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Diet of the Nonnative Greenhouse Frog (*Eleutherodactylus planirostris*) in Maui, Hawaii

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ABSTRACT.—The Greenhouse Frog (*Eleutherodactylus planirostris*) is one of the most widespread frog species in the world. Because of its high population densities, widespread distribution, and consumption of native invertebrates in some invaded sites, understanding its impacts in Hawaii is important. We analyzed stomach contents of 397 frogs from 10 study sites in Maui. Results suggest Greenhouse Frogs are active, ant-specialist predators in the leaf litter. Ants (Formicidae) were the dominant prey found in stomachs in both number and volume. Furthermore, only ants were consumed in a higher proportion than they were sampled in the environment. Because ants dominated their diets, and because all ants are nonnative to Hawaii, this means Greenhouse Frogs consumed primarily nonnative invertebrates (>80%) in the areas sampled. Although results suggest that most native taxa are not at risk from Greenhouse Frog predation, the only locations where we could currently find Greenhouse Frogs were in human-dominated lowlands, which have a lower proportion of native species. Greenhouse Frogs may consume more native species if they invade more native-dominated habitat. Alternatively, nonnative ants are known to impact negatively many native invertebrates in Hawaii, and their possible reduction through Greenhouse Frog predation could affect other species positively. Our research highlights the need to understand better the effects of Greenhouse Frog predation on both native and nonnative invertebrates in Hawaii.

Native to Cuba, the Greenhouse Frog, *Eleutherodactylus planirostris* (Cope, 1862), is one of the most widespread frog species in the world (Frost, 2014). It established on the Hawaiian Islands in the 1990s and is thought to be well-established on Kauai, Lanai, Maui, Oahu, and the island of Hawaii, although its distribution and diet have been studied only on the island of Hawaii (Kraus et al., 1999; Olson et al., 2012a). The Greenhouse Frog invaded Hawaii via the nursery trade (Kraus et al., 1999) and initially was found in nursery greenhouses and surrounding areas, but since that time has spread to residential areas, resorts and hotels, and public lands (Kraus and Campbell, 2002). The species spread mostly through the movement of infested nursery plants and other plant products, but also may spread through vehicle transport (Christy et al., 2007a). In a systematic survey conducted along major roads on the island of Hawaii in 2009, Greenhouse Frogs were found at 35% of 450 sites surveyed (Olson et al., 2012b).

Although the nonnative Greenhouse Frog is likely to be the most widespread amphibian in Hawaii, there has been little effort to manage it. This contrasts with its congener, the Puerto Rican Coqui, *Eleutherodactylus coqui* (Thomas 1966), which was introduced to Hawaii around the same time. Although Coquis still are managed in areas of the island of Hawaii and Maui, Hawaiian residents have little concern over the spread of the Greenhouse Frog, probably because of its quieter mating call (Kraus and Campbell, 2002). The one exception to this is that several resorts have tried to manage Greenhouse Frogs by regularly removing individuals (William Pitt, unpubl. data; Olson et al., 2012a).

Because Greenhouse Frogs are insectivorous, they most likely will affect invertebrate communities in Hawaii (Kraus et al., 1999). In some sites on the island of Hawaii, Greenhouse Frogs reach densities of 12,500 frogs ha⁻¹ and consume 129,000 invertebrates ha⁻¹ night⁻¹ (Olson and Beard, 2012); thus, Greenhouse Frogs may change invertebrate communities measurably. Previous studies suggest that most Greenhouse Frog populations are in the lowlands and they consume primarily ants

(Olson and Beard, 2012), all of which are nonnative to Hawaii. This may benefit native species, such as endemic ground crickets and endemic spiders, which are reduced by nonnative ants in some areas (Krushelnicky et al., 2005).

Even though eliminating the Coqui Frog from Maui is a high conservation priority for the Hawaiian Islands, Greenhouse Frogs have largely been ignored in Maui, even though they are likely to be more widespread. To begin understanding the potential ecological impacts of Greenhouse Frogs on this island, we first attempted to estimate the distribution of Greenhouse Frogs across Maui. We then compared their preferred diet to the composition of invertebrate communities across invaded sites, and the microhabitats where they forage.

MATERIALS AND METHODS

Study Sites.—To determine Greenhouse Frog distributions in Maui, Hawaii, USA (20°47'52"N, 156°18'33"W at its geometric center), we visited every other pixel (200 sites) with the use of a 1-km grid overlaid along major road networks of Maui (as in Bisrat et al., 2012:Appendix 1). We obtained the road layer from the Hawaii Data Clearinghouse website (<http://planning.hawaii.gov/gis/>). From 5 to 14 October 2010, we listened for Greenhouse Frogs for 5 min at each site. We did not hear Greenhouse Frogs calling at any of the sites, even though this method was used successfully on the island of Hawaii to determine Greenhouse Frog locations and detection probabilities (Olson et al., 2012b). Therefore, we selected sites for diet analysis based on known locations of Greenhouse Frogs determined through personal communication with land managers (Fig. 1). Based on this information, we selected 10 study sites with populations of Greenhouse Frogs sufficiently large to collect 30 frogs in one night at each site over a 100 × 100-m area (Fig. 1, Table 1). Three sites were located at vacation resorts (W1, W4, C5), six were at condominium estates (C1, C2, C3, C4, W2, W3), and one was on an organic farm (E1).

Dominant overstory across the sites included *Albizia saman* (C1), *Aleurites moluccana* (C3), *Artocarpus* spp. (E1), *Cocos nucifera* (C4, W1, W3, W4), *Dypsis lutescens* (C3, C5), and *Plumeria* spp. (C1, C2, W2). Dominant understory included *Cordyline fruticosa* (C4, E1, W4), *Croton* spp. (W2, W3), *Dypsis lutescens* (C1, C2, C3,

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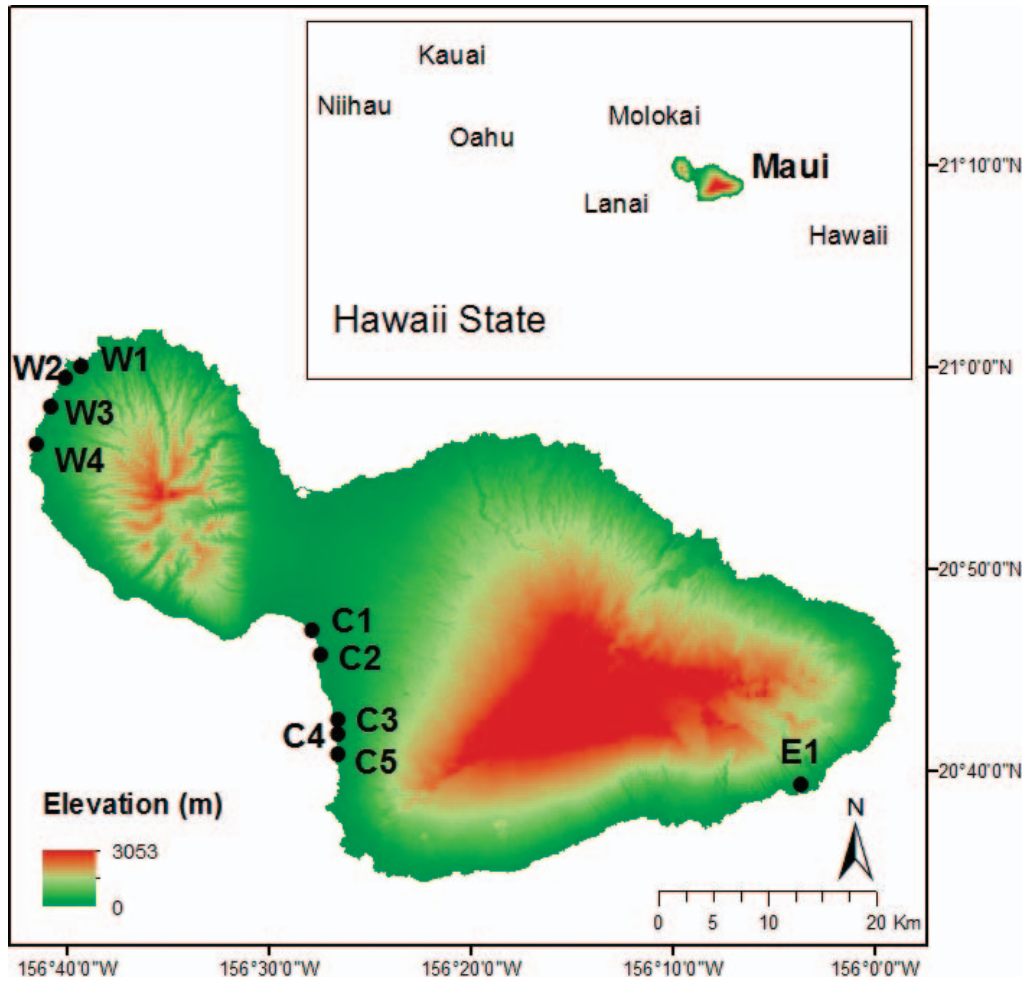


FIG. 1. Location of the 10 study sites of *Eleutherodactylus planirostris* in Maui, Hawaii. Study sites: W1 = Ritz Carlton, W2 = Napili Point, W3 = Kahana Villa, W4 = Westin Kaanapali, C1 = Maalaea Surf Resort, C2 = Kihei Resort, C3 = Maui Kamaole, C4 = Wailea Ekahi Village, C5 = Four Seasons, and E1 = Laulima Farm. See Table 1 for a complete description of each study site.

C4, W1), and *Zingiber officinale* (C1, C3, C5, W2). Sites varied in elevation from 2 to 134 m above sea level. Percent ground cover was measured using 1×1 -m quadrats at 20 similar points at each site (Table 1).

Frog Sampling. — We collected frogs from 2 to 27 November 2010 between 0900 and 1700 h. Two researchers searched the entire area of each site and hand-captured all frogs encountered. To locate frogs, researchers visually scanned the ground and vegetation while turning over rocks, leaf litter, debris, and man-made items. We kept hand-captured frogs in individual bags until they were euthanized with CO_2 at the end of the survey,

and then placed them in a -20°C freezer. We measured snout-vent length (SVL) of each frog with dial calipers to the nearest 0.1 mm. We assigned each frog to one of two basic color phases: 1) mottled tan and brown or 2) mottled tan and brown with two yellow dorsolateral stripes extending from the eye along the length of the body (Olson et al., 2012a). We dissected frogs and assigned them to a stage class (preadult, male, or female) based on examination of gonads. We removed, punctured, and stored stomachs in 70% ethanol until further analysis.

In the laboratory, we identified stomach contents to the lowest identifiable taxonomic unit, typically scientific Order, but

TABLE 1. Site name (abbreviation), elevation (m), dominant (>10%) groundcover (%), and number of *Eleutherodactylus planirostris* collected by site for Maui, Hawaii, USA.

Site name	Elevation (m)	Dominant groundcover (%)	Sample size
Ritz Carlton (W1)	50	Grass (47), herbaceous (25), leaf litter (11), soil (11)	42
Napili Point (W2)	22	Grass (42), herbaceous (20)	49
Kahana Villa (W3)	2	Herbaceous (60), rock (13), grass (12)	32
Westin Kaanapali (W4)	10	Herbaceous (42), leaf litter (25), soil (11)	34
Maalaea Surf Resort (C1)	4	Herbaceous (41), rock (21), cement (11)	42
Kihei Resort (C2)	35	Grass (22), soil (17), fern (13), herbaceous (12), rock (11)	30
Maui Kamaole (C3)	67	Grass (56), herbaceous (25)	54
Wailea Ekahi Village (C4)	42	Grass (58), soil (13)	31
Four Seasons (C5)	38	Grass (40), herbaceous (10), leaf litter (10)	30
Laulima Farm (E1)	134	Herbaceous (44), rock (50)	53

TABLE 2. Frequency of prey items (%), total number of prey items (%), volume of prey items (mm³; %), and importance (I) of each item in the diet of *Eleutherodactylus planirostris* collected from 10 sites in Maui, Hawaii based on the analysis of 397 stomachs. Asterisks indicate taxon with native representative(s) according to (Nishida, 2002).

Prey category	Frequency (%)	Number (%)	Volume (%)	I
Arachnida				
Acari: Oribatida*	72 (13.79)	218 (7.24)	72.46 (1.81)	22.84
Other Acari*	31 (5.94)	60 (1.99)	24.98 (0.62)	8.55
Araneae*	28 (5.36)	47 (1.56)	49.40 (1.23)	8.15
Chilopoda*	17 (3.26)	21 (0.70)	102.00 (2.55)	6.51
Diplopoda*	3 (0.58)	4 (0.13)	10.89 (0.27)	0.98
Gastropoda*	17 (3.26)	24 (0.80)	153.80 (3.84)	7.9
Insecta				
Blattodea	4 (0.77)	4 (0.13)	161.65 (4.03)	4.93
Coleoptera*				
Adult	30 (5.75)	45 (1.50)	181.81 (4.54)	11.79
Larvae	3 (0.58)	3 (0.10)	68.96 (1.72)	2.4
Collembola*	8 (1.53)	43 (1.43)	15.52 (0.39)	3.35
Dermaptera*	27 (5.18)	36 (1.20)	476.07 (11.88)	18.26
Diptera*	16 (3.07)	39 (1.30)	22.35 (0.56)	4.93
Hemiptera*				
Auchenorrhyncha	6 (1.15)	6 (0.20)	42.35 (1.06)	2.41
Heteroptera	1 (0.19)	1 (0.03)	5.10 (0.13)	0.35
Sternorrhyncha	3 (0.58)	4 (0.13)	1.11 (0.03)	0.74
Sternorrhyncha larvae	6 (1.15)	24 (0.80)	78.51 (1.96)	3.91
Hymenoptera				
Formicidae–Ant	207 (39.65)	2,331 (77.44)	2,162.58 (53.98)	171.07
Others*	7 (1.34)	9 (0.30)	3.87 (0.10)	1.74
Lepidoptera larvae*	1 (0.19)	1 (0.03)	38.85 (0.97)	1.19
Tricoptera	8 (1.53)	38 (1.26)	14.24 (0.36)	3.15
Malacostraca				
Amphipoda*	5 (0.96)	6 (0.20)	21.92 (0.55)	1.71
Isopoda*	12 (2.30)	31 (1.03)	124.96 (3.12)	6.45
Oligochaeta	3 (0.58)	4 (0.13)	78.94 (1.97)	2.68
Unidentified	6 (1.15)	10 (0.33)	12.56 (0.31)	1.79
Total	–	3,010	4,006.26	–
Detritus	5	36	66.21	–
Vegetation	39	55	169.11	–
Rock	65	196	134.35	–

in some cases Family (Table 2). For each item, we measured maximum length and width to 0.01 mm (Magnusson et al., 2003) with a 10-mm reticle. We calculated volume for each prey item using the formula: $v = 4/3 \pi \times l/2 \times (w/2)^2$, where l = prey length and w = prey width (Beard, 2007; Vitt et al., 2008). We determined prey importance (I) for each prey category by calculating: $I = (F\% + N\% + V\%)$, where $F\%$ = percentage of frogs in which the prey item occurred, $N\%$ = numeric percentage, and $V\%$ = volumetric percentage (Beard, 2007; Bonansea and Vaira, 2007). We did not consider detritus, vegetation, or rock prey categories, but we measured them.

Invertebrate Sampling.—We collected invertebrates at each study site during the same frog sampling period. We used three different collection methods to sample invertebrates potentially encountered by frogs. We collected leaf litter from eight 0.25 × 0.25-m subplots, a minimum of 10 m apart, located randomly within a 100 × 100-m plot. We placed the leaf litter in Berlese-Tullgren funnels within 4 h of collection and stored extracted invertebrates in 70% ethanol until identified. We collected flying invertebrates on 10 × 18-cm sticky traps (Chevron Ortho, Marysville, OH, USA) posted on stakes 10 cm above the forest floor. We randomly placed eight sticky traps, spaced a minimum of 10 m apart, within a 100 × 100-m plot for 48 h. We froze flying invertebrates until identified. Lastly, we collected foliage invertebrates with the use of a modified insect vacuum (Black & Decker, Towson, MI, USA) from eight 0.50 × 0.50-m subplots, spaced a minimum of 10 m apart, within a 100 × 100-m plot. We swept the insect vacuum across foliage below 0.50-m height, for a

total time of 30 sec in each subplot (Brook et al., 2008). We collected vacuumed invertebrates and stored them immediately in 70% ethanol until identified.

Statistical Analysis.—We used a one-way analysis of variance (ANOVA) to compare SVL between male and female frogs. We used a Pearson's chi-square exact test (χ^2) to test an expected 1 : 1 sex ratio across and within sites using a Monte Carlo simulation based on 999 replicates. We used a two-way factorial analysis of covariance (ANCOVA) to examine the effect of sex (2 levels) and site (10 levels) on total volume and number of prey items consumed. We included SVL as a covariate because it was positively related to both the total number of prey items ($R^2 = 0.137$; $F_{1,257} = -0.07$; $P < 0.001$) and prey volume ($R^2 = 0.137$; $F_{1,257} = 0.09$; $P < 0.001$). Because of the low number of preadults collected ($n = 7$ individuals), we excluded this stage class from all analyses.

Based on a Bray-Curtis dissimilarity matrix, we used nonmetric multidimensional scaling (NMDS) to compare stomach contents to invertebrate communities at each site, and analysis of similarity (ANOSIM) to calculate the dissimilarity statistic [to determine if sample type (stomach, leaf litter, foliage, and flying) and sites were different from one another]. We used the first NMDS axis as response variables in an ANOVA to determine which method of insect collection (leaf litter, foliage or flying) had an invertebrate community most similar to stomach content. We used a Tukey-Kramer analysis to test for differences across sampling type and stomach content. Because leaf litter samples resembled stomach contents more

than the other sample types (foliage and flying), we used another ANOVA to determine if stomach contents were more similar to each other across sites than to leaf litter samples from each site.

We estimated prey selection at each site with the Jacob's prey electivity formula (Jacobs, 1974): $e_i = (p_i - p_k) / [(p_i + p_k) - (2p_i p_k)]$, 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. We considered only prey categories representing $>1\%$ of available prey in the leaf litter. We used only leaf litter samples in this analysis because Greenhouse Frogs in our sites were mostly consuming leaf litter invertebrates (see Results). We present mean e_i values <-0.70 and >0.70 , which indicate strong avoidance or preference for invertebrates, respectively (Tuttle et al., 2009).

We confirmed data normality with Shapiro-Wilk tests and log-transformed data when necessary. We conducted all statistical analyses with the use of R 2.8.1 (R Development Core Team, 2004), and used $\alpha = 0.05$ for all tests. Means presented were first calculated within sites, and then across the 10 study sites. We present mean ± 1 SE throughout.

RESULTS

We collected a total of 397 frogs across the 10 sites (mean SVL = 21.1 ± 1.28 mm): 285 (71.8%) males (SVL range = 10.2–25.5; mean = 20.1 ± 0.79 mm), 105 (26.4%) females (SVL range = 18.6 to 30.1; mean = 24.8 ± 0.88 mm) and 7 (1.8%) preadults (SVL range = 5.9 to 11.2; mean = 8.0 ± 0.60 mm). Females were significantly larger than males ($F_{1,388} = 252.7$; $P < 0.001$). A 3 : 1 sex ratio was strongly biased toward males across all 10 sites ($\chi^2 = 122.33$; $P < 0.001$). Analysis within site showed that two sites had an equal sex ratio (C4: $\chi^2 = 2.56$; $P = 0.143$, C5: $\chi^2 = 0.36$; $P = 0.643$). All frogs collected had a mottled color pattern.

Diet Generalities.—Of the 397 collected individuals, 149 had empty stomachs: 106 (37%) males, 42 (40%) females, and one preadult (14%). We identified a total of 3,010 invertebrate items from the 248 stomachs that had prey items. On average, frogs had 7.6 ± 0.6 prey items per stomach. Average prey volume per stomach was $10.0 \text{ mm}^3 \pm 0.8$. Plant material was present in 39 (10%) stomachs and rocks in 65 (16%) stomachs.

Prey Categories.—The most important prey categories were Formicidae, Oribatida (an Order of Subclass Acari, and hereafter referred to as Oribatida), and Dermaptera, respectively (Table 2). Formicidae made up 77.4% of the total number of prey items ingested, followed by Oribatida with 7.2%; and other Acari were 2.0%. Formicidae represented 54.0% of the prey volume, followed by Dermaptera with 11.9%, and Coleoptera with 4.5%.

Diet by Sex.—After controlling for SVL, there was no difference in the total number of prey items consumed by males and females (7.6 ± 0.67 vs. 7.5 ± 1.3 ; $F_{1,244} = 0.260$, $P = 0.304$). On the other hand, the volume of prey per stomach was higher in females compared to males (15.8 ± 2.4 vs. $8.2 \pm 0.7 \text{ mm}^3$; $F_{1,234} = 131.7$, $P < 0.001$). The main items consumed by both sexes were Formicidae and Oribatida. Excluding frogs with empty stomachs, Formicidae filled on average 8.41 mm^3 in male stomachs and 10.4 mm^3 in female stomachs.

Diet by Site.—Ants (Formicidae) were the most numerous prey items consumed across all sites (ranging from 27% to 95% of the prey items consumed), except in C1 where Coleoptera (27%) and

Dermaptera (23%) also were important prey. The number of prey items consumed per frog differed by site ($F_{9,244} = 4.1$, $P < 0.001$), with means ranging from 2.6 (at C1) to 22.7 (at W4). Prey volume per frog differed by site ($F_{9,234} = 8.54$, $P < 0.001$), with means ranging from 1.1 mm^3 (at C1) to 18.9 mm^3 (at C4).

Foraging Location.—We collected and identified a total of 29,503 invertebrates in the environmental samples (Table 3). The most abundant invertebrates in the leaf litter samples were Collembola ($N = 4,295$ items; $N\% = 23$), Oribatida ($N = 3,896$; $N\% = 21$), other Acari ($N = 2,447$; $N\% = 13$), and Formicidae ($N = 2,107$; $N\% = 12$). The most abundant invertebrates on the sticky traps were Hymenoptera other than Formicidae ($N = 4,241$; $N\% = 54$), Diptera ($N = 1,950$; $N\% = 25$), and Thysanoptera ($N = 659$; $N\% = 8$). The most abundant invertebrates in the foliage samples were Formicidae ($N = 236$; $N\% = 44$), other Acari ($N = 66$; $N\% = 12$), and Diptera ($N = 54$; $N\% = 10$).

The first dimension of the NMDS separated stomach samples from invertebrates collected in sticky trap samples whereas the second dimension separated stomach samples and leaf litter samples from foliage samples (Fig. 2). Invertebrate composition differed among sample types (stomachs, leaf litter, foliage, and flying) (ANOSIM statistic = 0.847, $P < 0.001$), but sample types did not differ across sites (ANOSIM statistic = -0.148 , $P = 0.996$). The Tukey–Kramer analysis confirmed that leaf litter samples were more similar to stomach samples (Diff = -0.216 ; $P < 0.001$) than other sample types [foliage (Diff = 0.404; $P < 0.001$); flying (Diff = 1.147; $P < 0.001$)]; however, stomach samples were more similar to each other than to leaf litter samples from the same site ($F_{1,233} = 13.57$; $P < 0.05$).

Prey Preferences.—According to the Jacob's electivity index, only Formicidae was a preferred prey item across all sites (e_i range = 0.90–0.99). Although the proportion of prey type varied across sites, frogs consumed five invertebrate categories in lower proportion than was available in the environment, such as other Acari in four sites (C3, C4, C5, and W1; e_i range = -0.73 to -0.97), Oribatida in two sites (C5 and E1; e_i range = -0.82 to -0.97), Collembola in three sites (E1, W2, and W4; e_i range = -0.82 to -0.97), and Gastropoda in three sites (E1, W3, and W4; e_i range = -0.71 to -0.91).

DISCUSSION

Greenhouse Frog diets in Maui consist mostly of nonnative, leaf-litter invertebrates. This is primarily because of the high consumption of Formicidae (ants), all species of which are nonnative and were found mostly in the leaf litter. Formicidae was the dominant prey item in number (77%) and volume (54%). Furthermore, only Formicidae was consumed in higher proportion than was collected in the environment. This prey category also is an important dietary component in other parts of its introduced and native ranges. Formicidae was the most consumed prey item (32% of all prey items) on the island of Hawaii (Olson and Beard, 2012). In addition, it constituted 41% of prey items in Florida (Goin, 1947; Samways et al., 1996) and 63% in Jamaica (Stewart, 1977). In the native range of Cuba, only three stomachs were analyzed, and Formicidae represented 100% of the stomach content (Goin, 1947). Specializing in ants may be a conservative trait for Greenhouse Frogs across their native and introduced ranges, and may assist their establishment into previously uninvaded areas, especially considering that ants comprise 70% of invertebrate biomass in most tropical areas (Hölldobler and Wilson, 1990).

TABLE 3. Mean number (\pm SE) of invertebrate categories collected from 10 sites in Maui, Hawaii, extracted from the leaf litter ($n = 18,155$ individuals), collected on sticky traps ($n = 7,808$), and collected in vacuum samples ($n = 531$). Mean and SE were calculated within site before calculated across sites.

Invertebrate category	Leaf litter sample	Sticky trap sample	Vacuum sample
Arachnida			
Acari	27.81 (9.96)	0.06 (0.10)	0.84 (0.38)
Oribatida	44.27 (14.93)	0.09 (0.10)	0.03 (0.07)
Araneae	2.51 (0.90)	0.10 (0.11)	0.37 (0.20)
Pseudoscorpionida	0.18 (0.21)	0 (0)	0.06 (0.17)
Chilopoda	0.19 (0.22)	0 (0)	0 (0)
Diplopoda	0.27 (0.19)	0 (0)	0 (0)
Gastropoda	7.56 (2.23)	0 (0)	0.53 (0.31)
Insecta			
Blattodea	0.35 (0.31)	0 (0)	0.03 (0.45)
Coleoptera	2.47 (1.05)	0.48 (0.26)	0.10 (0.11)
Collembola	48.81 (19.26)	1.09 (0.80)	0.03 (0.07)
Dermaptera	0.62 (0.63)	0 (0)	0.17 (0.17)
Diptera			
Adult	1.74 (0.51)	22.16 (9.33)	0.68 (0.23)
Larvae	0.12 (0.35)	0 (0)	0 (0)
Hemiptera			
Auchenorrhyncha	3.19 (2.02)	2.26 (2.39)	0.04 (0.10)
Auchenorrhyncha larvae	0.19 (0.29)	0 (0)	0 (0)
Heteroptera	3.36 (5.00)	0.27 (0.11)	0.02 (0.04)
Heteroptera larvae	0.64 (0.97)	0 (0)	0 (0)
Sternorrhyncha	1.94 (4.45)	1.04 (0.62)	0.05 (0.10)
Sternorrhyncha larvae	0.03 (0.07)	0.02 (0.07)	0 (0)
Hymenoptera			
Formicidae–Ants	23.94 (22.95)	1.28 (0.60)	2.95 (3.35)
Other Hymenoptera	0.06 (0.06)	48.19 (16.35)	0.19 (0.11)
Odonata	0 (0)	0.02 (0.07)	0 (0)
Orthoptera	0.01 (0.04)	0.01 (0.03)	0 (0)
Lepidoptera	0.52 (0.33)	0.83 (0.94)	0 (0)
Psocoptera	0.50 (0.45)	1.44 (0.39)	0.03 (0.04)
Thysanoptera	2.48 (4.33)	7.49 (4.20)	0.16 (0.10)
Tricoptera	0.18 (0.29)	0.83 (1.68)	0 (0)
Malacostraca			
Amphipoda	5.78 (6.44)	0.01 (0.03)	0.13 (0.21)
Isopoda	20.11 (19.20)	0.03 (0.07)	0.19 (0.15)
Oligochaeta	0.33 (0.34)	0 (0)	0 (0)
Unidentified	1.18 (0.56)	0.92 (0.44)	0.18 (0.19)

There are differences in Greenhouse Frog diets across invaded localities. In addition to Formicidae, Oribatida and Dermaptera represented the most important prey categories in Maui. On the island of Hawaii, Formicidae, other Acari, and Collembola were the most important prey (Olson and Beard, 2012). In Florida, the most important prey categories were Formicidae, Coleoptera, and Blattodea (Goin, 1947) and in Jamaica the most important prey were Formicidae, Arachnida, and Isoptera (Stewart, 1977). In all these sites, Formicidae was the main prey item, but Greenhouse Frogs foraged on a variety of prey types, which is similar to other ant specialists (Toft, 1981; Ferreira et al., 2012). Differences in diets among invaded localities may be driven by differences in prey availability.

In Maui, Greenhouse Frogs consumed substantially fewer prey (7.6 items per stomach) compared to those found on the island of Hawaii (16.9 items per stomach) (Olson and Beard, 2012). In addition, frogs on Maui had a higher proportion of empty stomachs (37%) compared to frogs on Hawaii (3%) (Olson and Beard, 2012); however, Greenhouse Frogs also were larger on Maui than on Hawaii (mean SVL of males = 20.1 mm in Maui vs. 16.5 mm in Hawaii; females = 24.8 mm in Maui vs. 21.8 mm in Hawaii), and larger frogs often have fewer, larger prey items (Beard, 2007).

In addition to frog size differences between the islands, differences in both the number of prey per stomach and the number of empty stomachs between Maui and island of Hawaii

also could be attributed to differences in collection times. First, we expect frogs to consume more prey during the reproductive season (Gilbert, 2005; Taigen and Pough, 1985; Woolbright and Stewart, 1987). Based on the lack of calling males heard and few preadults collected during our sampling period, we expect this was not the reproductive season. Alternatively, Olson and Beard (2012) found calling males on the island of Hawaii as well as a large percentage of preadults (35.4%) during the May to June collections. Even though Greenhouse Frogs in Cuba have a reproductive season from April to January (Meshaka and Layne, 2005), we now suspect that Greenhouse Frogs in Hawaii have a reproductive season similar to that found in Florida, where choruses are heard from May to September (Goin, 1947; Meshaka et al., 2009) and hatchlings are seen from May to July (Lazell, 1989; Meshaka et al., 2009). Second, Greenhouse Frogs are nocturnal and they likely consume more prey items at night when they are active. We collected frogs during the day (to respect landowner preferences), whereas Olson and Beard (2012) collected frogs within a few hours of sunset. Because collecting times between these studies were different, comparing diet content between them may not be possible (Stewart and Woolbright, 1996).

All Greenhouse Frogs we collected were mottled, which is recessive to the dominant striped pattern (Olson et al., 2012a). In Cuba, there is a 3 : 1 ratio of striped to mottled individuals, whereas populations from Florida exhibit a 1 : 1 ratio (Goin,

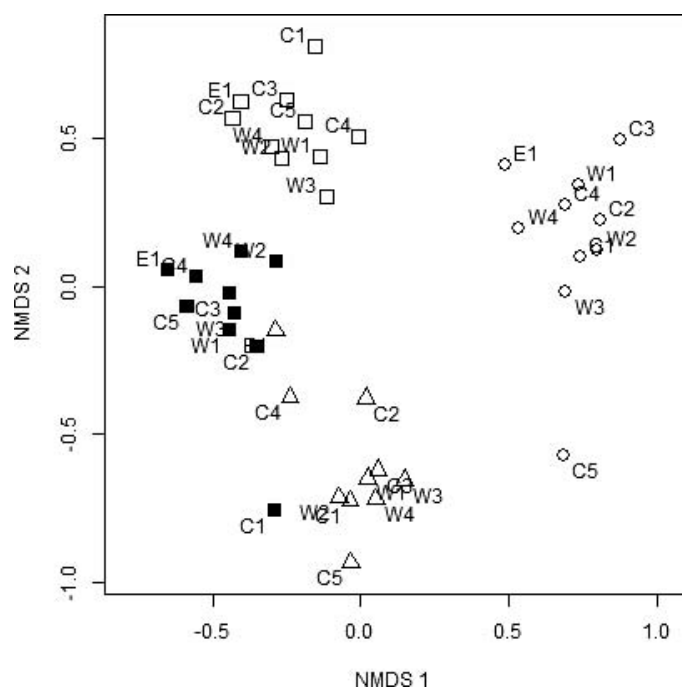


FIG. 2. Nonmetric multidimensional scaling (NMDS) of invertebrates found in the environment compared to *Eleutherodactylus planirostris* stomach contents (stress = 13.38) across 10 sites in Maui, Hawaii. Solid squares = stomach contents, open squares = leaf litter samples, triangles = foliage samples, and circles = stick trap samples.

1947). Olson and Beard (2012) found only mottled individuals across the island of Hawaii and in Lanai, although there are museum specimens of several striped individuals from Oahu (Olson et al., 2012a). The lack of striped individuals on Maui suggests these populations experienced either a bottleneck when they were introduced or selective pressure later (O'Neill et al., 2012).

In the only other study conducted on frog diets in Maui, the Coqui Frog was studied at two sites (Beard, 2007). One of these sites was in Kihei and the other was in Maliko Gulch, on the north side of the island and the last remaining stronghold of Coquis on the island (Beard and Pitt, 2012). Formicidae was the dominant prey in Kihei (92% of prey items; Beard, 2007); in Maliko Gulch, however, Amphipoda was the dominant prey (29% of prey items), followed by Isopoda (15%), Formicidae (13%), Acarina (7%), Collembola (6%), and Chilopoda (6%; Beard, 2007). In general, the diets of Coqui and Greenhouse Frogs appear similar in Hawaii: Both appear to consume primarily ants in the leaf litter. In both Maui and the island of Hawaii, however, Coqui frog diets appear more diverse than that of Greenhouse Frogs, which may result from its broader vertical distribution in the forest (Beard, 2007; Olson and Beard, 2012).

Nonnative invertebrates constitute >78% of the diet of Greenhouse Frogs in Maui. We expected this because all frogs were collected from human-modified landscapes dominated by nonnative vegetation, and are more likely to harbor nonnative invertebrates as well as frogs (Kraus and Campbell, 2002). In fact, these were the only locations where we found Greenhouse Frogs in Maui, and it remains unclear how widespread they are on the island. In other invaded areas, such as Florida, Guam, and the island of Hawaii, Greenhouse Frogs also have been recorded in highly modified human environments (Christy et al., 2007b, Meshaka et al., 2009; Olson et al., 2012b).

Among the most important taxa consumed by Greenhouse Frogs (Table 2), Araneae and Coleoptera are the most likely to contain native species, because natives comprise 71% and 75% of these taxa, respectively, in Maui (Nishida, 2002). As Olson and Beard (2012) suggest, it is likely at this stage in the invasion that Greenhouse Frogs do not commonly consume native species because of their current distributional patterns; most remaining native invertebrates occur in mid- to high elevations, whereas most Greenhouse Frogs occupy low elevations (Gagne, 1979; Gagne and Christensen, 1985; Olson and Beard, 2012). Greenhouse Frogs have been recorded, however, in pristine forests across its invaded range (Schwartz and Hendersen, 1991; Meshaka et al., 2009; Olson et al., 2012b), and if Greenhouse Frogs invade areas of highly endemic leaf litter invertebrates in Maui (Simon et al., 1984), their opportunistic feeding behavior and lack of specialized predators could potentially reduce native species.

Ants have had catastrophic impacts on native invertebrates, such as land snails, aquatic insects, major pollinators, and spiders across Hawaiian ecosystems (Gagne and Christensen, 1985; Cole et al., 1992; Gillespie and Reimer, 1993; Reimer, 1994; Krushelnycky et al., 2005). Native fauna proved highly vulnerable to introduced predatory ants because they evolved for millions of years without them. At least six of the 45 nonnative ants in Hawaii are highly destructive (Brian, 1983), and Greenhouse Frogs may reduce some of these populations. For example, Choi and Beard (2012) found that ant populations were 50% lower in some invaded sites along Coqui Frog invasion fronts on the island of Hawaii where densities ranged from 347 to 6,983 frogs/ha. Greenhouse Frogs reach densities of 12,000 frogs/ha in Hawaii, and Greenhouse Frogs are more specialized on ants. Thus, in more natural environments, Greenhouse Frogs may benefit native invertebrates indirectly by consuming large numbers of ants (Olson and Beard, 2012). A concern with such a conclusion is the general public may misinterpret it and disperse Greenhouse Frogs into natural environments, risking other unforeseen consequences. Therefore, we should remain cautious about the full impact of Greenhouse Frogs, especially considering the large number of unsuccessful biocontrol agents previously introduced into Hawaii (Howarth, 1999).

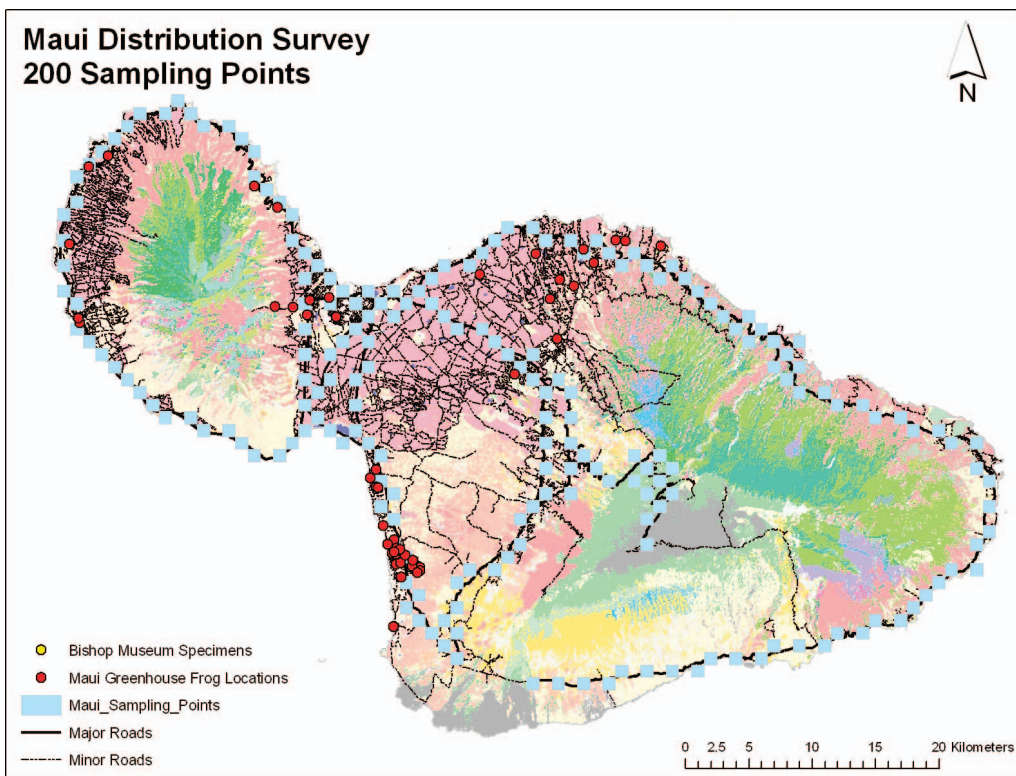
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APPENDIX 1. Map showing the points visited to determine the distribution of Greenhouse Frogs.