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Relationships Among Invasive Coqui Frogs, the Small Indian Mongoose and Rat Species in Hawaii

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RELATIONSHIPS AMONG INVASIVE COQUI FROGS, THE SMALL INDIAN MONGOOSE AND RAT SPECIES IN HAWAII

by

Shane A. Hill

A thesis submitted in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

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Logan, Utah

2018
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ABSTRACT

Relationships among Invasive Coqui Frogs, the Small Indian Mongoose and Rat Species in Hawaii

by

Shane A. Hill, Master of Science
Utah State University, 2018

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

With the increasing rate of species being introduced to areas outside of their native ranges, it is likely that non-natives interact in ways that influence each other’s population sizes. Rats (*Rattus* spp.) and mongooses (*Herpestes auropunctatus*) have been introduced to islands throughout the world where they impact native species. The coqui frog (*Eleutherodactylus coqui*) was introduced to Hawaii in the 1980’s, where rats and mongooses were already established. It has been hypothesized that the high densities of coqui frogs on Hawaii could increase mongoose and rat populations, and in turn increase bird nest predation rates.

We compared the relative abundances of rats and mongoose at 12 sites that had plots invaded and uninvaded by coqui frogs across the island of Hawaii. We also investigated at these 12 sites whether coquis influenced the rate at which mongooses and rats depredate bird nests using camera traps on artificial nests. We interpret our results considering mongoose and rat stomach analyses and camera trap data collected to
monitor coqui scavengers.

Our data showed that coqui presence was associated with 30% greater mongoose abundance and 17% less Pacific rat (*Rattus exulans*) abundance, possibly through apparent competition with coquis. Based on our diet analyses and scavenging data, both mongooses and rats consume coquis, but mongooses were more important consumers of dead coquis than other species. There were differences in mongoose and rat diets observed in plots with and without coquis. We speculate that coquis may be competing with rats for invertebrate prey due to the greater amount of fruit found in rat stomachs collected in coqui-invaded compared to uninvaded plots. Despite differences in the abundance of mongooses and rats in coqui invaded and uninvaded plots, we did not observe any difference in nest predation rates. Rats were the primary nest predators, depredating 57% of the artificial nests, while mongooses depredated 29% of the nests. Our results show that non-native amphibians may serve as novel prey and/or competitors to non-native mammals; differences at paired sites across invasion fronts with and without coqui suggest that coqui invasion may result in an increase or decrease non-native mammal populations.
Non-native species are increasing globally, and with this increase, it is likely that there will be new, unique relationships found among non-natives as well as additional impacts on native species. Rats and mongooses have been introduced to islands throughout the world where they impact native species, including birds, reptiles, and amphibians. The coqui frog was introduced to Hawaii in the 1980’s, where there were already abundant rat and mongoose populations. Previous research suggests that the high densities of coqui frogs may provide enough of a new food source for mongooses and rats that their populations would grow larger than they would without coqui frogs, and that this would exacerbate the negative effects that these predators have on native birds.

We investigated whether there are relationships between coqui presence, and the local abundance of introduced rats and mongoose on the island of Hawaii. We also investigated at these 12 sites whether there were indirect effects of coquis on bird nest predation rates using camera traps on artificial nests. Finally, we interpret our results in light of an analysis of the stomach contents of mongooses and rats, and data collected from remote cameras monitoring scavengers of dead coqui frogs.

We compared abundances of mammals in coqui invaded plots and uninvaded plots. In areas where coquis were present, we found a greater number of mongooses, and less Pacific rats. Both predators consume coquis, but mongooses were more important
consumers of live and dead coquis. Shifts in mongoose and rat diets were observed in coqui invaded and uninvaded plots. It may be that coqui frogs are competing with rats because we found more fruit in rat stomachs collected in coqui invaded compared to uninvaded plots. We did not observe any difference in nest predation rates with and without coquis. Our results show that the coqui may serve as novel prey and/or competitors to non-native mammals.
I would like to thank Dr. Karen Beard for the opportunity she has provided for me and my family to learn and experience so much that we would not have been able to otherwise. I thank her for her patience and guidance throughout this whole process. I would also like to thank my committee members: Dr. Julie Young for thoughtful and helpful insight on the writing of my thesis; Dr. Shane Siers for guidance and encouragement both in the field and at the computer to perform this research in the proper way; and Dr. Aaron Shiels for taking time out of his own work to allow me to learn proper data collection techniques from him in person. Thank you to Susan Durham for an enormous amount of help with statistical analyses.

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I give special thanks to my wife MarLyn Hill, who has undoubtedly sacrificed a lot in allowing me to pursue this degree and a profession in wildlife biology. No better support than that which you provide exists. I thank my children Taegan, Daphne, and
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Shane A. Hill
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CHAPTER 1
INTRODUCTION

The rate of biotic invasions has increased on a global scale due to rising trade worldwide (di Castri 1989). Additionally, invasions may begin to occur more rapidly and frequently as the global climate changes (Dukes and Mooney 1999; Hellman et al. 2008). These invasions are a significant threat to conservation (Wilcove et al. 1998; Bellard et al. 2016). As non-native species spread, they have the potential to affect ecosystems in their new ranges through predation (Fritts and Rodda 1998; Jones et al. 2008), competition (Mooney and Cleland 2001; Petren and Case 1996), and by altering fundamental properties of the ecosystem, such as nutrient cycle and plant productivity (Vitousek 1990; van der Putten et al. 2007; Sin et al. 2008; Weidenhamer and Callaway 2010).

Historically, the main negative effect of non-native fauna on islands is as novel predators and pathogens as opposed to novel competitors (Sax et al. 2002; Davis 2003), 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 ways that are difficult to predict (Simberloff and Von Holle 1999). Considering the growing number of non-natives and their potential for complex interactions, perhaps it is not surprising that there is also growing evidence that non-native species can serve as important prey for non-native predators (Gangoso et al. 2006; Rodriguez 2006; Beckmann and Shine 2011; Abernethy et al. 2016). Further, if predation or scavenging on non-native prey by non-native predators increases predator
populations, this can reduce the abundance or even cause extirpation of other prey species, a process termed “apparent competition” (Holt 1977). More specifically, apparent competition occurs when the abundance of one prey species increases the likelihood that another prey species is depredated by a shared predator, causing the appearance of competition between the two prey species. While these types of interactions would be most noteworthy if they negatively affect native species, these effects could also occur among non-native species in novel foodwebs. These types of complex interactions among non-natives, sometimes termed ‘invasional meltdowns’ (*sensu* Simberloff and Von Holle 1999), are just starting to be appreciated (O’Dowd et al. 2003; Green et al. 2011; O’Loughlin and Green 2017).

A well-known system that has experienced many invasions and the consequences associated with them is the Hawaiian Islands (Vitousek et al. 1987; Loope and Mueller-Dombois 1989; Wilcove et al. 1998; Lowe et al. 2000). There has been a large number of species introduced and established to the island chain, both intentionally and unintentionally (Moulton and Pimm 1986; Kraus 2003). Because there are no native ground-dwelling mammals, reptiles, or amphibians in Hawaii, the threat that invasive species pose is mostly limited to the native birds (Atkinson 1977; Hoshide et al. 1990; Reed et al. 2012), invertebrates (Hadfield et al. 1993; Choi and Beard 2012), and plants (Sugihara 1997; Sin et al. 2008; Shiels 2010; Weller et al. 2018).

One such introduction of an invasive species to Hawaii is that of the 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 coqui frog has become particularly widespread on the island of Hawaii, while
the remaining Hawaiian Islands have had more success controlling and preventing establishment (Beard et al. 2009). Previous studies have found that coqui frogs have both social impacts, including impacts on the economy and quality of life (Kraus and Campbell III 2002; Kaiser and Burnett 2006; Kalnicky et al. 2014), and ecological impacts through their interactions with other species (Tuttle et al. 2009; Choi and Beard 2012; Bernard and Mautz 2016; Smith et al. 2018).

Although previous research has determined some ecological consequences of the invasion and explored interactions between coquis and other species as described above, questions remain regarding interactions between coquis and invasive small mammals, in particular. The introduction of coquis to the island of Hawaii is recent relative to that of invasive mongoose (*Herpestes auropunctatus*) and rats (*Rattus* spp.) (Doty 1945; Baldwin et al. 1952; Kraus et al. 1999). When coquis arrived and established, they became potential prey to these predatory species already on the island. The introduction of coquis as novel prey could change the roles that mongooses and rats have within the Hawaiian food web. For example, coquis may increase rat and mongoose densities and therefore exacerbate the predation effects of both rats and mongooses 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 (Holt 1977). For example, if the presence of coquis causes an increase in mongooses, then there may be increased predation on rats by mongooses where coquis occur, eventually leading to a decrease in rats in those areas. Finally, coquis may directly compete with rats because both are nocturnal and insectivorous (Shiels et al. 2013; Wallis et al. 2016).
The purpose of this study was to investigate the trophic interactions among coquis, mongooses, and rats, and their abundances on the island of Hawaii. We tested the hypothesis that coquis are increasing the abundances of mongooses and rats through direct predation and therefore increasing nest predation rates in areas invaded by coqui frogs. We conducted this study at 12 sites across the island where the coqui has invaded and where there are neighboring areas where the coqui has not invaded, but that have similar vegetation and other habitat characteristics (Choi and Beard 2012; Smith et al. 2018).

More specifically, the three main objectives of this study were as follows: 1) to compare mongoose and rat abundances between coqui-invaded and non-invaded plots to determine if their population sizes differ in the presence or absence of coquis, or with coqui density; 2) to determine whether mongooses and rats consume coquis and how important of a prey item coquis are in their diets; and 3) to determine differences in potential predation rates on bird nests by mongooses and rats in the presence versus absence of coquis. Chapter 2 includes a more thorough literature review. The methods and results of our work are found in Chapters 3 and 4, respectively. Chapter 5 includes a discussion of the results. Finally, chapter 6 summarizes the implications of this research, future direction, and our conclusions.
Hawaiian Invasions

The effects of invasive species on isolated islands can be particularly pronounced due to the limited geographic range of islands, and some native species being unable to escape predation pressure of invasives to which they are not adapted (Case and Bolger 1991; Dickman et al. 1996; Fritts and Rodda 1998). Because the Hawaiian archipelago is so remote, it is characterized, as isolated islands tend to be, by high rates of endemism (Ziegler 2002) and as a global hotspot for biodiversity (Mlot 1995; Myers et al. 2000). But, unfortunately, the Hawaiian Islands are also well known for their extremely high number and abundance of non-native species (Moulton and Pimm 1986). There has been a near doubling of the number of plant species, an even greater increase in freshwater fish, and whole new taxa introduced, such as ground-dwelling mammals and terrestrial reptiles and amphibians, that did not naturally occur on these islands (Eldridge and Miller 1995; Sax and Gaines 2003). It is not surprising then that in many parts of Hawaii, complex interactions among native and non-native species are being observed (Loope and Mueller-Dombois 1989; Simberloff and Von Holle 1999). Hawaii’s combined factors of isolation, endemism, and number of invasions make it prone and less resistant to ecological disturbances and extinctions (Loope and Mueller-Dombois 1989). Hawaii’s sensitivity to disturbance and invasion is illustrated by the large number of species already affected; it has been estimated that approximately 80% of native Hawaiian birds have gone extinct (Pimm et al. 1994).
Mammalian Predators in Hawaii

While there are no native ground-dwelling mammals in Hawaii, invasive mammals are widespread, including the small Indian mongoose (*Herpestes auropunctatus*). The small Indian mongoose, native to the Middle East and southern Asia, is now a widespread pest due to intentional introductions to many islands in the Pacific Ocean (Gorman 1975; Yamada 2002), the Caribbean (Pimentel 1955) and Adriatic Seas (Barun et al. 2011b), and continental South America (Nellis and Small 1983). Mongooses were introduced to most of these areas in an effort to control rats in agricultural fields (Espeut 1882), as was the case for its introduction to the Hawaiian Islands in 1883 (Doty 1945; Baldwin et al. 1952). Studies have found that mongooses tend to have an initial effect on the densities and behavior of rats (Pemberton 1925; Barnum 1930; Doty 1945; Walker 1945; Seaman 1952; Pimentel 1955; Barun et al. 2011b). However, rats are still considered abundant pests where mongooses are established, and mongooses have now become a significant pest as well (Seaman and Randall 1962; Hays and Conant 2007). Research investigating whether mongooses effectively reduce rat abundance is equivocal (Pemberton 1925; Barnum 1930; Doty 1945; Seaman 1952; Baldwin et al. 1952); however, it is more likely that mongoose reduce less arboreal rat species (Walker 1945; Pimentel 1955).

The mongoose has been introduced to at least 64 islands around the world (Barun et al. 2011a) and has contributed to the decline and extirpation of many native and endemic species of amphibians, birds, mammals, and reptiles (Baldwin et al. 1952; Pimentel 1955; Seaman and Randall 1962; Nellis and Everard 1983; Yamada 2002). For example, the relative abundance of native amphibians in Croatia on mongoose-invaded
islands were lower compared to mongoose-free islands (Barun et al. 2010). Also, the Smoky jungle frog (*Leptodactylus pentadactylus*) was extirpated from among the Lesser Antilles islands with mongooses, while they persisted on islands without mongooses (Barbour 1930). For the most part, mongooses have been shown to reduce birds that nest on the ground through nest depredation (Baldwin et al. 1952); past research has not shown much threat to birds that nest higher in the canopy (Morley and Winder 2013). In Hawaii, mongooses have been shown to affect populations of the Hawaiian goose (*Branta sandvicensis*) mainly through nest predation (Hoshide et al. 1990). Kauai has a more successful breeding population of Hawaiian geese than populations on other the other islands, which may be due to the failure of the mongoose to establish on that island (U.S. Fish and Wildlife Service 2004; Duffy et al. 2015).

Three species of rat are found in Hawaii: black rats (*Rattus rattus*), Pacific rats (*Rattus exulans*), and Norway rats (*Rattus norvegicus*). Each of these rat species were unintentional introductions to Hawaii, starting with the Pacific rat around 800 years ago followed by the black rat and Norway rat, which arrived with the Europeans in 1778. These rats are now widespread and are considered noxious pests (Atkinson 1977; Scott et al. 1988; Amarasekare 1993). Rats, most notably the black rat, are abundant omnivores, and have been shown to negatively affect native birds through nest predation (Atkinson 1977; Amarasekare 1993; VanderWerf and Smith 2002; Caut et al. 2008). Control of rats on O’ahu has been shown to decrease predation on ‘Elepaio (*Chasiempis sandwichensis ibidis*) nests (VanderWerf 2001; VanderWerf and Smith 2002). Little research has been conducted regarding the predation effects of rats on taxa other than birds; reptiles and amphibians are uncommonly found in diet studies of rats. A diet study in Hawaii did not
find any frogs in the diets of rats, despite the large densities of coqui frogs in the areas in which the rats were captured (Beard and Pitt 2006). However, other studies have shown that rats do tend to have an influence on reptile populations. For example, one such study observed rats negatively affecting lizard assemblages in New Zealand (Towns 1991). Furthermore, another study found an increase in Antiguan racer (*Alsophis antiquae*) populations on Great Bird Island, which doubled within 18 months after the eradication of rats (Daltry 2006).

Eradication attempts of both mongooses and rats have been most effective on small islands (Nellis and Everard 1983; Keitt et al. 2015). Very few attempts at eradication of mongooses have been successful, but over 580 islands have had rats successfully eradicated (Keitt et al. 2015). The primary methods of control include live trapping for mongooses (Barun et al. 2011a) and bait stations or kill traps for rats. Eradication of rats is attempted through aerial broadcasting of rodenticide bait (Howald et al. 2007). While resources that would lead to effective control of mongoose and rat populations on a large scale in Hawaii are not being allocated, the U.S. Department of Agriculture and others have conducted research investigating the efficacy of trapping and baiting methods on the Hawaiian Island (Tobin et al. 1997; Pitt et al. 2015; Spurr et al. 2015).

**Coqui Frogs in Hawaii**

The Hawaiian Islands also have no native reptiles or amphibians (except sea turtles); however, 31 non-native reptiles and amphibians have been introduced both intentionally, as biocontrol for agricultural pests, and accidentally, as stowaways in cargo and nursery plants, and through the pet trade (Kraus 2009). The coqui frog
(Eleutherodactylus coqui) was introduced accidentally to Hawaii in the late 1980’s via the nursery trade and has become a successful invader (Kraus et al. 1999). In its home range of Puerto Rico, this frog is well known and beloved by locals, but in Hawaii, it is considered a nuisance because of its loud two-note mating (“cō-kee”) call (90 decibels at 0.5 m), from which its name is derived (Dodd 2013). Coquis have been found to reach extremely high densities in Hawaii, up to 91,000 frogs/ha (Beard et al. 2008), which surpasses its known native range density (estimated to be around 20,570 frog/ha) (Stewart and Woolbright 1996).

A study of the economic effects of coqui frogs in Hawaii showed a $7.6 million reduction to property values island-wide directly related to the noise pollution produced by coqui frogs (Kaiser and Burnett 2006). Furthermore, nursery owners have had to pay to treat exported plants and have experienced loss of sales because frogs are often spread by transporting nursery plants (Kraus and Campbell III 2002). Funds for control efforts of coquis [exceeding $4 million in 2007 ((HISC) 2007)] are mostly procured by federal and state agencies (Pimentel et al. 2005; Loope and Kraus 2009), adding to the private economic cost of coqui frogs in Hawaii. Moreover, private landowners and volunteers have invested a great deal of financial resources and time towards the control of coquis (Kalnicky et al. 2014). While there are no state or federal efforts to control coquis on the Island of Hawaii, many private home owners actively control coqui on their property.

Studies of the ecological impact of the coqui have revealed that coqui frogs have changed invertebrate communities through direct predation of leaf litter insects and has increased other invertebrates that likely consume their carrion or fecal matter (Tuttle et al. 2009; Choi and Beard 2012; Kalnicky et al. 2013). Coquis also appear to have affected
the abundance of some birds on the island of Hawaii, specifically they are associated with increases in non-native predatory bird species that may utilize them as a prey source (Smith et al. 2018). Because coquis are insectivorous and can reach such high densities, there is also a possibility of competition between coquis and the only bat species found in Hawaii, the insectivorous hoary bat (*Lasiurus cinereus semotus*) (Bernard and Mautz 2016). Finally, coquis have been shown to alter ecosystems in a fundamental way by increasing the rate of nitrogen and phosphorous cycling in a way that favors non-native plants (Sin et al. 2008). It is thought that their high abundance and biomass might make coquis an important source of nutrients and energy as prey and carrion for other non-native consumers in Hawaii (Abernethy et al. 2016). Given that coquis have been shown to be a detriment to some aspects of society and capable of changing the ecology of Hawaii, it is worth investigating other impacts they may have on Hawaiian wildlife communities (Fig. 1).

In their native range of Puerto Rico, coquis are known to be prey for a variety of invertebrate and vertebrate species suggesting that species do not require any special adaptations to consume them. Species that are known to consume frogs include arachnids, centipedes, crabs, hawks, song birds, cats, mongooses and rats (Reagan and Waide 1996). It is likely that they are consumed by a similar suite of species in their non-native range of Hawaii.

It has been hypothesized that coquis may serve as novel prey for non-native mammals in Hawaii (Kraus et al. 1999; Beard and Pitt 2005, 2006); however, prior to this study, this hypothesis had not been thoroughly tested. It remains unknown whether coquis make up a large portion of mongooses and rats diets, and whether coquis increase
or decrease mongoose or rat populations where they invade. A recent study on the island of Hawaii documented scavenging of coqui frogs by non-native mammals in three native habitat types (Abernethy et al. 2016). This study found that coqui carcasses were removed by mongooses 12.5% of the time and rats 7.3% of the time, indicating that the high density of coqui may produce enough necromass to provide an important resource for these invasive predators. Further, it has been hypothesized that if coquis increase mongoose and rat populations they may influence bird-nest predation rates, thereby potentially negatively affecting native birds indirectly through apparent competition (Kraus et al. 1999).

**Fig. 1** Web of possible direct interactions of coqui frogs within Hawaiian ecosystems. Citations marked with (*) refer to hypothesized effects of coqui and the focus of this study. (1 Kraus et al. 1999; 2 Beard and Pitt 2005; 3 Baldwin et al. 1952; 4 VanderWerf 2001, 2002; 5 Choi and Beard 2012; 6 Smith and Beard 2018; 7 Beard et al. 2002; 8 Sin et al. 2008; 9 Vitousek et al. 1987; 10 Walker 1945; Pimentel 1955).
Study Sites

We conducted research at 12 sites on the island of Hawaii in areas with ‘coqui invasion fronts’ (Fig. 2). Coqui invasion fronts are defined as the edge of established coqui populations, and where habitat in close proximity and 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. 2) 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 coqui invasion front had moved. These are the only known locations on the island where there is sufficient area on either side of the invasion front to conduct our research and where habitat has been determined previously to be similar on both sides of the front (Choi and Beard 2012; Smith et al. 2018).
Fig 2. 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).

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 invasion front had a mean distance of 1163 m (range: 297 to 2954 m) between them. We wanted plots to be close to each other to maintain similar habitats on either side of the front (Fig. 3), but not so close that many individual mammals would be moving between them. 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 some sites were adjusted, we tested for differences in habitat across coqui and non-coqui plots by measuring the following variables in both plots of each site: elevation, canopy cover, vegetated ground cover, percent understory density, and determination of the dominant canopy and dominant understory species (explained in further detail in Appendix A). For each variable, we tested for differences in habitat across coqui and non-coqui plots using a one-way analysis of variance (ANOVA) test with site as a block. We detected no differences in these variables across coqui and non-coqui plots (Table A-2). It should be noted that 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 potential sites from their analysis that were sufficiently different in terms of habitat
variables, such that differences across the front might not be attributed primarily to coquis (Choi 2011).

Further, 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.

Mongoose and Rat Abundance

To test whether the abundance of non-native mammals is related to coqui frog presence or absence (Objective 1), 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 (Fig. 4). We baited live traps with uncooked Hillshire Farms 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. Trapped rats were identified to species (black rat or Pacific rat). We euthanized each individual captured in
a live trap via CO₂ saturation. Because traps were check twice a day, we were able to reset the 5-10% of traps that had sprung each trap night.

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 (Appendix 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). We set up 30 m x 30 m plots placed 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. It should be noted that this method was used to develop a relative coqui density among sites, and not necessarily a precise estimate of coqui density, which may be better attained using longer term, mark-recapture techniques, such as those used in Beard et al. (2008) and Woolbright et al. (2006). 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 model weights for the most supported detection distributions and p-values for Freeman-Tukey goodness of fit tests are provided (see Table B-2 for Results). For this and all other tests, we establish statistical significance at $\alpha = 0.05$.

To determine the effect of coqui presence and absence on the abundance indices of small mammal predators, 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 predator species (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 the log(trap nights) (to allow interpretation of estimates as CPUE), coqui presence or absence as the fixed effect, and site as a random effect to account for the non-independence between paired trap webs at each site. We also tested correlation of coqui density estimates 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.

A competing hypothesis to the coqui effect on mongoose and rat abundances includes the pairwise interaction among the three mammalian predators (mongoose, black rats and Pacific rats) influencing their abundances. We tested this competing hypothesis by running a similar model 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 then compared the models AIC values to determine the top model for each predator species.

**Rat and Mongoose Diet**

To address Objective 2, the analysis of mongoose and rat diets, we removed the stomachs of the euthanized specimens collected from our trapping efforts. We froze the stomachs at -20° C for later analysis in the laboratory. We thawed each sample and removed stomach contents. We swirled the contents of each sample for 5 min in water and a mild detergent (Joy® brand) 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, which included 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 at 10-20x magnification. Some stomachs were too big for the Petri dish, we gently stirred these samples for 30 seconds and took sub-samples by pouring 50% of the contents onto 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 and relative abundance of each food type using a
method similar to Shiels et al. (2013). We determined the frequency of each food type by
noting the occurrence of that food type in each sample. 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.

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. First, we tested
for differences in groups defined by species and then for differences in groups of the
same species separated by the plot type in which they were found. We tested for
differences in diets using multiple iterations of the analysis, one including all food types
or the total composition of their diets, and one for each food type sub-group.

**Coqui Scavengers**

To further address Objective 2, we sought to observe actual scavenging of 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 7 days. We recorded each visitation of all carcasses regardless of species. We summarized the camera trap data to illustrate which species were the most frequent scavengers of coquis. All camera data for rats were pooled into one group, as discrimination between black rats and Pacific rats based on camera trap images was not reliable.

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. 2) 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; Fig. 5). Following methods from the previous field season, we placed 21 to 24 cameras in each coqui plot, evenly 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 to potentially be important based on the 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.

![Image](image_url)

**Fig. 5** Example photos from one site (Hamakua, Fig. 2) showing similar location of camera sites A) with (coqui circled in yellow) and B) without dead coquis.

**Nest Predation**

To address Objective 3, 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, obtained from an online retailer, and constructed of weaved plant fibers. We placed nests randomly but at least 15 m apart, 0.5 m to 1.5 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 7 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 7 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 ran our models with the dependent variable being depredated or not depredated, and plot type (coqui or non-coqui) as the independent variable. We tested the effect of coquis on the number of predation events by each predator, again, with a GLMM assuming a Poisson distribution of the count data and number of predation events by each predator as the dependent variable and plot type as the independent variable. For all models, variation among sites and plots were accounted for by including them as random effects.
CHAPTER 4
RESULTS

Mongoose and Rat Abundance

Mongooses 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 (7 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 catch per unit effort (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 (Sugihara 1997; Puan et al. 2011). Depletion estimate results are reported in Appendix Table B-1.

In total, 705 small mammals were collected across all sites: 194 mongooses, 262 black rats, and 209 Pacific rats. Seven Norway rats (Rattus norvegicus) were trapped at one site (ER) and 33 house mice (Mus musculus) were trapped at five sites but were not included in any analyses.

Among all the models we ran, coqui presence or absence only was the top predictor of the relative abundance of mongoose and Pacific rats. Pacific rat CPUE was top predictor in the black rat model (Table 1). The mean predicted relative abundance estimates from the mongoose model were significantly higher for plots with coqui (2.13/100 trap nights) than without coqui (1.64/100 trap nights; \( p < 0.001 \); Fig. 6) and
show a 30% higher abundance of mongooses. Mean predicted relative abundance for Pacific rats was significantly lower for plots with coqui than without (1.75 vs. 2.1/100 trap nights; \( p = 0.012 \); Fig. 6), showing a 17% difference. Mean predicted black rat abundances were negatively correlated with Pacific rat abundance (\( p = 0.028 \)) 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. 6).

Fig. 6 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: * \( p < 0.05 \).
Table 1 Generalized linear mixed models testing the pairwise interactions among the three mammalian predators (mongoose, black rats and Pacific rats) capture per unit effort and coqui presence or absence (i.e. coqui). DOF represent degrees of freedom for each model. Best fitting models have largest change from baseline models Akaike information criterion (Δ AIC), maximized log-likelihood (logLik) and lowest deviance. Estimates show direction and degree of change for top models * Indicates top model for each predator species.

<table>
<thead>
<tr>
<th>Model</th>
<th>DOF</th>
<th>AIC</th>
<th>Δ AIC</th>
<th>logLik</th>
<th>deviance</th>
<th>p-value</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>mongoose</td>
<td>2</td>
<td>157</td>
<td>0</td>
<td>-76</td>
<td>153</td>
<td>&lt; 0.001</td>
<td>0.48</td>
</tr>
<tr>
<td>mongoose ~ coqui*</td>
<td>3</td>
<td>148</td>
<td>-9</td>
<td>-71</td>
<td>142</td>
<td>&lt; 0.001</td>
<td>0.48</td>
</tr>
<tr>
<td>mongoose ~ black rat</td>
<td>3</td>
<td>158</td>
<td>1</td>
<td>-76</td>
<td>152</td>
<td>0.261</td>
<td></td>
</tr>
<tr>
<td>mongoose ~ Pacific rat</td>
<td>3</td>
<td>156</td>
<td>-2</td>
<td>-75</td>
<td>150</td>
<td>0.095</td>
<td></td>
</tr>
<tr>
<td>black rat</td>
<td>2</td>
<td>201</td>
<td>0</td>
<td>-98</td>
<td>197</td>
<td></td>
<td></td>
</tr>
<tr>
<td>black rat ~ Pacific rat*</td>
<td>3</td>
<td>198</td>
<td>-3</td>
<td>-96</td>
<td>192</td>
<td>0.029</td>
<td>-0.32</td>
</tr>
<tr>
<td>black rat ~ mongoose</td>
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<td>200</td>
<td>-1</td>
<td>-97</td>
<td>195</td>
<td>0.127</td>
<td></td>
</tr>
<tr>
<td>black rat ~ coqui</td>
<td>3</td>
<td>202</td>
<td>1</td>
<td>-98</td>
<td>196</td>
<td>0.262</td>
<td></td>
</tr>
<tr>
<td>Pacific rat</td>
<td>2</td>
<td>152</td>
<td>0</td>
<td>-74</td>
<td>148</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific rat ~ coqui*</td>
<td>3</td>
<td>148</td>
<td>-4</td>
<td>-71</td>
<td>142</td>
<td>0.012</td>
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</tr>
<tr>
<td>Pacific rat ~ mongoose</td>
<td>3</td>
<td>152</td>
<td>0</td>
<td>-73</td>
<td>146</td>
<td>0.169</td>
<td></td>
</tr>
<tr>
<td>Pacific rat ~ black rat</td>
<td>3</td>
<td>152</td>
<td>0</td>
<td>-73</td>
<td>146</td>
<td>0.159</td>
<td></td>
</tr>
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</table>

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 from distance sampling (mongoose, r = 0.05, p = 0.87; black rats, r = -0.25, p = 0.43; Pacific rats, r = -0.25, p = 0.42; Appendix Fig. B-1).

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, 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).
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; and not statistically distinguishable from zero.

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. 7). 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. 7). The remaining food type categories had such low percentages that they were not compared.
Fig. 7 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.

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 both rat species, there was a greater percent of fruit in stomachs in coqui plots (black rat: $p = 0.003$, Pacific rat: $p = 0.054$), although only marginally significant for Pacific rats. Marginally significant results also suggest trends toward greater percent of arthropods in stomachs in non-coqui than coqui plots (black rat: $p = 0.09$, Pacific rat: $p = 0.10$), most notably caterpillars in Pacific rat diets ($p = 0.068$; Table 2).
**Table 2** Comparison of mean percent (%) ± 1 SE of food types identified in stomachs of predators between plots. P-values indicate significance of MRPP tests comparing food type proportions between coqui and non-coqui plots for each predator. P-values not given for food type categories that were zero percent relative abundance for one of the plot types.

<table>
<thead>
<tr>
<th>Food type</th>
<th>Mongoose Coqui plots (n=69)</th>
<th>Mongoose Non-coqui plots (n=37)</th>
<th>p</th>
<th>Black rat Coqui plots (n=79)</th>
<th>Black rat Non-coqui plots (n=60)</th>
<th>p</th>
<th>Pacific rat Coqui plots (n=87)</th>
<th>Pacific rat Non-coqui plots (n=79)</th>
<th>p</th>
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</thead>
<tbody>
<tr>
<td>Coqui</td>
<td>3.7 ± 1.9</td>
<td>0</td>
<td>0.212</td>
<td>0.1 ± 0.1</td>
<td>0</td>
<td>0</td>
<td>1.3 ± 1.3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Plant</td>
<td>22.9 ± 7.3</td>
<td>14.5 ± 7</td>
<td>0.128</td>
<td>87.8 ± 1.2</td>
<td>77.9 ± 11.8</td>
<td>0.059</td>
<td>77.7 ± 9.5</td>
<td>65.1 ± 9.8</td>
<td>0.070</td>
</tr>
<tr>
<td>Fruit</td>
<td>9.8 ± 3.1</td>
<td>1.3 ± 0.8</td>
<td>0.045*</td>
<td>9.2 ± 0.3</td>
<td>51 ± 5.3</td>
<td>0.003</td>
<td>66.2 ± 5.7</td>
<td>51.2 ± 5.3</td>
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<tr>
<td>Seed</td>
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<td>1.1 ± 1.1</td>
<td>1</td>
<td>72.3 ± 6.5</td>
<td>6.3 ± 2.4</td>
<td>*</td>
<td>0.6 ± 0.3</td>
<td>3.4 ± 1.6</td>
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<tr>
<td>Other plant material</td>
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<td>12.1 ± 5.1</td>
<td>0.580</td>
<td>4.5</td>
<td>20.4 ± 4.1</td>
<td>0.857</td>
<td>10.9 ± 3.5</td>
<td>10.5 ± 2.9</td>
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</tr>
<tr>
<td>Arthropod</td>
<td>22.5 ± 9.5</td>
<td>20.2 ± 10.7</td>
<td>0.537</td>
<td>9.9 ± 3.8</td>
<td>17.4 ± 5.4</td>
<td>0.099</td>
<td>20.2 ± 7.6</td>
<td>31.8 ± 8.2</td>
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<tr>
<td>Caterpillars</td>
<td>5 ± 2.5</td>
<td>5.3 ± 2.8</td>
<td>0.537</td>
<td>5.8 ± 1.9</td>
<td>10.5 ± 2.8</td>
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<td>5.6 ± 2.4</td>
<td>13.7 ± 3.3</td>
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<tr>
<td>Dipteran</td>
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<td>4.8 ± 3.3</td>
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</tr>
<tr>
<td>Other arthropod</td>
<td>9.5 ± 3.1</td>
<td>9.4 ± 3.9</td>
<td>0.866</td>
<td>4.1 ± 1.9</td>
<td>6.9 ± 2.6</td>
<td>0.368</td>
<td>13.1 ± 3.8</td>
<td>16.1 ± 3.7</td>
<td>0.641</td>
</tr>
<tr>
<td>Bird</td>
<td>1.5 ± 1.5</td>
<td>0.9 ± 0.9</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1 ± 0.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Lizard</td>
<td>10.5 ± 3.2</td>
<td>15 ± 5.2</td>
<td>0.548</td>
<td>0</td>
<td>0.1 ± 0.1</td>
<td>0</td>
<td>0.1 ± 0.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Rodent</td>
<td>24.9 ± 4.9</td>
<td>32 ± 7.6</td>
<td>0.446</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.6 ± 0.6</td>
<td>0</td>
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</tr>
<tr>
<td>Other</td>
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<td>18.5 ± 6.1</td>
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<td>2.2 ± 1</td>
<td>4.3 ± 2.2</td>
<td>0.371</td>
<td>0.2 ± 0.2</td>
<td>3.3 ± 1.6</td>
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</tbody>
</table>

**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%) (Fig. 8, Fig.9).
Fig. 8 Photos of species observed scavenging dead coqui frogs during sampling. A) Mongoose (*Herpestes auropunctatus*) B) Rat species C) Feral pig (*Sus scrofa*) D) Domestic cat (*Felis catus*) E) Female Northern Cardinal (*Cardinalis cardinalis*).
Fig. 9 Total number of photos showing scavenging of adult coqui frog by all observed species across all sites for field seasons 2016 and 2017.

In 2017 comparison of coqui carcass-baited cameras (n = 57) with unbaited control cameras (n = 58), 84.2% of the baited cameras recorded images of potential scavengers, while only 50% of the unbaited cameras recorded such visits. This difference was significant (p = 0.030) (Fig. 10).
Fig. 10 Mean number of cameras visited and not visited (±SE) (n=5) by any animal at five sites (Eden Rock, Hamakua, Kalopa, Manuka, and Waipio).

**Nest Predation**

We observed 564 artificial nests for nest predation (n = 283 in coqui plots and 281 in non-coqui plots, positioned at a range of heights between 0.5 m and 2 m) (Table C-1). 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 (Fig. 11).
Fig. 11 Mean predation rates (%) with standard error bars for plot type across all sites (n=12).

On average 56.7% of nests were confirmed to be depredated by rats and 28.9% by mongooses; 14.4 % were depredated by unidentified predators (cameras failed to capture an image) (Fig. 12, Fig. 13). Neither of the nest predation rates for rats and mongooses differed between coqui and non-coqui plots (p = 0.451 and 0.391, respectively; Fig. 13).

Fig. 12 Photos of rats and mongooses depredated quail eggs from artificial nests.
Fig. 13 Mean predation rates (%) with standard error bars of each predator species at coqui and non-coqui plots across all 12 sites (n=12 in the figure). Across sites, there were 283 nests monitored at coqui plots and 281 nests monitored at non-coqui plots.
CHAPTER 5
DISCUSSION

This study found that differences in the average densities and diets of the invasive small mammals across coqui invasion fronts on the island of Hawaii is associated with coqui frog presence. We did not find, however, any correlation between coqui density estimates and predator abundance. Mongoose, followed by rats, were the most important scavengers for coquis. Although there was only a small number of coqui frogs found in the diets for all the predator stomachs we collected, we found a shift in their diets that may be influenced by the presence of coqui in the environment. For mongoose and rats, there was a greater relative abundance of fruit in stomachs from the coqui than the non-coqui plots. Also, in both rat species, we found a pattern, although non-significant, of a greater relative abundance of arthropods in stomachs from non-coqui than coqui plots. Despite the differences found in predator abundances between coqui and non-coqui plots, we did not find any difference in the predation rate of the artificial nests we placed in those plots.

Our results suggest that either: 1) coquis are acting on the abundances, distributions, and dietary behavior of mongooses and rats in a manner that influences them either directly or indirectly; or 2) mongooses and rats are responding to some other factor, independent of coquis, that varies across with coqui and non-coqui plots. In an attempt to reduce bias caused by other factors in our comparisons, we placed our plots in areas on either side of coqui invasion fronts that visually had similar habitat and tested whether habitat variables differed between paired plots. None of the variables we measured (canopy cover, understory density, ground cover, and elevation) were different
across invasion fronts (Table A-2). As further support for this, two other studies have tried to identify habitat differences across these fronts using different methods and have been unable to do so (Choi and Beard 2012; Smith et al. 2018). This suggests that the presence or absence of coqui frogs in our plots was not dependent on the structure and composition of vegetation (since they were similar in both plot types at all sites) but likely due to some other factor (i.e., time to colonize). While we cannot rule out that some other factor contributed to the differences we observed in these plots (i.e., mongoose and rat abundances), we think our study design is adequate to test relationships between the coqui invasion and abundances of small mammal predators, and to develop hypotheses that can be tested using more controlled experimental designs.

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 mongoose by showing that frog species decline where mongoose invade (Barbour 1930; Gorman 1975; Watari et al. 2008; Barun et al. 2010). We are not aware of other studies showing that frogs increase mongoose populations, although this might be more expected at invasion fronts. Mongooses were the most common scavengers of coquis and they had a greater number of frogs in their stomachs than rats. While direct predation likely contributed to, rather than solely caused, the increased abundance of mongooses we observed, the relative abundance and frequency of coquis in the 106 stomachs we investigated seems too 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 one mongoose stomach containing
four frogs. It may be that coqui densities in the plot were not high enough for them to become an abundant food source, although we did not see any correlation with coqui density and mongoose abundance (Appendix Fig. B-1). Or, it may be that coqui frogs are digested quickly and passed through the digestive track before we observed them, this may explain the high amount of scavenging but low amount of coquis in stomachs, and potentially the large proportion of empty stomachs among all the stomachs collected. A potential explanation for the increase in mongoose abundance is that mongooses may be opportunistic consumers of coquis and may only consume them at particular times of year or life stages (Yamada 2002; Barun et al. 2010), which was not captured in our sampling. Alternatively, coquis alter the habitat (e.g. increasing non-native fruiting trees; Sin et al. 2008) in a way that better suits mongooses causing a shift in mongoose diets that might improve fitness.

In general, we found both rat species had marginally lower indices of relative abundance in coqui than in non-coqui plots; black rats were on average 13% lower, though non-significant, while Pacific rats were significantly lower on average by 35%. A plausible explanation for this pattern is apparent competition between coquis and rats, or more specifically, that greater mongoose numbers in plots with coqui resulted in greater mongoose predation on rats or rat avoidance of coqui plots (Pemberton 1925; Barnum 1930; Doty 1945; Walker 1945; Seaman 1952; Pimentel 1955; Barun et al. 2011b), we found that rodents made up 27% of mongoose diets. Although, the top models for predicting either rat species relative abundance did not include mongoose as the best predictor and did include coqui frog presence for Pacific rats. Our results could be interpreted as to suggest that coquis are associated with the increase of mongooses and
that mongooses in turn reduce populations of rats (non-arboreal rats, in particular; Walker 1945; Pimentel 1955). Pacific rats often use the ground and den underground, while black rats tend to be more arboreal (Shiels 2010). Thus, it makes sense that mongoose threaten Pacific rats more than black rats.

For both rat species, we found a greater relative abundance of arthropods in diets, although only marginally significant, in non-coqui than coqui plots. Coquis are insectivores, and most directly impact, and primarily reduce, leaf litter invertebrates (Choi and Beard 2012). Therefore, coquis might compete with rats for invertebrate prey, and this could be an additional explanation for the lower rat abundances in coqui than non-coqui plots. The Pacific rat abundance models support this explanation because coquis are a better explanatory variable for Pacific rats than are mongoose. Additionally, according to our study, Pacific rats consume more arthropods than black rats. Because coquis reduce leaf litter invertebrates (Choi and Beard 2012), one would hypothesize that coquis are in greater competition for these resources with Pacific rats than black rats. Other research associating coqui presence with non-native bird abundance suggests that coquis generally increase some non-native bird abundance (Smith et al. 2018), which could in turn lead to increased bird predation on arthropods in plots with coqui. These potential mechanisms may contribute to explaining why rats appear to be consuming more insects, caterpillars in particular, which are often a key component of bird diets, in non-coqui plots.

While our results do not show any significant correlation between coqui densities and predator abundance, the direction of these relationships matched the patterns with coqui presence and absence. It should be noted that the densities we estimated in our
plots differ significantly from previous density estimates in other studies. Beard et al. (2008) reported coqui densities of 91,000 frogs/ha and Woolbright et al. (2006) reported coqui densities of 89,000 frogs/ha on the island of Hawaii. The highest density estimate that we made was 2,879 frog/ha. First, in this study we used a one-night distance sampling approach to estimate coqui densities, and while this approach can be used to determine relative abundance among treatments (Smith et al. 2018), it does not give as precise an estimate of coqui abundance as does the longer-term mark-recapture techniques used in Beard et al. (2008) and Woolbright et al. (2006). Another potential explanation for this difference may be that our study focused on the edges or “fronts” of the coquis range (i.e., where they are still invading), and densities of coquis may be lower at the edges than at the center of the range (Estoup et al. 2004). Finally, if the lower estimates made in our study actually reflect much lower densities of coquis in our study plots, this may provide an explanation for the low number of predator stomachs containing coqui remains and may suggest that coqui may not become a significant part of rat and mongoose diets until they reach greater densities.

There seems to be a dietary shift for mongooses and rats across the coqui invasion front, in which mongooses and rats were consuming more fruit in areas with frogs compared to areas without frogs. This result is similar to previous research that found that frugivorous house finches (*Haemorhous mexicanus*) increase in coqui plots compared to non-coqui plots (Smith et al. 2018). Previous research has shown that the growth rate of non-native plants, 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; whether coquis have a causative effect on this relationship remains undetermined.

Our study shows that other invasive species, most frequently mongoose, scavenge on coqui frogs. We found a much higher rate of scavenging on coquis than Abernethy et al. (2016). That study reported that vertebrates scavenge coquis 22% of the frogs placed in the field, while we found vertebrates scavenge them 84% of the time. This may be due to the fact that coquis were not established at 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 (arthropods 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, such as our study 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. Although our methods were similar to those used in Abernethy et al. (2016), the higher rate of overall removal by vertebrates we observed may not be natural. It could be that our positioning of dead coquis was more conspicuous than may occur naturally. Based on our experience, it is rare to observe a dead coqui frog in the field, except as roadkill.

Even though we found differences in the densities of mongooses and rats where coquis occur, we were unable to detect any difference in percent of depredated artificial
nests between plot types. Despite the changes in their relative abundances across coqui and non-coqui plots, the number of nests depredated between coqui and non-coqui plots was similar for both mongooses and rats. We observed a greater number of rats (56.7%) depredating our nests compared to mongooses (28.9%), which is to be expected because we placed our nests ~1 m off the ground and rats are more arboreal than mongooses, black rats in particular (Shiels 2010). However, it is worth noting that 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 (Table C-1; Fig. C-1). Studies have found that rat control can increase nest success for native birds; therefore, it can be inferred that an area with less rats would have lower nest predation (VanderWerf 2001; VanderWerf and Smith 2002). In our study, coquis were associated with an increase of mongooses, but a decrease of Pacific rats, and no significant difference of black rat abundances. Because black rats tend to be more arboreal, they are likely a more important nest predator than Pacific rats. Our results suggest that birds that nest within the range of 0-2 m from the forest floor are at an equally significant risk of nest depredation in both coqui invaded and uninvaded areas.

Some of the limitations of our research revolve around the fact that 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). It can be argued that larger areas would be more appropriate for estimating mongoose abundance. 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, being more arboreal, can depredate nests higher in the canopy (VanderWerf 2001; VanderWerf and Smith 2002; Shiels 2010). Because we were focusing on both mongooses and rats, our artificial nests were placed 0.5-2 m from the ground to capture mongoose and rat nest predation rats. Future studies may focus solely on mongooses or rats to capture more robust data on the target species. A study on the effects of coquis on mongoose should also accommodate the large home ranges (8.6 to 70.2 ha) of mongooses (Pitt et al. 2015), which may limit the sites suitable for such a project.
In conclusion, the results of our research partially support the hypothesis proposed by Kraus et al. (1999) and Beard and Pitt (2005). The presence of coquis is associated with greater mongoose abundance, perhaps through direct consumption of a novel prey, or indirectly, through other effects that coquis have within the ecosystem. It may be that the effect that coquis have on non-native plant growth creates slightly more suitable habitat for mongooses or that the increased number of non-native birds in coqui invaded areas attracts mongooses (Sin et al. 2008, Smith et al. 2018). On the other hand, rat abundances seem to be lower in coqui-invaded plots, possibly through competition for resources as our data and diet analysis suggest or, again, through the coquis affecting the overall web of interactions within the invaded habitats.

With our data, we have determined that mongooses and rats are the top scavengers of coqui frogs, but we cannot confirm that coquis are an important resource for non-native mammalian predators. With the ever-growing likelihood of future introductions of invasive species to Hawaii, it is conceivable that 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.

The association of increased mongoose abundances in areas where coqui frogs occur is a cause for concern for individuals or agencies who have objectives revolving around the conservation and/or restoration of birds that have been negatively affected by mongooses, such as the Hawaiian goose (*Branta sandvicensis*). Because the coqui frog is
unlikely to be extirpated and potentially may spread to new areas, their associative effect on mongooses may, according to our results, continue to grow, therefore efforts to restore Hawaiian goose populations will be more difficult in areas with coqui frogs. An increase in mongooses also raises concern regarding the spread of diseases. Mongooses are known vectors of the rabies virus and, although it has never been reported to occur in Hawaii, the increased abundance of mongooses would cause the virus to be more prevalent and spread faster if it were ever to make it to the island.

Future studies should include more robust sampling focused on mongooses because our results suggest that the detrimental effects of mongooses on Hawaiian birds may be exacerbated by the presence of coqui frogs. More specifically, we were only able to calculate indices of abundance of mongooses and stronger methods of abundance estimation, such as capture mark recapture methods, would provide better estimates of abundance. Also, our estimates of coqui density differ from the estimates of studies using more robust sampling methods; future research should incorporate these methods. A combination of more robust abundance and density estimations may capture stronger effects of coquis on mongooses, possibly showing effects of coqui density on mongooses, but at a minimum would improve our understanding of their relationship. Also, to determine if there are actual increased impacts on bird nests, tests should focus at a level that mongooses are more likely to have an effect (e.g. lower to the ground).

A study focusing on the effects of coqui frogs on small mammalian predators may also utilize geographic information systems and remote sensing tools to map out the spatial distribution of species. More specifically, the use of satellite transmitters on mongooses will provide data on their movement and resource selection (Pitt et al. 2015).
Mongoose spatial data, in conjunction with a map delineating current coqui distribution, would provide data researchers could use to develop resource selection function models (Boyce et al. 2002) and determine if mongooses utilize coqui invaded areas more than uninvaded areas. This study would be limited by the ability to properly map coqui distributions (Bisrat et al. 2012; Olson et al. 2012).
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APPENDICES
APPENDIX A

SITE DESCRIPTION AND HABITAT VARIABLES
Table A-1 Mean values of plot-level environmental covariates included in Plot-level habitat differences analysis in each of the 12 sites. C= coquis present, N = coquis absent. Full names for sites are in Fig. 2.

<table>
<thead>
<tr>
<th>Site</th>
<th>Annual rainfall* (mm)</th>
<th>Annual temperature†(°C)</th>
<th>Plot type</th>
<th>Coqui density (frogs/ha)</th>
<th>Canopy cover (%)</th>
<th>Dominant canopy</th>
<th>Understory density (%)</th>
<th>Dominant understory</th>
<th>Vegetation ground cover (%)</th>
<th>Elevation (m)</th>
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<td>838</td>
<td>17.7</td>
<td>C</td>
<td>433</td>
<td>98</td>
<td>Eucalyptus</td>
<td>38</td>
<td>Tree Fern</td>
<td>19.4</td>
<td>689</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>N</td>
<td>99</td>
<td>99</td>
<td>Eucalyptus</td>
<td>60</td>
<td>Tree Fern</td>
<td>17.5</td>
<td>694</td>
</tr>
<tr>
<td>US</td>
<td>838</td>
<td>16.4</td>
<td>C</td>
<td>197</td>
<td>51</td>
<td>Strawberry Guava</td>
<td>51</td>
<td>Strawberry Guava</td>
<td>30.6</td>
<td>730</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>N</td>
<td>51</td>
<td>51</td>
<td>Strawberry Guava</td>
<td>53</td>
<td>Strawberry Guava</td>
<td>32.2</td>
<td>786</td>
</tr>
<tr>
<td>VC</td>
<td>5759</td>
<td>17</td>
<td>C</td>
<td>267</td>
<td>44</td>
<td>Ohia</td>
<td>56</td>
<td>Uluhe Fern</td>
<td>75.3</td>
<td>935</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>N</td>
<td>52</td>
<td>52</td>
<td>Ohia</td>
<td>61</td>
<td>Uluhe Fern</td>
<td>71.9</td>
<td>1081</td>
</tr>
<tr>
<td>WP</td>
<td>4815</td>
<td>20.9</td>
<td>C</td>
<td>314</td>
<td>97</td>
<td>Eucalyptus</td>
<td>80</td>
<td>Cane Grass</td>
<td>55.3</td>
<td>372</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>N</td>
<td>99</td>
<td>99</td>
<td>Eucalyptus</td>
<td>70</td>
<td>Cane Grass</td>
<td>56.3</td>
<td>420</td>
</tr>
</tbody>
</table>

Habitat Variables

Previous studies in 11 of 12 of our sites found no 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, we wanted to confirm that plots on either side of the fronts at each site still differed only in their presence and absence of coqui. We measured and tested for differences in following variables in all plots: elevation, percent canopy cover, percent vegetated ground cover, percent understory density, dominant canopy and dominant understory. Elevation was collected from the center of each plot with a Garmin Etrex® 20x. To take vegetation measurements, we established four 40-m long transects radiating from the center of each plot in each cardinal direction. Every 10 m for four points on each transect, we determined percent canopy cover using a spherical crown densitometer (Forestry Suppliers, Convex Model A), for a total of 16 measurements per plot. We measured ground cover at the same points using a 20 point intercept method in a 1 m x 1 m quadrat and categorized ground cover types as vegetation, leaf litter, bare ground, moss, logs, and rocks. We calculated percent vegetated ground cover (ferns and other shrubs, grass, and forbs) by dividing the number of points with vegetation by the total number of points observed (16 quadrats x 20 points/quadrat = 320 points).

We measured understory density at the center of each plot and at the end of each 40-m long transect, for five measurements per plot. We measured understory vegetation density by taking a photograph of a 0.5 m wide x 2 m tall white sheet from a distance of 5 m facing away from the center of plot, except for at the center point where we faced south, and 1.5 from the forest floor. We imported each photo into Adobe Photoshop®
(Adobe Systems Inc., San Jose, CA), used the cropping tool to crop the photos to the desired portions of each image, and used the threshold function to convert the color image into a binary black and white image. Once we had a binary image, we used the histogram feature to calculate percentage of black or vegetation pixels relative to the total number of pixels in the image (Limb et al. 2007).

We determined dominant vegetation in five, 5 m x 5 m subplots at the center of the plot and at the end of each 40-m long transects by recording the diameter at breast height of all trees and the species of the three largest trees within each subplot. We calculated the percent of each species per plot by dividing the number of individuals of each species by the total number of recorded trees (15 per plot). The species with the highest percentage was used to describe the dominant vegetation type (Table A-1).

We tested for differences in habitat across coqui and non-coqui plots using a one-way analysis of variance (ANOVA) test for each variable with site as a block with a significance level of $p < 0.05$.

Plot-level habitat differences

None of the habitat variables we measured differed across coqui and non-coqui plots (Table A-2).
Table A-2 One-way ANOVA results for environmental differences between coqui and non-coqui sites.

<table>
<thead>
<tr>
<th>Habitat Variable</th>
<th>Plot type effect and Site block effect</th>
<th>Sum of Squares</th>
<th>Degrees of freedom</th>
<th>F statistic</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy Cover</td>
<td>Coqui Site</td>
<td>0.0018</td>
<td>1</td>
<td>1.852</td>
<td>0.201</td>
</tr>
<tr>
<td></td>
<td>Coqui Site</td>
<td>2.1668</td>
<td>11</td>
<td>198.565</td>
<td>5.28e-11 *</td>
</tr>
<tr>
<td>Understory Density</td>
<td>Coqui Site</td>
<td>0.0063</td>
<td>1</td>
<td>1.408</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>Coqui Site</td>
<td>0.8305</td>
<td>11</td>
<td>16.774</td>
<td>2.59e-05 *</td>
</tr>
<tr>
<td>Ground cover</td>
<td>Coqui Site</td>
<td>0</td>
<td>1</td>
<td>0.016</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>Coqui Site</td>
<td>24269</td>
<td>11</td>
<td>352.034</td>
<td>2.31e-12 *</td>
</tr>
<tr>
<td>Elevation</td>
<td>Coqui Site</td>
<td>376</td>
<td>1</td>
<td>0.099</td>
<td>0.758882</td>
</tr>
<tr>
<td></td>
<td>Coqui Site</td>
<td>528509</td>
<td>11</td>
<td>12.653</td>
<td>0.000103 *</td>
</tr>
</tbody>
</table>

*indicates significant difference

Table A-3 Variance inflation factors (VIF) and univariate correlation coefficients (r) between coqui density and four habitat variables. A conservative estimate of collinearity is based on a threshold of VIF > 3 (Zuur et al. 2010).

<table>
<thead>
<tr>
<th>Canopy Cover</th>
<th>Understory Density</th>
<th>Percent Ground cover</th>
<th>Elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td>VIF</td>
<td>2.5</td>
<td>1.56</td>
<td>2.66</td>
</tr>
<tr>
<td>r</td>
<td>0.03</td>
<td>0.21</td>
<td>-0.31</td>
</tr>
</tbody>
</table>
APPENDIX B

PREDATOR DEPLETION ANALYSIS, PLOT LEVEL COQUI DENSITIES AND PREDATOR/CORRELATION TESTS
In addition to using CPUE as an index we estimated rat and mongoose abundance in each plot using a depletion analysis processed in program MARK accessed in R with the package RMARK. Our depletion sampling resulted in small sample sizes at all sites that were unlikely to provide us with actual density estimates. Thus, our results served as a density index rather than actual density, which satisfies the requirements of this study, comparing the density of predators between our coqui and non-coqui plots. Plots at which we only trapped individuals 3 or less days of total 7 trap days were not given estimated 95% confidence intervals (CI) because they did not meet the criteria to be used in the analysis. Plot density estimates that did not receive confidence intervals included 15 for mongoose, 12 for Pacific rats, and 13 for black rats. In these instances, we used the total number of individuals trapped, assuming that we had removed all individuals of a given species from the plot.

The mean estimated densities of mongooses were 5.09 mongooses/ha at coqui sites and 3.13 mongooses/ha at non-coqui sites (Table B-1). Black rat mean estimated densities were 5.85 individuals/ha at both coqui sites and 6.21 individuals/ha at non-coqui sites (Table B-1). Finally, the mean estimated densities of Pacific rats were 3.79 individuals/ha at coqui sites and 5.63 individuals/ha at non-coqui sites (Table B-1).
Table B-1 Estimates of coqui density calculated from line-transect distance sampling surveys and rats and mongoose density indices calculated in depletion analysis for all sites and plots. CI was not estimable when species were only caught on 3 or less days.

<table>
<thead>
<tr>
<th>Site</th>
<th>Point *</th>
<th>Coqui density (frogs/ha)</th>
<th>Mongoose density index (#/ha) (95% CI)</th>
<th>Black rat density index (#/ha) (95% CI)</th>
<th>Pacific rat density index (#/ha) (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eden Rock (ER)</td>
<td>C</td>
<td>236</td>
<td>0</td>
<td>20 (18-29)</td>
<td>12 (10-27.5)</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>1</td>
<td>5.5 (5.5-10.5)</td>
<td>20 (19-27)</td>
</tr>
<tr>
<td>Fern Forest (FF)</td>
<td>C</td>
<td>356</td>
<td>5.5 (5.5-10.5)</td>
<td>15.5 (5.5-37.5)</td>
<td>7.5 (7.5-18)</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>4</td>
<td>9.5 (8.5-17.5)</td>
<td>9 (7-26.5)</td>
</tr>
<tr>
<td>Hamakua (HM)</td>
<td>C</td>
<td>289</td>
<td>4.5 (4.5-7)</td>
<td>5 (3.5-24.5)</td>
<td>8.5 (8-14)</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>5 (5-9.5)</td>
<td>5.5 (5.5-6.5)</td>
<td>8.5 (8-14.5)</td>
</tr>
<tr>
<td>Kalopa (KP)</td>
<td>C</td>
<td>158</td>
<td>16 (15.5-20.5)</td>
<td>8 (7-16.5)</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>7 (7-12)</td>
<td>4</td>
<td>3 (2.5-15)</td>
</tr>
<tr>
<td>Kaupakuea Homestead (KH)</td>
<td>C</td>
<td>123</td>
<td>2</td>
<td>1</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>1</td>
<td>1.5</td>
<td>5.5 (5.5-1.5)</td>
</tr>
<tr>
<td>Manuka A (MA)</td>
<td>C</td>
<td>2878</td>
<td>6 (5.5-13)</td>
<td>2</td>
<td>2 (2-5)</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>2.5</td>
<td>10 (10-13.5)</td>
<td>2</td>
</tr>
<tr>
<td>Manuka B (MB)</td>
<td>C</td>
<td>1299</td>
<td>8 (7-20)</td>
<td>4</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>4</td>
<td>17 (17-21.5)</td>
<td>2</td>
</tr>
<tr>
<td>Saddle Road (SR)</td>
<td>C</td>
<td>433</td>
<td>3.5 (3.5-6.5)</td>
<td>1.5</td>
<td>3 (3-7)</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Stainback (SB)</td>
<td>C</td>
<td>801</td>
<td>2</td>
<td>1</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>3</td>
<td>4</td>
<td>3 (3-8.5)</td>
</tr>
<tr>
<td>Upper Stainback (US)</td>
<td>C</td>
<td>197</td>
<td>1</td>
<td>3.5</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>2.5</td>
<td>5.5</td>
<td>1.5</td>
</tr>
<tr>
<td>Volcano (VC)</td>
<td>C</td>
<td>267</td>
<td>5 (5-10.5)</td>
<td>10.5 (10-17)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>1</td>
<td>7 (7-12)</td>
<td>1</td>
</tr>
<tr>
<td>Waipio (WP)</td>
<td>C</td>
<td>370</td>
<td>9.5 (9.5-13)</td>
<td>0</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
<td>5</td>
<td>2.5</td>
<td>10.5 (8.5-26.5)</td>
</tr>
</tbody>
</table>

* C=coqui, N=non-coqui
Table B-2 Estimates of coqui density (frogs/ha) estimated from line-transect distance-sampling surveys for all sites and plots using the unmarked package in R. We observed 1577 frogs during surveys. All distance sampling data was modeled with null models for both detection and density using either half-normal (HN), hazard (HZ), or exponential (E) distributions (Akaike model weights, $w$, are provided for the most supported detection distributions, as are and $p$-values for Freeman-Tukey goodness of fit tests [GOF; acceptable fit determined for modeling assumptions if $p > 0.10$]). Other abbreviations are as follows: C= coquis present, N = coquis absent.

<table>
<thead>
<tr>
<th>Site</th>
<th>Plot</th>
<th>Density</th>
<th>Top model</th>
<th>$w$</th>
<th>GOF</th>
</tr>
</thead>
<tbody>
<tr>
<td>ER</td>
<td>C</td>
<td>236</td>
<td>E</td>
<td>0.39</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FF</td>
<td>C</td>
<td>356</td>
<td>E</td>
<td>0.42</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HM</td>
<td>C</td>
<td>289</td>
<td>E</td>
<td>0.41</td>
<td>0.03</td>
</tr>
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<td>N</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>C</td>
<td>123</td>
<td>E</td>
<td>0.42</td>
<td>0.17</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>KP</td>
<td>C</td>
<td>158</td>
<td>E</td>
<td>0.52</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>N</td>
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<td></td>
</tr>
<tr>
<td>MA</td>
<td>C</td>
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<td>E</td>
<td>0.85</td>
<td>0.78</td>
</tr>
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<td></td>
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</tr>
<tr>
<td>MB</td>
<td>C</td>
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<td>E</td>
<td>0.51</td>
<td>0.91</td>
</tr>
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<td></td>
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</tr>
<tr>
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<td>C</td>
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<td>E</td>
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<td>0.01</td>
</tr>
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</tr>
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<td>C</td>
<td>801</td>
<td>E</td>
<td>0.52</td>
<td>0.20</td>
</tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>US</td>
<td>C</td>
<td>197</td>
<td>E</td>
<td>0.43</td>
<td>0.56</td>
</tr>
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<td>N</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VC</td>
<td>C</td>
<td>267</td>
<td>E</td>
<td>0.46</td>
<td>0.13</td>
</tr>
<tr>
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<td>N</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WP</td>
<td>C</td>
<td>314</td>
<td>E</td>
<td>0.45</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. B-1 Scatterplots and regression of the trap night indices of A) mongooses B) Black rats and C) Pacific rats on the estimated density of coqui frogs from 12 sites.
APPENDIX C

ARTIFICIAL NEST HEIGHT SUMMARY
Table C-1 Height profiles of percent of all nests monitored during study (depredated and not depredated) and percent nests depredated by each predator species.

<table>
<thead>
<tr>
<th>Nest Heights (m)</th>
<th>0 – 0.25 m</th>
<th>0.30 – 0.50 m</th>
<th>0.60 – 0.75 m</th>
<th>0.80 – 1.00 m</th>
<th>1.1 – 1.25 m</th>
<th>1.30 – 1.50 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>All nests Percent monitored</td>
<td>0.7</td>
<td>12.1</td>
<td>19.8</td>
<td>39.8</td>
<td>17.8</td>
<td>9.8</td>
</tr>
<tr>
<td>Mongoose Percent depredated</td>
<td>0</td>
<td>10.9</td>
<td>25.3</td>
<td>33.7</td>
<td>19.3</td>
<td>10.8</td>
</tr>
<tr>
<td>Rat Percent depredated</td>
<td>0</td>
<td>11.2</td>
<td>19.8</td>
<td>44.8</td>
<td>15.5</td>
<td>6.9</td>
</tr>
<tr>
<td>Unknown Percent depredated</td>
<td>2.9</td>
<td>11.4</td>
<td>20</td>
<td>37</td>
<td>28.6</td>
<td>0</td>
</tr>
</tbody>
</table>

Fig. C-1 Percent of all depredated nests across entire study area and their heights including the portion of nests depredated by mongooses, rats and unknowns.