bc}$ |
| Larvae | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.7$^{a}$ | 1.3$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 23.6$^{a}$ | 8.1$^{a}$ | 0.3$^{a}$ |
| Collembola | 30.5$^{cde}$ | 9.4$^{e}$ | 28.2$^{bcde}$ | 41.1$^{bcd}$ | 37.9$^{bc}$ | 26.3$^{bcde}$ | 6.2$^{de}$ | 55.8$^{b}$ | 228.5$^{a}$ | 21.3$^{bcde}$ |
| Dermaptera | 100.7$^{ab}$ | 14.7$^{ab}$ | 78.6$^{ab}$ | 105.6$^{ab}$ | 12.4$^{b}$ | 4.6$^{b}$ | 27.2$^{ab}$ | 319.1$^{a}$ | 0.0$^{b}$ | 0.0$^{b}$ |
| Diptera | | | | | | | | | | |
| Adult | 275.6$^{b}$ | 13.0$^{b}$ | 15.9$^{b}$ | 26.8$^{b}$ | 12.1$^{b}$ | 5.0$^{b}$ | 17.2$^{b}$ | 556.9$^{a}$ | 36.8$^{b}$ | 49.4$^{b}$ |
| Larvae | 2.4$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.2$^{a}$ | 0.0$^{a}$ | 0.2$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |
| Egg mass | 1.0$^{a}$ | 0.0$^{a}$ | 0.5$^{a}$ | 0.1$^{a}$ | 0.1$^{a}$ | 2.3$^{a}$ | 0.0$^{a}$ | 0.5$^{a}$ | 0.0$^{a}$ | 0.6$^{a}$ |
| Hemiptera | | | | | | | | | | |
| Auchenorrhyncha | 11.8$^{a}$ | 2.1$^{a}$ | 0.0$^{a}$ | 8.4$^{a}$ | 1.2$^{a}$ | 2.0$^{a}$ | 0.0$^{a}$ | 8.3$^{a}$ | 6.7$^{a}$ | 0.0$^{a}$ |
| Heteroptera | 159.6$^{ab}$ | 19.9$^{bc}$ | 1.2$^{bc}$ | 78.0$^{bc}$ | 342.8$^{a}$ | 133.5$^{ab}$ | 97.9$^{ab}$ | 129.7$^{bc}$ | 32.4$^{c}$ | 79.9$^{c}$ |
| Sternorrhyncha | 0.2$^{b}$ | 2.7$^{b}$ | 1.1$^{ab}$ | 8.6$^{a}$ | 0.4$^{b}$ | 4.8$^{b}$ | 0.5$^{b}$ | 0.8$^{b}$ | 0.4$^{b}$ | 0.9$^{b}$ |
| Hymenoptera | 6.5$^{a}$ | 2.4$^{a}$ | 2.1$^{a}$ | 1.6$^{a}$ | 6.3$^{a}$ | 5.6$^{a}$ | 0.4$^{a}$ | 30.7$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |
| Formicidae | 54.7$^{cde}$ | 56.1$^{cde}$ | 43.7$^{cde}$ | 703.5$^{ab}$ | 1401.3$^{a}$ | 300.1$^{bc}$ | 175.1$^{bcd}$ | 14.0$^{de}$ | 20.7$^{e}$ | 29.3$^{cde}$ |
| Lepidoptera larvae | 3.6$^{b}$ | 0.0$^{b}$ | 0.3$^{b}$ | 0.0$^{b}$ | 0.0$^{b}$ | 0.2$^{b}$ | 0.0$^{b}$ | 262.2$^{a}$ | 69.0$^{b}$ | 10.7$^{b}$ |
| Neuroptera | 0.9$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.1$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |
| Orthoptera | 0.0$^{a}$ | 108.2$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 8.1$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |
| Other larvae | 1.9$^{a}$ | 0.0$^{a}$ | 0.1$^{a}$ | 0.7$^{a}$ | 2.0$^{a}$ | 1.4$^{a}$ | 4.2$^{a}$ | 22.7$^{a}$ | 0.7$^{a}$ | 0.1$^{a}$ |
| Psocoptera | 28.5$^{bc}$ | 0.0$^{c}$ | 3.1$^{bc}$ | 64.1$^{a}$ | 16.5$^{b}$ | 6.4$^{bc}$ | 0.0$^{bc}$ | 0.4$^{c}$ | 6.8$^{c}$ | 0.1$^{bc}$ |
| Pupa | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.1$^{a}$ | 0.2$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |
| Thysanoptera | 0.2$^{a}$ | 0.1$^{a}$ | 0.5$^{a}$ | 0.5$^{a}$ | 0.0$^{a}$ | 0.3$^{a}$ | 0.0$^{a}$ | 0.2$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |
| Malacotraca | | | | | | | | | | |
| Amphipoda | 0.0$^{c}$ | 134.3$^{ab}$ | 12.2$^{bc}$ | 45.4$^{bc}$ | 1.4$^{c}$ | 6.1$^{bc}$ | 9.2$^{bc}$ | 0.0$^{c}$ | 409.7$^{a}$ | 109.4$^{abc}$ |
| Isopoda | 100.7$^{bc}$ | 91.7$^{bc}$ | 3.7$^{c}$ | 35.5$^{c}$ | 48.9$^{c}$ | 34.1$^{bc}$ | 32.1$^{bc}$ | 155.2$^{a}$ | 76.6$^{b}$ | 21.9$^{bc}$ |
| Oligochaeta | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ | 23.4$^{a}$ | 0.0$^{a}$ | 0.0$^{a}$ |

Table A-3. *Eleutherodactylus planirostris* prey selection of invertebrates by collection method, using Jacobs Prey Electivity Formula from ten study sites on the island of Hawaii, USA, in 2009. Prey categories > 2% of the total stomach contents and environmental sample are shown.

| Prey category | Leaf litter |
|---|---|
| Acari | -0.6800 |
| Amphipoda | 0.3126 |
| Araneae | 0.5898 |
| Collembola | 0.1047 |
| Diptera | - |
| Formicidae | 0.7455 |
| Hymenoptera | - |
| Isopoda | 0.1088 |
| Psocoptera | - |
| Sternorrhyncha | 0.2109 |
| Thysanoptera | - |

Table A-4. Five highest ranked models for *Eleutherodactylus planirostris* mark-recapture study at site Keaau Macadamia Orchard (KM), island of Hawaii, USA, in 2009.

| Model | BIC | ΔBIC | BIC weights | Model likelihood | Number parameters | Deviance |
|---|---|---|---|---|---|---|
| p(SVL) = c(SVL) | 4188.53 | 0.00 | 0.76 | 1.00 | 2 | 4171.67 |
| p(g+SVL) = c(g+SVL) | 4191.47 | 2.94 | 0.18 | 0.23 | 3 | 4166.18 |
| p(SVL) = c(SVL), c(toes) | 4194.03 | 5.50 | 0.05 | 0.06 | 3 | 4168.74 |
| p(g+SVL) = c(g+SVL), c(toes) | 4197.29 | 8.77 | 0.01 | 0.01 | 4 | 4163.58 |
| p(g) = c(g) | 4199.68 | 11.15 | 0.00 | 0.00 | 2 | 4182.82 |

Table A-5. Minimum, maximum and average temperature (Temp) and relative humidity (Rh), sky cover, number of preadults, number of adults, and preadult to adult ratio for each day of the seven day survey period for the *Eleutherodactylus planirostris* mark- recapture study at site Keaau Macadamia Orchard (KM), island of Hawaii, USA, 2009.

| Day | Min temp (°C) | Max temp (°C) | Ave temp (°C) | Min Rh | Max Rh | Ave Rh | Sky cover | Pre-adults | Adults | Preadult to adult ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 20.19 | 21.33 | 20.71 | 101.90 | 103.70 | 102.85 | drizzle | 204 | 117 | 1.74 |
| 2 | 20.19 | 22.48 | 20.71 | 94.50 | 103.90 | 101.89 | cloudy | 145 | 101 | 1.44 |
| 3 | 20.95 | 22.86 | 21.78 | 93.80 | 101.90 | 99.49 | clear | 160 | 159 | 1.01 |
| 4 | 19.42 | 22.09 | 20.19 | 92.20 | 102.50 | 99.21 | clear | 130 | 117 | 1.11 |
| 5 | 19.81 | 23.24 | 21.09 | 87.10 | 99.60 | 96.05 | clear | 138 | 135 | 1.02 |
| 6 | 19.81 | 22.86 | 21.16 | 88.40 | 99.90 | 96.25 | partly cloudy | 155 | 141 | 1.10 |
| 7 | 19.42 | 23.24 | 21.30 | 85.40 | 98.90 | 94.51 | partly cloudy | 145 | 157 | 0.92 |

# Appendix B

## Diet analysis ANOVA tables

Table B-1. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Acari per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 33.1 | <0.0001 |
| Site | 9 | 413 | 10.6 | <0.0001 |

Table B-2. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Amphipoda per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 0.3 | 0.7479 |
| Site | 9 | 413 | 3.1 | 0.0015 |

Table B-3. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Araneae per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 2.5 | 0.0861 |
| Site | 9 | 413 | 1.7 | 0.0946 |

Table B-4. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Chilopoda per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 1.8 | 0.1745 |
| Site | 9 | 413 | 1.8 | 0.0619 |

Table B-5. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Coleoptera per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 6.0 | 0.0026 |
| Site | 9 | 413 | 2.8 | 0.0035 |

Table B-6. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Collembola per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 8.8 | 0.0002 |
| Site | 9 | 413 | 12.4 | <0.0001 |

Table B-7. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Diptera per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 3.4 | 0.0193 |
| Site | 9 | 413 | 4.8 | 0.0639 |

Table B-8. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Hemiptera: Heteroptera per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 11.7 | <0.0001 |
| Site | 9 | 413 | 3.2 | 0.001 |

Table B-9. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (9 levels) on total number of Hymenoptera: Formicidae per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 350 | 4.1 | 0.0180 |
| Site | 8 | 350 | 15.7 | <0.0001 |
| Stage class*Site | 16 | 350 | 3.2 | <0.0001 |

Table B-10. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (9 levels) on total number of Isopoda per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 350 | 0.0 | 1 |
| Site | 8 | 350 | 2.6 | 0.0101 |
| Stage class*Site | 16 | 350 | 1.8 | 0.0255 |

Table B-11. Model results of two-way factorial ANOVA with negative binomial distribution to estimate the effect of stage class (3 levels) and site (10 levels) on total number of Psocoptera per stomach.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 2.6 | 0.075 |
| Site | 9 | 413 | 8.4 | <0.0001 |

Table B-12: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Acari volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 18.9 | <0.0001 |
| Site | 9 | 413 | 9.6 | <0.0001 |

Table B-13: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Amphipoda volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 0.7 | 0.5134 |
| Site | 9 | 413 | 5.5 | <0.0001 |

Table B-14: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Araneae volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 0.7 | 0.5134 |
| Site | 9 | 413 | 5.5 | <0.0001 |

Table B-15: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Chilopoda volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 2.4 | 0.937 |
| Site | 9 | 413 | 1.6 | 0.1031 |

Table B-16: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Coleoptera volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 11.7 | <0.0001 |
| Site | 9 | 413 | 4.5 | <0.0001 |

Table B-17: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Collembola volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 2.0 | 0.1311 |
| Site | 9 | 413 | 19.2 | <0.0001 |

Table B-18: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Dermaptera volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 5.0 | 0.0069 |
| Site | 9 | 413 | 2.5 | 0.0077 |

Table B-19: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Diplopoda volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 2.4 | 0.0965 |
| Site | 9 | 413 | 1.7 | 0.0871 |

Table B-20: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Diptera volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 3.4 | 0.362 |
| Site | 9 | 413 | 4.8 | <0.0001 |

Table B-21: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Hemiptera: Heteroptera volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 24.7 | <0.0001 |
| Site | 9 | 413 | 4.1 | <0.0001 |

Table B-22: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Hymenoptea: Formicidae volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 350 | 4.3 | 0.0142 |
| Site | 8 | 350 | 8.7 | <0.0001 |
| Stage class*Site | 16 | 350 | 3.6 | <0.0001 |

Table B-23: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Isopoda volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 350 | 1.4 | 0.2616 |
| Site | 8 | 350 | 4.4 | <0.0001 |
| Stage class*Site | 16 | 350 | 3.1 | <0.0001 |

Table B-24: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Lepidoptera larvae volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 2.4 | 0.0945 |
| Site | 9 | 413 | 6.0 | <0.0001 |

Table B-25: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Orthoptera volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 1.8 | 0.1698 |
| Site | 9 | 413 | 1.0 | 0.4517 |

Table B-26: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Pseudoscorpiones volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 1.3 | 0.2673 |
| Site | 9 | 413 | 5.0 | <0.0001 |

Table B-27: Model results of two-way factorial ANOVA to estimate the effect of stage class (3 levels) and site (10 levels) on total Psocoptera volume per stomach. Volume data were log transformed to meet necessary model assumptions of normality and homogeneity of variance.

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Stage class | 2 | 413 | 4.0 | 0.02 |
| Site | 9 | 413 | 8.6 | <0.0001 |

# Appendix C

## Chapter 3 Supplemental Tables

Table C-1. Set of all competing single-season, single species models for *Eleutherodactylus coqui* from the island of Hawaii, USA, 2009. ($AIC_c$ = small-sample size Akaike Information Criterion, $w_i$ = model weights, K = number of parameters).

| Model | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | Model likelihood | K | -2log (likelihood) |
|---|---|---|---|---|---|---|
| $\Psi$(ELEV),$p$(t+RH+WIND+SKY) | 463.80 | 0.00 | 0.18 | 1.00 | 8 | 447.47 |
| $\Psi$(ELEV),$p$(t+RH+WIND+SKY+GHF) | 463.87 | 0.07 | 0.18 | 0.97 | 9 | 445.46 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+WIND) | 464.05 | 0.25 | 0.16 | 0.88 | 8 | 447.72 |
| $\Psi$(ELEV),$p$(t+RH+WIND) | 464.17 | 0.37 | 0.15 | 0.83 | 7 | 449.91 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+WIND+SKY) | 464.17 | 0.37 | 0.15 | 0.83 | 9 | 445.76 |
| $\Psi$(ELEV),$p$(t+WIND+SKY) | 465.71 | 1.91 | 0.07 | 0.38 | 7 | 451.45 |
| $\Psi$(ELEV),$p$(t+WIND) | 466.55 | 2.75 | 0.05 | 0.25 | 6 | 454.36 |
| $\Psi$(ELEV),$p$(t+TEMP+WIND+SKY) | 467.33 | 3.53 | 0.03 | 0.17 | 8 | 451.00 |
| $\Psi$(ELEV),$p$(t+TEMP+WIND) | 467.88 | 4.08 | 0.02 | 0.13 | 7 | 453.62 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+SKY) | 487.10 | 23.30 | 0.00 | 0.00 | 8 | 470.77 |
| $\Psi$(ELEV),$p$(t+TEMP+RH) | 489.59 | 25.79 | 0.00 | 0.00 | 7 | 475.33 |
| $\Psi$(ELEV),$p$(t+RH+SKY) | 491.14 | 27.34 | 0.00 | 0.00 | 7 | 476.88 |
| $\Psi$(ELEV),$p$(t+ SKY) | 491.98 | 28.18 | 0.00 | 0.00 | 6 | 479.79 |
| $\Psi$(ELEV),$p$(t+TEMP+SKY) | 493.25 | 29.45 | 0.00 | 0.00 | 4 | 485.16 |
| $\Psi$(ELEV),$p$(t+TEMP) | 493.69 | 29.89 | 0.00 | 0.00 | 6 | 481.50 |
| $\Psi$(ELEV),$p$(t+RH) | 494.15 | 30.35 | 0.00 | 0.00 | 6 | 481.96 |
| $\Psi$(ELEV),$p$(t) | 495.27 | 31.47 | 0.00 | 0.00 | 5 | 485.13 |
| $\Psi$(ELEV),$p$(.) | 495.34 | 31.54 | 0.00 | 0.00 | 3 | 489.29 |
| $\Psi$(ELEV),$p$(T) | 497.38 | 33.58 | 0.00 | 0.00 | 4 | 489.29 |
| $\Psi$(ELEV),$p$(T+T^2) | 498.91 | 35.11 | 0.00 | 0.00 | 5 | 488.77 |
| $\Psi$(ELEV),$p$(t+WIND+SKY) | 526.26 | 62.46 | 0.00 | 0.00 | 7 | 512.00 |
| $\Psi$(.),$p$(.) | 564.41 | 100.61 | 0.00 | 0.00 | 2 | 560.38 |

Table C-2. Set of all competing single-season, single species models for *Eleutherodactylus planirostris* from the island of Hawaii, USA, 2009. ($AIC_c$ = small-sample size Akaike Information Criterion, $w_i$ = model weights, K = number of parameters).

| Model | $QAIC_c$ | $\Delta QAIC_c$ | $w_i$ | Model likelihood | K | -2log (likelihood) |
|---|---|---|---|---|---|---|
| $\Psi$(ELEV),$p$(t+SKY+COQUI) | 452.65 | 0.00 | 0.18 | 1.00 | 7 | 495.39 |
| $\Psi$(ELEV),$p$(t+SKY) | 452.84 | 0.19 | 0.17 | 0.91 | 6 | 497.93 |
| $\Psi$(ELEV),$p$(t+TEMP+SKY+COQUI) | 454.11 | 1.46 | 0.09 | 0.48 | 8 | 494.69 |
| $\Psi$(ELEV),$p$(t+TEMP+SKY) | 454.18 | 1.53 | 0.09 | 0.47 | 7 | 497.11 |
| $\Psi$(ELEV),$p$(t+WIND+SKY+COQUI) | 454.49 | 1.84 | 0.07 | 0.40 | 8 | 495.12 |
| $\Psi$(ELEV),$p$(t+RH+SKY+COQUI) | 454.51 | 1.86 | 0.07 | 0.39 | 8 | 495.14 |
| $\Psi$(ELEV),$p$(t+RH+SKY) | 454.80 | 2.15 | 0.06 | 0.34 | 7 | 497.82 |
| $\Psi$(ELEV),$p$(t+WIND+SKY) | 454.88 | 2.23 | 0.06 | 0.33 | 7 | 497.91 |
| $\Psi$(ELEV),$p$(t+TEMP+WIND+SKY+COQUI) | 456.02 | 3.37 | 0.03 | 0.19 | 9 | 494.50 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+SKY+COQUI) | 456.17 | 3.52 | 0.03 | 0.17 | 9 | 494.66 |
| $\Psi$(ELEV),$p$(t+TEMP+WIND+SKY) | 456.25 | 3.60 | 0.03 | 0.17 | 8 | 497.11 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+SKY) | 456.25 | 3.60 | 0.03 | 0.17 | 8 | 497.11 |
| $\Psi$(ELEV),$p$(t+RH+WIND+SKY+COQUI) | 456.38 | 3.73 | 0.03 | 0.15 | 9 | 494.90 |
| $\Psi$(ELEV),$p$(t+RH+WIND+SKY) | 456.86 | 4.21 | 0.02 | 0.12 | 8 | 497.80 |
| $\Psi$(ELEV), $p$(t+TEMP+RH+WIND+SKY+COQUI) | 458.09 | 5.44 | 0.01 | 0.07 | 10 | 494.47 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+WIND+SKY) | 458.33 | 5.68 | 0.01 | 0.06 | 9 | 497.11 |
| $\Psi$(ELEV),$p$(t) | 462.43 | 9.78 | 0.00 | 0.01 | 5 | 511.09 |
| $\Psi$(ELEV),$p$(T+T^2) | 462.99 | 10.34 | 0.00 | 0.01 | 5 | 511.73 |
| $\Psi$(ELEV),$p$(t+RH) | 463.39 | 10.74 | 0.00 | 0.00 | 6 | 509.85 |
| $\Psi$(ELEV),$p$(t+COQUI) | 463.66 | 11.01 | 0.00 | 0.00 | 6 | 510.16 |
| $\Psi$(ELEV),$p$(t+WIND) | 464.07 | 11.42 | 0.00 | 0.00 | 6 | 510.62 |
| $\Psi$(ELEV),$p$(t+TEMP) | 464.27 | 11.62 | 0.00 | 0.00 | 6 | 510.85 |
| $\Psi$(ELEV),$p$(t+RH+COQUI) | 464.28 | 11.63 | 0.00 | 0.00 | 7 | 508.53 |
| $\Psi$(ELEV),$p$(T) | 464.63 | 11.98 | 0.00 | 0.00 | 4 | 515.89 |
| $\Psi$(ELEV),$p$(t+WIND+COQUI) | 464.94 | 12.29 | 0.00 | 0.00 | 7 | 509.27 |
| $\Psi$(ELEV),$p$(t+RH+WIND) | 465.18 | 12.53 | 0.00 | 0.00 | 7 | 509.55 |
| $\Psi$(ELEV),$p$(t+TEMP+RH) | 465.43 | 12.78 | 0.00 | 0.00 | 7 | 509.83 |
| $\Psi$(ELEV),$p$(t+TEMP+COQUI) | 465.55 | 12.90 | 0.00 | 0.00 | 7 | 509.96 |
| $\Psi$(ELEV),$p$(t+RH+WIND+COQUI) | 465.76 | 13.11 | 0.00 | 0.00 | 8 | 507.86 |
| $\Psi$(ELEV),$p$(t+TEMP+WIND) | 465.97 | 13.32 | 0.00 | 0.00 | 7 | 510.44 |
| $\Psi$(ELEV),$p$(.) | 466.05 | 13.40 | 0.00 | 0.00 | 3 | 519.80 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+COQUI) | 466.36 | 13.71 | 0.00 | 0.00 | 8 | 508.53 |
| $\Psi$(ELEV),$p$(t+TEMP+WIND+COQUI) | 466.90 | 14.25 | 0.00 | 0.00 | 8 | 509.15 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+WIND) | 467.25 | 14.60 | 0.00 | 0.00 | 8 | 509.54 |
| $\Psi$(ELEV),$p$(t+TEMP+RH+WIND+COQUI) | 467.84 | 15.19 | 0.00 | 0.00 | 9 | 507.85 |
| $\Psi$(.),$p$(.) | 478.60 | 25.95 | 0.00 | 0.00 | 2 | 536.27 |

# Appendix D

Co-author permission letter

October 12, 2010

Christina Olson
Utah State University
Department of Wildland Resources
Logan, UT 84322-5230
(941) 266-6643

Dear Dr. Will Pitt:

I am in the process of preparing my thesis in the Ecology Department at Utah State University. I hope to complete in the fall of 2010.

I am requesting your permission to include the co-authored attached material. I will include acknowledgments to your work and copyright and reprint rights information in a special appendix.

Please indicate your approval of this request by signing in the space provided. If you have any questions please call me at the above number.

Thank you for your cooperation,

Christina Olson

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I hereby give permission to Christina Olson to include the following material in her dissertation:

> Olson, CA, KH Beard, WC Pitt. 2010. Biology and impacts of Pacific Island Invasive Species*: Eleutherodactylus planirostris*, the greenhouse frog (Anura: Eleutherodactylidae). Pacific Science. In progress.

Signed _____

Date 25 OCT 10