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Shane A. Hill
Utah State University

Karen H. Beard
Utah State University

Shane R. Siers
National Wildlife Research Center, Hawaii Field Station

Aaron B. Shiels
National Wildlife Research Center, Ft. Collins

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Running head: Interactions among an invasive frog and invasive mammals

Invasive coqui frogs are associated with differences in mongoose and rat abundances and diets in Hawaii

Shane A. Hill¹, Karen H. Beard^{1*}, Shane R. Siers² and Aaron B. Shiels³

1 Department of Wildland Resources and Ecology Center, Utah State University, Logan, UT 84322-5230, U.S.A.

2 USDA APHIS, Wildlife Services, National Wildlife Research Center, Hawaii Field Station, Hilo, Hawaii 96720, U.S.A.

3 USDA APHIS, Wildlife Services, National Wildlife Research Center, Ft. Collins, CO 80521, U.S.A.

* Email address: karen.beard@usu.edu; Orcid: 0000-0003-4997-2495; ph.: +1 435-797-8220

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Abstract

With the increasing rate of species being introduced to areas outside of their native ranges, non-natives are likely to interact in ways that influence each other's populations. The high densities of invasive coqui frogs (*Eleutherodactylus coqui*) in Hawaii have been hypothesized to increase non-native mongoose (*Herpestes auropunctatus*) and rat (*Rattus* spp.) abundances, and in turn increase bird nest depredation rates. We compared the relative abundances of rats and mongooses and artificial bird nest predation rates at 12 sites that had plots with similar habitat invaded and not invaded by coqui frogs across the island of Hawaii. We interpret our results considering mongoose and rat stomach analyses and camera trap data collected to monitor coqui scavengers. We found that coqui presence was associated with 30% greater mongoose abundance and 17% lower Pacific rat (*Rattus exulans*) abundance. Based on our diet analyses and scavenging data, both mongooses and rats consume coquis, but mongooses were the most important consumers of coquis, which may have contributed to their increase in coqui plots. We speculate that coquis are competing with rats for invertebrate prey due to reduced Pacific rat abundance and greater amounts of fruit in rat stomachs collected in coqui-invaded compared to uninvaded plots. We did not observe any difference in nest predation rates in coqui-invaded and uninvaded plots. Our results suggest that the coqui invasion may increase or decrease non-native mammal populations, and non-native amphibians may serve as both novel prey and competitors to non-native mammals.

Introduction

A main negative effect of non-native fauna on islands is as novel predators (Davis 2003; Sax et al. 2002), and the consequences are particularly noteworthy when these introduced predators eliminate or greatly reduce native species (Atkinson 1985; Savidge 1987). However, as invasive species become increasingly widespread and abundant, they are starting to interact with one another in complex and difficult to predict ways (Simberloff and Von Holle 1999). Given the growing number of non-natives and their potential for complex interactions, it is not surprising that there is also growing evidence that non-native species can serve as important prey for non-native predators (Abernethy et al. 2016; Beckmann and Shine 2011; Gangoso et al. 2006; Rodriguez 2006). While these types of interactions might be most noteworthy if they negatively affect native species, these effects can also occur among non-native species in completely novel food webs. There is growing support for these types of complex interactions among non-natives, sometimes termed invasional meltdowns (*sensu* Simberloff and Von Holle 1999), with examples from yellow ant and scale insects on Christmas Island, and green crabs and clams in North America (Grosholz 2005; O'Dowd et al. 2003; reviewed in O'Loughlin and Green 2017).

A region of the world that has experienced a large number of intentional and unintentional invasions is the Hawaiian archipelago (Loope and Mueller-Dombois 1989; Vitousek et al. 1987; Wilcove et al. 1998). Because there are no native ground-dwelling mammals, reptiles, or amphibians, the ecological threat that non-natives pose is mostly limited to native birds (Atkinson 1977; Hoshida et al. 1990; Reed et al. 2012), invertebrates (Choi and Beard 2012; Hadfield et al. 1993), and plants (Shiels 2010; Sugihara 1997; Weller et al. 2018). One such introduction of a non-native to Hawaii is that of the Puerto Rican coqui frog (*Eleutherodactylus coqui*) (Kraus et al. 1999). The coqui has received a great deal of attention

since it was introduced via the horticultural trade in the late 1980's (Kraus et al. 1999). The frog is particularly widespread on the island of Hawaii, while the other Hawaiian Islands have had more success in preventing its establishment and controlling populations (Beard et al. 2009). Previous studies have found that coquis have both societal impacts, including economic and quality of life impacts (Kaiser and Burnett 2006; Kalnicky et al. 2014; Kraus and Campbell 2002), and ecological impacts through their interactions with other species (Bernard and Mautz 2016; Choi and Beard 2012; Smith et al. 2018; Tuttle et al. 2009).

Although previous research has determined some ecological consequences of the coqui invasion, questions remain regarding interactions between coquis and invasive small mammals. The introduction of coquis to the island of Hawaii is recent relative to that of the mongooses (*Herpestes auro-punctatus*) and rats (*Rattus* spp.) (Baldwin et al. 1952; Doty 1945; Kraus et al. 1999), and, when coquis established, they became potential prey to these species. Further, if coquis serve as novel prey to these species, it could change the roles that mongooses and rats have within the Hawaiian food web. For example, coquis may increase rat and mongoose abundances and exacerbate the predation effects of both mongooses and rats on native birds (Kraus et al. 1999; VanderWerf 2001; Beard and Pitt 2006). Interactions observed in native communities may also occur within this non-native dominated system, such as apparent competition (*sensu* Holt 1977). For example, if the presence of coquis causes an increase in mongooses, then there may be increased predation on rats by mongooses in coqui-infested areas, eventually leading to a decrease in rats. Finally, coquis may compete directly with rats for prey because both are nocturnal and insectivorous (Shiels et al. 2013; Wallis et al. 2016).

Our primary goal was to test the hypothesis proposed by Kraus et al. (1999) that coquis may increase the abundances of mongooses and rats through direct predation and thereby

increase bird nest predation. However, this hypothesis provides only a simple view of the potential interactions among these species, especially between coquis and rats. Therefore, we investigated likely alternative, but not mutually exclusive, hypotheses between coquis and rats, such as apparent competition and resource competition. If coquis serve as important prey for mongooses and rats, we predict that mongoose and rat abundance will be higher in areas with coquis and we expect coquis to be important in mongoose and rat diets. If coquis interact with rats through apparent competition, we predict that mongoose populations will be higher and rat populations will be lower in areas with coquis. We would also expect mongooses to have rats in their diets. If coquis compete with rats for resources, we predict that rat abundance will be lower in areas with coquis, and that rats and coquis will consume similar prey. Finally, if coquis increase bird nest predation through either increases in mongoose or rat abundances, we expect nest predation rates will be higher in areas with coquis than in areas without coquis.

To address these hypotheses and predictions, we determined the relationship among coquis, mongooses, and rats to determine if coquis or the other invasive mammal were important predictors of mongoose and rat abundance. To determine whether predation or competition might be occurring between coquis, mongooses, and rats, we investigated mongoose and rat stomach contents in the presence and absence of coquis, and direct scavenging on coquis. Finally, to determine if coquis indirectly influenced bird nest predation, we investigated nest predation rates in the presence and absence of coquis.

Methods

Study sites

We conducted research at 12 sites on the island of Hawaii in areas with coqui invasion fronts (Fig. 1). Coqui invasion fronts are defined as the edge of established coqui populations, and where habitat in close proximity differs only in the presence or absence of the frog. Eleven of these sites were located near areas used in previous studies investigating the impacts of coquis on invertebrates and birds (Choi and Beard 2012; Smith et al. 2018). We added one site (site Upper Stainback [US]; Fig. 1) and adjusted the location of the plots at four sites (sites Eden Rock [ER] Kalopa [KP] Stainback [SB], and Volcano [VC]) from the locations used in Smith et al. (2018) because the invasion front had moved since that study. These were the only known locations on the island where there was sufficient area on either side of the invasion front to conduct our research and where habitat had been determined previously to be similar on both sides of the front (Choi and Beard 2012; Smith et al. 2018).

At each site, we set up two circular 2.01-ha plots (diameter: 160 m), one on either side of the invasion front, in which all measurements were made. Plots on either side of the front had a mean distance of 1163 m (range: 297 to 2954 m) between them, with the fronts roughly half way between them. We wanted plots to be close enough to each other to maintain similar habitats, but not so close that many individual mammals would be moving between them. While we cannot assume complete independence between either side of the invasion front, we feel that it is safe to assume that any movement of small mammals across the front occurred at random and did not affect our ability to address our objectives (as in Smith et al. 2018). Because coqui populations are often near roads (Olson et al. 2012), we placed both coqui and non-coqui plots the same distance (> 50 m) from roads, trails, buildings, agricultural fields, or other such habitat edges to

avoid biasing small mammal observations. We confirmed coqui presence and absence on both sides of the front by listening for 20 minutes during peak calling hours, 1900 to 0200 h (Woolbright 1985), for the male's two-note mating call on at least three separate nights no more than two months prior to sampling.

Previous studies in 11 of 12 of our sites found no measurable differences in habitat on either side of the front (Choi and Beard 2012; Smith et al. 2018). Because this study was initiated two years after the previous study (Smith et al. 2018) and the location of some sites were adjusted, we tested for differences in habitat across fronts by measuring the following variables in both plots at each site: elevation, canopy cover, vegetated ground cover, percent understory density, and dominant canopy and dominant understory species (explained in detail in Supplemental Material A). For each variable, we tested for differences in habitat across paired plots using a one-way analysis of variance (ANOVA) with coqui presence/absence as the fixed effect, and site as a random block effect. We detected no differences in these variables across coqui and non-coqui plots (Supplemental material A). Of note, a previous study more thoroughly tested, both statistically and in terms of the field variables collected, habitat difference between these sites and dropped 5 of 20 sites from their analysis that were sufficiently different in terms of habitat variables (Choi 2011). We used 11 of the sites remaining after that analysis. In summary, these 11 sites had no measurable habitat differences across the front, in either of the previous studies or this study.

Mongoose and rat abundance

To test whether the abundance of non-native mammals is related to coqui frog presence or absence, we estimated mongoose and rat abundances in coqui and non-coqui plots at each of

the 12 sites with trapping webs. We conducted mongoose and rat trapping from December 2015 to July 2016. Each trapping web consisted of 16, 80-m transects radiating from a central point and covering 2.01 ha, with one web on either side of the invasion front. We set eight live cage traps (Tomahawk Live Trap Company, Tomahawk, WI), one every 10 m, along each alternating transect. On the remaining transects, we placed eight snap traps (Victor rat traps, Woodstream Corporation, Lititz, PA), one every 10 m. We baited live traps with uncooked cocktail links soaked in fish oil, suspended by a hook in the back of each trap, while snap traps were baited with chunks of coconut. We checked each trap twice daily, once at dawn and again at dusk, for seven days at each site. We identified trapped rats to species. We euthanized each individual captured in a live trap via CO₂ saturation. Mongoose and rat relative abundance indices were defined as the number of individuals caught relative to the total number of trap nights (1 trap night is equal to a trap set for one night) at each site or capture per unit effort (CPUE). We also estimated rat and mongoose abundances using depletion analysis for all plots (Supplemental Material B).

Coqui density, in addition to presence, may affect rat and mongoose abundances. Within each invaded plot, we estimated coqui density using the line-transect distance-sampling survey methods (Buckland et al. 2001) used by and described in Choi and Beard (2012), Kalnicky et al. (2013), and Smith et al. (2018). In summary, we placed 30 m x 30 m plots in the center of the 2.01 ha plots on the coqui side of the invasion front. Then, for one night at each site, we walked down the center of each of six 5-m wide, 30-m long transects for 30 minutes (for a total of 180 minutes per plot) and recorded all frogs at any height seen or heard and their distance from the center of the transect. Coqui densities were estimated using the distance-sampling functions in the package “unmarked” (Fiske and Chandler 2011) in R (R Core Team 2016). All distance

sampling data was modeled with null models for density using either half-normal, hazard, or exponential distributions. Akaike Information Criterion (AIC) values for the most supported detection distributions and p -values for Freeman-Tukey goodness of fit tests are provided (see Supplemental material B).

To determine the effect of coqui presence and absence on the abundance indices of small mammals, we used generalized linear mixed models (GLMM) in R (R Core Team 2016) using the “glmer” function within the “lme4” package (Bates et al. 2015). Each mammal species (e.g., mongoose, black rat, and Pacific rat) was modeled separately, assuming a Poisson distribution, with number of captures at each plot as the dependent variable offset by $\log(\text{trap nights})$ to allow interpretation of estimates as CPUE. We tested for differences in abundance using coqui presence/absence as the fixed effect, and site as a random block effect to account for the non-independence between paired trap webs at each site. We also tested correlation of coqui density estimates from coqui plots with abundance indices of rats and mongooses using Pearson’s correlation coefficient to determine the strength and significance of the relationships between each species and coqui frogs using the “cor.test” function in R.

The predation and resource competition hypotheses only include the possibility of coquis influencing invasive mammals. The alternative hypothesis regarding apparent competition includes interactions among mammalian species. We tested this competing hypothesis by running a model similar to that previously described substituting plot type (i.e., coqui presence/absence) as the independent variable with rat species CPUE in the mongoose model, mongoose CPUE in both black rat and Pacific rat models, Pacific rat CPUE in black rat model, and vice versa for the Pacific rat model. We identified top models as those with the lowest AIC

values using a $\Delta AIC < 2$ criteria. We also did a Pearson's correlation test between each of these species abundances.

Rat and mongoose diet

We removed the stomachs of the euthanized specimens collected from our trapping efforts to analyze mongoose and rat diets. We froze stomachs at -20°C for later analysis in the laboratory. After thawing, we swirled the contents of each sample for 5 min in water and a mild detergent to dissolve any stomach fluids and oils, poured the contents through a 0.4 mm sieved and preserved them in 95% ethanol (Sugihara 1997). For each sample, we performed a thorough search of the stomach contents for coqui remains, such as skin and bones, under a dissecting scope. We then used a grid of 5 mm x 5 mm squares laid under a Petri dish to inspect each sample with a dissecting scope 10-20x magnification. For stomach samples too large for Petri dishes, we gently stirred these samples for 30 seconds and took sub-samples by pouring 50% of the contents onto a grid. We recorded the food type found within each grid-square (i.e. 40 evenly spaces grid-boxes). We categorized food into seven major types: plant, arthropod, reptile, amphibian, bird, rodent and other (as in Shiels et al. 2013). We were able to distinguish between reptile and amphibian remains through skin fragments and portions of head, claws, tails, and other body parts present in the samples. We sub-categorized plant food types as fruit, seed, and other plant material (flowers, vegetative material, and unknown), and arthropods as Coleoptera, Diptera, Lepidoptera, and other arthropod material (other included Hymenoptera, Chilopoda, Odonata, Orthoptera, Gastropoda, Arachnida, and unknown arthropod material). Stomach contents placed in the "other" category were items that we could not identify. We removed

parasitic roundworms from the analysis and excluded empty stomachs and samples that contained a volume greater than 50% of roundworms or trap bait from the study.

We determined the frequency of each food type by noting the occurrence of that food type in each sample (Shiels et al. 2013). We calculated relative abundance in each sample by dividing the number of squares with a certain food type by the total number of squares covered by the contents of each stomach (Shiels et al. 2013). We compared relative abundances or percent of food types among all species, and tested for differences in the diets of each species individually between coqui plots and non-coqui plots, using the non-parametric analysis Multi-Response Permutation Procedure (MRPP), an analysis for testing for difference between two or more groups (Mielke et al. 1981) in the “vegan” package (Oksanen et al. 2017) for R. We tested for differences in diet composition among the three species using all plots. We then assessed differences in diet composition between coqui and non-coqui plots for each predator species individually. For all statistical tests in this study, we used $\alpha < 0.05$ as significant, except for diet analyses of invertebrates, where we also discuss results with $\alpha < 0.10$ because of the high degree of spatial and temporal variability observed with invertebrate data (sensu Holmes and Schultz 1988; Tuttle et al. 2009).

Coqui scavengers

To determine scavenging on coquis, from December 2015 to July 2016, the week before we began nest predation tests at each site (see below), we placed 25 dead coquis in the 2.01-ha plot on the coqui invaded side of the front. We collected these coquis from near each coqui-invaded plot, but not within plots, and euthanized them. Each dead coqui was placed on the ground or within 50 cm of the ground on varying substrates to simulate where frogs might be if

they had died naturally. Frogs were placed randomly but at least 15 m apart. We made observations of scavenging events with a motion-activated camera (Reconyx HyperFire models, Reconyx Inc., WI, USA) on each carcass positioned 1 to 2 m from the dead coqui. Cameras remained in the field for seven days. We recorded each visitation of all carcasses regardless of species. We summarized the camera trap data to determine which species were the most frequent scavengers of coquis. Species were differentiated based on known distinguishing characteristics except for black rats and Pacific rats, which were pooled because they could not be reliably distinguished. Individuals were assumed the same until they left the field of view. We could not reliably distinguish individuals from one another across multiple scavenging events.

From May to July 2017, we returned to the five sites with the greatest number of visits from scavengers (sites ER, HM, KP, MB, and WP; Fig. 1) to validate our method by characterizing differences in observations between cameras baited with a coqui carcass (treatment cameras) and cameras without a coqui as bait (control cameras). Following methods from the previous field season, we placed 21 to 24 cameras in each coqui plot, balanced between treatment and control. Because there were no coquis to be scavenged from the control cameras, the data collected here were counts of visits to the field of view of each camera that triggered the motion sensor. In addition, to capture invertebrate scavengers that would not activate the cameras' motion sensors, we placed all frog carcasses on pressure-sensitive external lever triggers that would activate cameras when a frog was removed. These were not used in the previous field season but were thought potentially to be important based on results from Abernethy et al. (2016). To test for differences in the number of visits to cameras with frogs and control cameras, we used a GLMM with camera set type (coqui or control) as a fixed effect, site

as a random effect, and the sum of visits to each camera set type for each site as the dependent variable, assuming a Poisson distribution.

Nest predation

To test whether nests are visited by predators at higher rates in sites where coqui occur, we monitored artificial nests with quail eggs in our plots (VanderWerf 2001). From December 2015 to July 2016, the week before we began trapping at each site, we placed 25 artificial nests in each of the 2.01-ha plots on both sides of the invasion front. Artificial nests were 10-cm in diameter, 3-cm deep, and constructed of weaved plant fibers. We placed nests randomly but at least 15 m apart, 0.25 m to 2.0 m from the ground, and on a variety of plant substrates, depending on the site, including crooks of branches, along horizontal branches, and within bundles of ferns. Within each nest, we placed one locally farmed quail egg. Between 1 and 2 m from each nest, we placed a motion-activated camera to identify which species depredated the egg. Each nest was monitored for seven nights. Nests were counted as depredated if the eggs were gone, removed from nest, or had received damage in any way from predators during the seven nights. We reused nests among sites after waiting at least seven days for odors that may have attracted or repelled predators to the nest to dissipate between each use (VanderWerf 2001).

We tested the effect of coqui presence on the rate that the nests were depredated and the number of predation events by rats and mongooses individually. To test coqui effect on depredation rates, we ran a GLMM in R using the “glmer” function within the “lme4” package. Using binomial distributions, we tested for differences in nest depredation using coqui presence/absence as the fixed effect and site as a random block effect. We tested the effect of coquis on the number of predation events by each predator with a similar GLMM, but assuming

a Poisson distribution of the count data and number of predation events by each predator as the dependent variable.

Results

Mongoose and rat abundance

Mongoose were caught exclusively in live traps, while rats were caught in both trap types, but most frequently (86% of the time) in snap traps. Because mongoose were only caught in Tomahawk live traps, mongoose trapping effort was 448 trap nights per plot (7 days of trapping with 64 live traps). Because rats were caught in both types of traps, we had 896 trap nights per plot (seven days of trapping with 128 traps). There were no trap nights or days in which two individuals were caught in the same trap. We compared CPUE (captures per 100 trap nights) with results from depletion modeling, but because results were not qualitatively different and showed the same patterns with coquis, we only present capture data per 100 trap-nights in the text for comparability with other studies (Puan et al. 2011; Sugihara 1997). Depletion estimate results are reported in Supplemental material B.

In total, 705 small mammals were collected across all sites: 194 mongooses, 262 black rats, and 209 Pacific rats. Seven Norway rats (*R. norvegicus*) were trapped at one site (ER), and 33 house mice (*Mus musculus*) were trapped at five sites and but not further analyzed due to low sample size and zero counts at many sites.

Among all the models run, coqui presence or absence was the top predictor of the relative abundance of mongoose and of Pacific rats. Pacific rat CPUE was the top predictor in the black rat model (Table 1). The mean predicted relative abundance estimates from the mongoose model were significantly greater for plots with coqui (2.13/100 trap nights) than

without coqui (1.64/100 trap nights; $p < 0.001$; Fig. 2) and showed a 30% greater abundance of mongooses. Mean predicted relative abundance for Pacific rats was significantly less for plots with coqui than without (1.75 vs. 2.10/100 trap nights; $p = 0.012$; Fig. 2), showing a 17% difference. Mean predicted black rat abundances were negatively correlated with Pacific rat abundance ($df = 11$, $z = -2.186$, $p = 0.028$) but were also lower in sites with coqui (1.92 vs. 2.21/100 trap nights), though this effect was not significant ($p = 0.262$; Fig. 2).

While the directions of the estimated relationships were consistent with the presence or absence results, mongoose and rat abundance indices were not significantly correlated with coqui density estimates (mongooses, $r = 0.05$, $p = 0.87$; black rats, $r = -0.25$, $p = 0.43$; Pacific rats, $r = -0.25$, $p = 0.42$; Supplemental material B).

Rat and mongoose diet

Trapping efforts yielded 194 mongoose stomach samples, of which 72 were empty and 16 contained >50% by volume intestinal parasites or bait. There was a total of 262 black rat stomachs, of which 63 were empty and 33 were >50% parasites or bait. Finally, out of 209 Pacific rat stomachs, 54 were empty and 14 contained >50% parasites or bait. In total, there were 413 stomachs (106 mongoose, 166 black rat, and 141 Pacific rat) included in analyses.

Coqui frogs were found only in stomach contents from mammals trapped in coqui plots. The frequency of stomachs from coqui plots ($n=216$) containing coquis was low for all species: five out of 69 (7.2%) mongoose stomachs, two out of 87 (2.3%) black rat stomachs, and one out of 60 (1.7%) Pacific rat stomachs. The abundance of coqui frogs relative to all stomach contents of individuals trapped in coqui plots was also low for all species: 3.7% of mongoose diet, 0.1% of black rat diet, and 1.3% of Pacific rat diet on average.

Relative abundance of each food type was calculated from stomachs of 106 mongooses, 141 Pacific rats, and 166 black rats regardless of the plot type in which they were caught. Mongoose diets contained all recorded food types, and the composition of all food types differed significantly from those of black rats and Pacific rats ($p = 0.001$; Fig. 3). When we compared black rat and Pacific rat diets, we found a higher percent of plant material in black rat stomachs ($p = 0.005$), and a higher percent of arthropods in Pacific rat stomachs ($p = 0.002$; Fig. 3). The remaining food type categories had low percentages and were not compared.

For mongoose, only the mean percent of fruit differed between coqui and non-coqui plots ($p = 0.045$), with a greater percent of fruit found in stomachs in coqui plots. Similarly, for black rats, there was a greater percent of fruit ($p = 0.003$) and other plant material ($p = 0.027$) in stomachs in coqui plots. Results also suggest a greater percent of invertebrates in rat stomachs in non-coqui than coqui plots (black rat: $p = 0.099$), most notably more caterpillars in Pacific rat diets ($p = 0.068$; Table 2).

Coqui scavengers

Of the 384 dead frogs placed in study plots, 267 (70%) were removed. Of those scavenging events, we could determine the scavenger in 228 cases (85.4%). In the remaining cases, the camera failed to capture an image of the scavenger. Average time to removal was 56 hours (SD = 36.8 hours). We observed six species scavenging coquis. Mongooses were the most frequently observed scavengers (60.5% of 228 confirmed events), followed by rats (34.2%), pigs (*Sus scrofa*, 3.1%), ants (species unidentified, 1.3%), one domestic cat (*Felis catus*, 0.4%) and one northern cardinal (*Cardinalis cardinalis*, 0.4%). In 2017, there were more images recorded

of potential scavengers at coqui carcass-baited cameras (84.2% recorded images, $n = 57$) than at unbaited control cameras (50% recorded images, $n = 58$) ($z = 2.145$, $p = 0.03$).

Nest predation

We observed 564 artificial nests for nest predation ($n = 283$ in coqui plots and 281 in non-coqui plots, Supplemental material C). In total, 40.6% of the nests were depredated; there was no difference in the percentage of nests depredated in coqui versus non-coqui plots. On average 56.7% of nests were confirmed to be depredated by rats, 28.9% by mongooses, and 14.4% were depredated by unidentified predators (cameras failed to capture an image). Neither of the nest predation rates for rats nor mongooses differed between coqui or non-coqui plots ($z = 0.754$, $p = 0.45$ and $z = 0.858$, $p = 0.39$, respectively).

Discussion

We set out to address the hypothesis originally proposed by Kraus et al. (1999) that mongoose and rats depredate coqui frogs, which in turn increases mongoose and rat abundance, and subsequently increases bird nest predation. In support of this hypothesis, we found 30% more mongoose where coquis were present on the island of Hawaii and mongoose were also the most important scavengers of coqui. In contrast, we found 17% fewer Pacific rats where coquis were present, which suggests they are not important predators of coqui, and provides support for both the apparent competition or resource competition hypotheses for coquis and rats. We found more support for the resource competition hypothesis than the apparent competition hypothesis, primarily because coquis were in the top model for Pacific rat abundance, were a better explanatory variable than mongoose, and because rat diets shifted towards more fruit and less

invertebrates in the presence of coquis. Perhaps because mongoose increased and rats decreased in abundance in the presence of coquis, we found no support for the hypothesis that coquis indirectly increase bird-nest predation rates.

Where coqui frogs occur, we found, on average, 30% more mongooses than in areas without frogs. Other studies have shown the importance of interactions between frogs and mongooses by showing that frog species decline where mongooses invade (Barbour 1930; Barun et al. 2010; Gorman 1975; Watari et al. 2008). We are not aware of other studies showing that frogs increase mongoose abundance, although we might expect this relationship more frequently at the beginning of an invasion or at an invasion front (Simberloff and Gibbons 2004). In our study, mongooses were the most common predators and scavengers of coquis. While direct predation likely contributed to the increased abundance of mongooses we observed, the relative abundance (4%) and frequency (7%) of coquis in the stomachs we investigated from coqui plots seems low to explain the increase entirely.

Previous research in Hawaii has shown an individual mongoose can consume a high number of coquis (remains of 15 frogs in one stomach) (Beard and Pitt 2006). We did not find that to be the case in our study; rather we found at most four frogs in one mongoose stomach. We offer several potential explanations for this pattern. First, perhaps mongoose consumed more coquis than we observed, but they were digested quickly. Second, mongoose may only opportunistically consume coquis, such as at particular times of year or life stages (Barun et al. 2010; Yamada 2002) that were not captured in our sampling. Finally, our results could reflect that coquis indirectly increase mongooses, such as by altering available forage (e.g. by increasing non-native fruit as discussed below; Sin et al. 2008).

In general, we found both rat species had lower indices of relative abundance in coqui than in non-coqui plots, but only Pacific rats were significantly lower, on average by 17%. A possible explanation for this pattern is apparent competition between coquis and rats, or more specifically, that greater mongoose abundance in coqui plots resulted in greater mongoose predation on rats or rat avoidance of coqui plots (Barnum 1930; Barun et al. 2011; Doty 1945; Pimentel 1955; Seaman and Randall 1962; Walker 1945). We expected greater potential for apparent competition with the less-arboreal Pacific rats because they are more likely to interact with mongooses (Pimentel 1955; Shiels 2010; Walker 1945). Our results support this because Pacific rat abundances were lower in coqui plots. Further, we found that rodents made up 27% of mongoose diets. However, the top models for predicting either rat species' relative abundance did not include mongoose. Therefore, while apparent competition may play a role in reducing rats where coquis are present, it is likely not the only factor.

We expected that coquis may compete with less-arboreal Pacific rat, in particular, for invertebrate prey. Coquis are, after all, insectivores, and most directly impact and reduce leaf litter invertebrates (Beard 2007; Choi and Beard 2012). In support of the resource competition hypothesis, coquis were in the top model and were a better explanatory variable of Pacific rat abundance than mongooses. Further, Pacific rats consumed more arthropods than black rats in our study, so we would expect to observe a greater reduction in Pacific than black rats if competition for invertebrates was important. Finally, we found a greater relative abundance of arthropods (in general or some type) in rat diets from non-coqui plots than coqui plots. Therefore, competition for invertebrate resources appears to be another, at least partial, explanation for the lower Pacific rat abundance in coqui plots.

There seems to be a dietary shift for mongooses and rats across the coqui invasion front, in which both mongooses and black rats, in particular, were consuming more fruit in areas with frogs compared to areas without frogs. Previous research suggests that the growth rate of strawberry guava, *Psidium cattleianum*, in particular, a dominant non-native plant in many of these sites, is greater in areas with coqui frogs (Sin et al. 2008). We did not measure the number of fruits produced per plot, but future research should determine if fruit availability differs between coqui and non-coqui plots. Our results are consistent with greater frugivory by mongooses and rats in areas invaded by coqui than in areas not invaded.

Our study shows that other invasive species, most frequently mongooses, scavenge on coquis. Abernethy et al. (2016) found that vertebrates scavenge 22% of the frogs placed in the field, while we found vertebrates scavenge them 84% of the time. This difference may be due to the fact that coquis were not established in the native-dominated sites used by Abernethy et al. (2016) and the fauna present were not conditioned to search for such small-bodied amphibians. We also observed a much lower rate of frogs removed by invertebrates. Abernethy et al. (2016) observed 78% of frog carcasses removed by invertebrates. The only invertebrates we observed scavenging frogs were ants, 6.3% of the time (invertebrates were only evaluated in 2017 field season, but 86% of our predation events were accounted for in the 2016 field season). Our results suggest that in non-native dominated sites with established coqui populations, vertebrates are more important scavengers than invertebrates, and that they consume a high percentage of dead coqui frogs if they are readily available.

Even though we found differences in the abundance of mongooses and rats where coquis occur, we were unable to detect any difference in the percent of depredated artificial nests for mongoose or rats in coqui invaded and uninvaded areas. We observed a greater number of rats

(56.7%) depredating nests compared to mongooses (28.9%), which was expected because we placed nests 0.25-2 m off the ground, and black rats, in particular, are more arboreal than mongooses (Shiels 2010). However, of note, we frequently observed mongooses climbing to remove eggs from relatively high nests; 64% of the nests that mongooses depredated were between 0.75 m and 1.75 m (Supplemental material C). Studies have found that rat control can increase nest success for native birds; we can infer that areas with less rats would have lower nest predation (VanderWerf 2001; VanderWerf and Smith 2002). However, because coquis were associated with increased mongoose abundance, decreased Pacific rat abundance, and no difference in black rat abundance, we might expect a similar risk of nest depredation in both coqui invaded and uninvaded areas.

We were simultaneously studying the effects of coquis on predators with differing life histories. Our methods may have been adequate to capture the data we wanted for one species while failing to do so for another. For example, the size of our plots remained constant despite the difference in home ranges between mongooses and rats (Lindsey et al. 1999; Pitt et al. 2015). A study on the effects of coquis on mongoose maybe should accommodate the large home ranges (8.6 to 70.2 ha) of mongooses (Pitt et al. 2015). Also, most empirical evidence suggests that mongooses are a larger threat to ground foraging and nesting birds (Hoshide et al. 1990; Morley and Winder 2013) while rats can depredate nests higher in the canopy (Shiels 2010; VanderWerf 2001; VanderWerf and Smith 2002). Future studies focused solely on mongooses or rats may capture more robust data on the target species.

Our results suggest that either: 1) coquis are either directly or indirectly influencing the abundance and dietary behavior of mongooses and rats, or 2) mongooses and rats are responding to some other factor, independent of coquis, that varies between coqui and non-coqui plots. The

similarities in vegetation structure across the invasion fronts as assessed by the current and past studies suggests that vegetation structure and composition did not drive the differences we found in mammal abundance and diets across the fronts (Choi and Beard 2012; Smith et al. 2018). While we cannot rule out that some other factor contributed to the differences we found, we think our study design is adequate to test relationships between coquis and mammals, and to develop hypotheses that can be tested using more targeted experimental designs.

In conclusion, the results of our research partially support the hypothesis proposed by Kraus et al. (1999) that coquis may increase populations of invasive small mammals in Hawaii. The presence of coquis is associated with greater mongoose abundance, probably through direct consumption of a novel prey. The association of increased mongoose abundances in areas with coqui frogs should concern managers interested in conserving or restoring birds that mongooses negatively affect. On the other hand, rat abundances seem to be lower in coqui-invaded plots, possibly through both competition for resources and apparent competition. With the ever-growing likelihood of future introductions of invasive species to Hawaii, coquis could facilitate the successful establishment of other invasive predators. We recommend that managers continue to monitor and prevent coqui movement across the island of Hawaii and to other locations, such as Kauai and Oahu, which presently have no coquis.

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Author Contributions

Conceived and designed the research: Karen Beard and Aaron Shiels. Performed the research: Shane Hill. Analyzed the data: Shane Hill and Shane Siers. Wrote the paper: Shane Hill and Karen Beard. Helped revise the paper: all authors.

Compliance with ethical standards

Conflict of interest

The authors have declared that no competing interests exist.

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Fig 1. Twelve study sites on the island of Hawaii. Each site was comprised of paired study plots on either side of the coqui invasion front. Site abbreviations are Eden Roc (ER), Fern Forest (FF), Hamakua FR (HM), Kaupukuea Homestead (KH), Kalopa (KP), Manuka A (MA), Manuka B (MB), Stainback (SB), Upper Stainback (US), Saddle Road (SR), Volcano (VC), Waipio (WP).

Fig. 2 Mean relative abundance indices (individuals/100 trap nights) with standard error bars for small mammals across 12 coqui and non-coqui sites. Significance based on GLMMs: * $p < 0.05$

Fig. 3 Mean percent (%) of major food types found in the stomachs of mongooses, black rats, and Pacific rats compared by plot type. Differences in percent of coqui in stomach contents between coqui plots and non-coqui plots were statistically non-significant for all three species. C=coqui plots N=non-coqui plots. *n does not include empty stomachs

Table 1 Generalized linear mixed models testing the importance of other species as an explanatory variable in the capture per unit effort models of mongoose, black rats and Pacific rats. Akaike Information Criteria (AIC), model weights, logLik, deviance, *p*-values, and model estimates are provided. * Indicates top model(s) for each predator species based on $\Delta AIC < 2$ criteria.

Model	DOF	AIC	ΔAIC	weight	logLik	deviance	<i>p</i> -value	estimate
mongoose ~ coqui*	3	148	0	0.976	-71	142	< 0.001	0.48
mongoose ~ Pacific rat	3	156	7	0.016	-75	150	0.095	
mongoose ~ black rat	3	158	10	0.007	-76	152	0.261	
black rat ~ Pacific rat*	3	198	0	0.716	-96	192	0.029	-0.32
black rat ~ mongoose	3	200	2	0.181	-97	195	0.127	
black rat ~ coqui	3	202	4	0.103	-98	196	0.262	
Pacific rat ~ coqui*	3	148	0	0.812	-71	142	0.012	-0.35
Pacific rat ~ black rat	3	152	4	0.096	-73	146	0.159	
Pacific rat ~ mongoose	3	152	4	0.092	-73	146	0.169	

Table 2 Comparison of mean percent (%) $\pm$ 1 SE food types identified in stomachs of predators between coqui and non-coqui plots. n = the number of stomachs from up to 12 sites. *p*-values indicate significance from Multi-Response Permutation Procedure tests comparing food type between plots for each predator. *p*-values are not given for food type categories that were zero for one of the plot types. * $p < 0.05$; † $p < 0.10$

Food type	Mongoose			Black rat			Pacific rat		
	Coqui plots (n=69)	Non-coqui plots (n=37)	<i>p</i> - value	Coqui plots (n=79)	Non-coqui plots (n=60)	<i>p</i> - value	Coqui plots (n=87)	Non-coqui plots (n=79)	<i>p</i> - value
Coqui	3.7 $\pm$ 1.9	0	-	0.1 $\pm$ 0.1	0	-	1.3 $\pm$ 1.3	0	-
Plant	22.9 $\pm$ 7.3	14.5 $\pm$ 7	0.128	87.8 $\pm$ 9.2	77.9 $\pm$ 11.8	0.059†	77.7 $\pm$ 9.5	65.1 $\pm$ 9.8	0.070†
Fruit	9.8 $\pm$ 3	1.3 $\pm$ 0.8	0.045*	72.3 $\pm$ 4.5	51 $\pm$ 5.3	0.003*	66.2 $\pm$ 5.7	51.2 $\pm$ 5.3	0.054†
Seed	1.3 $\pm$ 1.2	1.1 $\pm$ 1.1	1.000	6.6 $\pm$ 2.1	6.5 $\pm$ 2.4	0.857	0.6 $\pm$ 0.3	3.4 $\pm$ 1.6	0.105
Other plant material	11.8 $\pm$ 3.1	12.1 $\pm$ 5.1	0.580	8.9 $\pm$ 2.6	20.4 $\pm$ 4.1	0.027*	10.9 $\pm$ 3.5	10.5 $\pm$ 2.9	0.926
Arthropod	22.5 $\pm$ 9.5	20.2 $\pm$ 10.7	0.537	9.9 $\pm$ 3.8	17.4 $\pm$ 5.4	0.099†	20.2 $\pm$ 7.6	31 $\pm$ 8.2	0.112
Caterpillars	5.0 $\pm$ 2.5	5.3 $\pm$ 2.8	0.527	5.8 $\pm$ 1.9	10.5 $\pm$ 2.8	0.222	5.6 $\pm$ 2.4	13.7 $\pm$ 3.3	0.068†
Coleopteran	4.6 $\pm$ 2.2	0.7 $\pm$ 0.7	0.173	0	0	-	0.2 $\pm$ 0.1	0	-
Dipteran	3.4 $\pm$ 1.7	4.8 $\pm$ 3.3	0.758	0	0	-	1.3 $\pm$ 1.3	1.2 $\pm$ 1.2	1.000
Other arthropod	9.5 $\pm$ 3.1	9.4 $\pm$ 3.9	0.866	4.1 $\pm$ 1.9	6.9 $\pm$ 2.6	0.368	13.1 $\pm$ 3.8	16.1 $\pm$ 3.7	0.641
Bird	1.5 $\pm$ 1.5	0.9 $\pm$ 0.9	1.000	0.4 $\pm$ 0.4	0	-	0	0.1 $\pm$ 0.1	-
Lizard	10.5 $\pm$ 3.2	15 $\pm$ 5.2	0.548	0	0.1 $\pm$ 0.1	-	0	0.1 $\pm$ 0.1	-
Rodent	24.9 $\pm$ 4.9	32 $\pm$ 7.6	0.446	0	0	-	0.6 $\pm$ 0.6	0	-
Other	13.8 $\pm$ 3.7	18.5 $\pm$ 6.1	0.566	2.2 $\pm$ 1.0	4.3 $\pm$ 2.2	0.371	0.2 $\pm$ 0.2	3.3 $\pm$ 1.6	0.123