Utah State University

DigitalCommons@USU

Ecology Center Publications   Ecology Center

3-19-2019

Invasive Coqui Frogs Are Associated With Differences in Mongoose and Rat Abundances and Diets in Hawaii

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

Follow this and additional works at: https://digitalcommons.usu.edu/eco_pubs

Part of the Life Sciences Commons

Recommended Citation

1 **Running head: Interactions among an invasive frog and invasive mammals**

2

3 **Invasive coqui frogs are associated with differences in mongoose and rat abundances and**

4 **diets in Hawaii**

5

6 **Shane A. Hill[1], Karen H. Beard[1]*, Shane R. Siers[2] and Aaron B. Shiels[3]**

7

8 **1 Department of Wildland Resources and Ecology Center, Utah State University, Logan,**

9 **UT 84322-5230, U.S.A.**

10

11 **2 USDA APHIS, Wildlife Services, National Wildlife Research Center, Hawaii Field**

12 **Station, Hilo, Hawaii 96720, U.S.A.**

13

14 **3 USDA APHIS, Wildlife Services, National Wildlife Research Center, Ft. Collins, CO**

15 **80521, U.S.A.**

16

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

18

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; Hoshide 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

65   since it was introduced via the horticultural trade in the late 1980's (Kraus et al. 1999). The frog

66   is particularly widespread on the island of Hawaii, while the other Hawaiian Islands have had

67   more success in preventing its establishment and controlling populations (Beard et al. 2009).

68   Previous studies have found that coquis have both societal impacts, including economic and

69   quality of life impacts (Kaiser and Burnett 2006; Kalnicky et al. 2014; Kraus and Campbell

70   2002), and ecological impacts through their interactions with other species (Bernard and Mautz

71   2016; Choi and Beard 2012; Smith et al. 2018; Tuttle et al. 2009).

72   Although previous research has determined some ecological consequences of the coqui

73   invasion, questions remain regarding interactions between coquis and invasive small mammals.

74   The introduction of coquis to the island of Hawaii is recent relative to that of the mongooses

75   (*Herpestes auropunctatus*) and rats (*Rattus* spp.) (Baldwin et al. 1952; Doty 1945; Kraus et al.

76   1999), and, when coquis established, they became potential prey to these species. Further, if

77   coquis serve as novel prey to these species, it could change the roles that mongooses and rats

78   have within the Hawaiian food web. For example, coquis may increase rat and mongoose

79   abundances and exacerbate the predation effects of both mongooses and rats on native birds

80   (Kraus et al. 1999; VanderWerf 2001; Beard and Pitt 2006). Interactions observed in native

81   communities may also occur within this non-native dominated system, such as apparent

82   competition (*sensu* Holt 1977). For example, if the presence of coquis causes an increase in

83   mongooses, then there may be increased predation on rats by mongooses in coqui-infested areas,

84   eventually leading to a decrease in rats. Finally, coquis may compete directly with rats for prey

85   because both are nocturnal and insectivorous (Shiels et al. 2013; Wallis et al. 2016).

86   Our primary goal was to test the hypothesis proposed by Kraus et al. (1999) that coquis

87   may increase the abundances of mongooses and rats through direct predation and thereby

88 increase bird nest predation. However, this hypothesis provides only a simple view of the

89 potential interactions among these species, especially between coquis and rats. Therefore, we

90 investigated likely alternative, but not mutually exclusive, hypotheses between coquis and rats,

91 such as apparent competition and resource competition. If coquis serve as important prey for

92 mongooses and rats, we predict that mongoose and rat abundance will be higher in areas with

93 coquis and we expect coquis to be important in mongoose and rat diets. If coquis interact with

94 rats through apparent competition, we predict that mongoose populations will be higher and rat

95 populations will be lower in areas with coquis. We would also expect mongooses to have rats in

96 their diets. If coquis compete with rats for resources, we predict that rat abundance will be lower

97 in areas with coquis, and that rats and coquis will consume similar prey. Finally, if coquis

98 increase bird nest predation through either increases in mongoose or rat abundances, we expect

99 nest predation rates will be higher in areas with coquis than in areas without coquis.

100   To address these hypotheses and predictions, we determined the relationship among

101 coquis, mongooses, and rats to determine if coquis or the other invasive mammal were important

102 predictors of mongoose and rat abundance. To determine whether predation or competition

103 might be occurring between coquis, mongooses, and rats, we investigated mongoose and rat

104 stomach contents in the presence and absence of coquis, and direct scavenging on coquis.

105 Finally, to determine if coquis indirectly influenced bird nest predation, we investigated nest

106 predation rates in the presence and absence of coquis.

107

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

131 avoid biasing small mammal observations. We confirmed coqui presence and absence on both

132 sides of the front by listening for 20 minutes during peak calling hours, 1900 to 0200 h

133 (Woolbright 1985), for the male's two-note mating call on at least three separate nights no more

134 than two months prior to sampling.

135   Previous studies in 11 of 12 of our sites found no measurable differences in habitat on

136 either side of the front (Choi and Beard 2012; Smith et al. 2018). Because this study was initiated

137 two years after the previous study (Smith et al. 2018) and the location of some sites were

138 adjusted, we tested for differences in habitat across fronts by measuring the following variables

139 in both plots at each site: elevation, canopy cover, vegetated ground cover, percent understory

140 density, and dominant canopy and dominant understory species (explained in detail in

141 Supplemental Material A). For each variable, we tested for differences in habitat across paired

142 plots using a one-way analysis of variance (ANOVA) with coqui presence/absence as the fixed

143 effect, and site as a random block effect. We detected no differences in these variables across

144 coqui and non-coqui plots (Supplemental material A). Of note, a previous study more thoroughly

145 tested, both statistically and in terms of the field variables collected, habitat difference between

146 these sites and dropped 5 of 20 sites from their analysis that were sufficiently different in terms

147 of habitat variables (Choi 2011). We used 11 of the sites remaining after that analysis. In

148 summary, these 11 sites had no measurable habitat differences across the front, in either of the

149 previous studies or this study.

150

151 Mongoose and rat abundance

152   To test whether the abundance of non-native mammals is related to coqui frog presence

153 or absence, we estimated mongoose and rat abundances in coqui and non-coqui plots at each of

154   the 12 sites with trapping webs. We conducted mongoose and rat trapping from December 2015

155   to July 2016. Each trapping web consisted of 16, 80-m transects radiating from a central point

156   and covering 2.01 ha, with one web on either side of the invasion front. We set eight live cage

157   traps (Tomahawk Live Trap Company, Tomahawk, WI), one every 10 m, along each alternating

158   transect. On the remaining transects, we placed eight snap traps (Victor rat traps, Woodstream

159   Corporation, Lititz, PA), one every 10 m. We baited live traps with uncooked cocktail links

160   soaked in fish oil, suspended by a hook in the back of each trap, while snap traps were baited

161   with chunks of coconut. We checked each trap twice daily, once at dawn and again at dusk, for

162   seven days at each site. We identified trapped rats to species. We euthanized each individual

163   captured in a live trap via CO_2 saturation. Mongoose and rat relative abundance indices were

164   defined as the number of individuals caught relative to the total number of trap nights (1 trap

165   night is equal to a trap set for one night) at each site or capture per unit effort (CPUE). We also

166   estimated rat and mongoose abundances using depletion analysis for all plots (Supplemental

167   Material B).

168   Coqui density, in addition to presence, may affect rat and mongoose abundances. Within

169   each invaded plot, we estimated coqui density using the line-transect distance-sampling survey

170   methods (Buckland et al. 2001) used by and described in Choi and Beard (2012), Kalnicky et al.

171   (2013), and Smith et al. (2018). In summary, we placed 30 m x 30 m plots in the center of the

172   2.01 ha plots on the coqui side of the invasion front. Then, for one night at each site, we walked

173   down the center of each of six 5-m wide, 30-m long transects for 30 minutes (for a total of 180

174   minutes per plot) and recorded all frogs at any height seen or heard and their distance from the

175   center of the transect. Coqui densities were estimated using the distance-sampling functions in

176   the package "unmarked" (Fiske and Chandler 2011) in R (R Core Team 2016). All distance

177 sampling data was modeled with null models for density using either half-normal, hazard, or

178 exponential distributions. Akaike Information Criterion (AIC) values for the most supported

179 detection distributions and *p*-values for Freeman-Tukey goodness of fit tests are provided (see

180 Supplemental material B).

181   To determine the effect of coqui presence and absence on the abundance indices of small

182 mammals, we used generalized linear mixed models (GLMM) in R (R Core Team 2016) using

183 the "glmer" function within the "lme4" package (Bates et al. 2015). Each mammal species (e.g.,

184 mongoose, black rat, and Pacific rat) was modeled separately, assuming a Poisson distribution,

185 with number of captures at each plot as the dependent variable offset by log(trap nights) to allow

186 interpretation of estimates as CPUE. We tested for differences in abundance using coqui

187 presence/absence as the fixed effect, and site as a random block effect to account for the non-

188 independence between paired trap webs at each site. We also tested correlation of coqui density

189 estimates from coqui plots with abundance indices of rats and mongooses using Pearson's

190 correlation coefficient to determine the strength and significance of the relationships between

191 each species and coqui frogs using the "cor.test" function in R.

192   The predation and resource competition hypotheses only include the possibility of coquis

193 influencing invasive mammals. The alternative hypothesis regarding apparent competition

194 includes interactions among mammalian species. We tested this competing hypothesis by

195 running a model similar to that previously described substituting plot type (i.e., coqui

196 presence/absence) as the independent variable with rat species CPUE in the mongoose model,

197 mongoose CPUE in both black rat and Pacific rat models, Pacific rat CPUE in black rat model,

198 and vice versa for the Pacific rat model. We identified top models as those with the lowest AIC

199 values using a ΔAIC < 2 criteria. We also did a Pearson's correlation test between each of these

200 species abundances.

201

202 Rat and mongoose diet

203   We removed the stomachs of the euthanized specimens collected from our trapping

204 efforts to analyze mongoose and rat diets. We froze stomachs at -20° C for later analysis in the

205 laboratory. After thawing, we swirled the contents of each sample for 5 min in water and a mild

206 detergent to dissolve any stomach fluids and oils, poured the contents through a 0.4 mm sieved

207 and preserved them in 95% ethanol (Sugihara 1997). For each sample, we performed a thorough

208 search of the stomach contents for coqui remains, such as skin and bones, under a dissecting

209 scope. We then used a grid of 5 mm x 5 mm squares laid under a Petri dish to inspect each

210 sample with a dissecting scope 10-20x magnification. For stomach samples too large for Petri

211 dishes, we gently stirred these samples for 30 seconds and took sub-samples by pouring 50% of

212 the contents onto a grid. We recorded the food type found within each grid-square (i.e. 40 evenly

213 spaces grid-boxes). We categorized food into seven major types: plant, arthropod, reptile,

214 amphibian, bird, rodent and other (as in Shiels et al. 2013). We were able to distinguish between

215 reptile and amphibian remains through skin fragments and portions of head, claws, tails, and

216 other body parts present in the samples. We sub-categorized plant food types as fruit, seed, and

217 other plant material (flowers, vegetative material, and unknown), and arthropods as Coleoptera,

218 Diptera, Lepidoptera, and other arthropod material (other included Hymenoptera, Chilopoda,

219 Odonata, Orthoptera, Gastropoda, Arachnida, and unknown arthropod material). Stomach

220 contents placed in the "other" category were items that we could not identify. We removed

221 parasitic roundworms from the analysis and excluded empty stomachs and samples that

222 contained a volume greater than 50% of roundworms or trap bait from the study.

223 We determined the frequency of each food type by noting the occurrence of that food

224 type in each sample (Shiels et al. 2013). We calculated relative abundance in each sample by

225 dividing the number of squares with a certain food type by the total number of squares covered

226 by the contents of each stomach (Shiels et al. 2013). We compared relative abundances or

227 percent of food types among all species, and tested for differences in the diets of each species

228 individually between coqui plots and non-coqui plots, using the non-parametric analysis Multi-

229 Response Permutation Procedure (MRPP), an analysis for testing for difference between two or

230 more groups (Mielke et al. 1981) in the "vegan" package (Oksanen et al. 2017) for R. We tested

231 for differences in diet composition among the three species using all plots. We then assessed

232 differences in diet composition between coqui and non-coqui plots for each predator species

233 individually. For all statistical tests in this study, we used $\alpha < 0.05$ as significant, except for diet

234 analyses of invertebrates, where we also discuss results with $\alpha < 0.10$ because of the high degree

235 of spatial and temporal variability observed with invertebrate data (sensu Holmes and Schultz

236 1988; Tuttle et al. 2009).

237

238 Coqui scavengers

239 To determine scavenging on coquis, from December 2015 to July 2016, the week before

240 we began nest predation tests at each site (see below), we placed 25 dead coquis in the 2.01-ha

241 plot on the coqui invaded side of the front. We collected these coquis from near each coqui-

242 invaded plot, but not within plots, and euthanized them. Each dead coqui was placed on the

243 ground or within 50 cm of the ground on varying substrates to simulate where frogs might be if

244   they had died naturally. Frogs were placed randomly but at least 15 m apart. We made

245   observations of scavenging events with a motion-activated camera (Reconyx HyperFire models,

246   Reconyx Inc., WI, USA) on each carcass positioned 1 to 2 m from the dead coqui. Cameras

247   remained in the field for seven days. We recorded each visitation of all carcasses regardless of

248   species. We summarized the camera trap data to determine which species were the most frequent

249   scavengers of coquis. Species were differentiated based on known distinguishing characteristics

250   except for black rats and Pacific rats, which were pooled because they could not be reliably

251   distinguished. Individuals were assumed the same until they left the field of view. We could not

252   reliably distinguish individuals from one another across multiple scavenging events.

253   From May to July 2017, we returned to the five sites with the greatest number of visits

254   from scavengers (sites ER, HM, KP, MB, and WP; Fig. 1) to validate our method by

255   characterizing differences in observations between cameras baited with a coqui carcass

256   (treatment cameras) and cameras without a coqui as bait (control cameras). Following methods

257   from the previous field season, we placed 21 to 24 cameras in each coqui plot, balanced between

258   treatment and control. Because there were no coquis to be scavenged from the control cameras,

259   the data collected here were counts of visits to the field of view of each camera that triggered the

260   motion sensor. In addition, to capture invertebrate scavengers that would not activate the

261   cameras' motion sensors, we placed all frog carcasses on pressure-sensitive external lever

262   triggers that would activate cameras when a frog was removed. These were not used in the

263   previous field season but were thought potentially to be important based on results from

264   Abernethy et al. (2016). To test for differences in the number of visits to cameras with frogs and

265   control cameras, we used a GLMM with camera set type (coqui or control) as a fixed effect, site

266 as a random effect, and the sum of visits to each camera set type for each site as the dependent

267 variable, assuming a Poisson distribution.

268

269 Nest predation

270   To test whether nests are visited by predators at higher rates in sites where coqui occur,

271 we monitored artificial nests with quail eggs in our plots (VanderWerf 2001). From December

272 2015 to July 2016, the week before we began trapping at each site, we placed 25 artificial nests

273 in each of the 2.01-ha plots on both sides of the invasion front. Artificial nests were 10-cm in

274 diameter, 3-cm deep, and constructed of weaved plant fibers. We placed nests randomly but at

275 least 15 m apart, 0.25 m to 2.0 m from the ground, and on a variety of plant substrates,

276 depending on the site, including crooks of branches, along horizontal branches, and within

277 bundles of ferns. Within each nest, we placed one locally farmed quail egg. Between 1 and 2 m

278 from each nest, we placed a motion-activated camera to identify which species depredated the

279 egg. Each nest was monitored for seven nights. Nests were counted as depredated if the eggs

280 were gone, removed from nest, or had received damage in any way from predators during the

281 seven nights. We reused nests among sites after waiting at least seven days for odors that may

282 have attracted or repelled predators to the nest to dissipate between each use (VanderWerf 2001).

283   We tested the effect of coqui presence on the rate that the nests were depredated and the

284 number of predation events by rats and mongooses individually. To test coqui effect on

285 depredation rates, we ran a GLMM in R using the "glmer" function within the "lme4" package.

286 Using binomial distributions, we tested for differences in nest depredation using coqui

287 presence/absence as the fixed effect and site as a random block effect. We tested the effect of

288 coquis on the number of predation events by each predator with a similar GLMM, but assuming

289 a Poisson distribution of the count data and number of predation events by each predator as the

290 dependent variable.

291

Results

293 Mongoose and rat abundance

294   Mongooses were caught exclusively in live traps, while rats were caught in both trap

295 types, but most frequently (86% of the time) in snap traps. Because mongoose were only caught

296 in Tomahawk live traps, mongoose trapping effort was 448 trap nights per plot (7 days of

297 trapping with 64 live traps). Because rats were caught in both types of traps, we had 896 trap

298 nights per plot (seven days of trapping with 128 traps). There were no trap nights or days in

299 which two individuals were caught in the same trap. We compared CPUE (captures per 100 trap

300 nights) with results from depletion modeling, but because results were not qualitatively different

301 and showed the same patterns with coquis, we only present capture data per 100 trap-nights in

302 the text for comparability with other studies (Puan et al. 2011; Sugihara 1997). Depletion

303 estimate results are reported in Supplemental material B.

304   In total, 705 small mammals were collected across all sites: 194 mongooses, 262 black

305 rats, and 209 Pacific rats. Seven Norway rats (*R. norvegicus*) were trapped at one site (ER), and

306 33 house mice (*Mus musculus*) were trapped at five sites and but not further analyzed due to low

307 sample size and zero counts at many sites.

308   Among all the models run, coqui presence or absence was the top predictor of the

309 relative abundance of mongoose and of Pacific rats. Pacific rat CPUE was the top predictor in

310 the black rat model (Table 1). The mean predicted relative abundance estimates from the

311 mongoose model were significantly greater for plots with coqui (2.13/100 trap nights) than

312   without coqui (1.64/100 trap nights; $p < 0.001$; Fig. 2) and showed a 30% greater abundance of

313   mongooses. Mean predicted relative abundance for Pacific rats was significantly less for plots

314   with coqui than without (1.75 vs. 2.10/100 trap nights; $p = 0.012$; Fig. 2), showing a 17%

315   difference. Mean predicted black rat abundances were negatively correlated with Pacific rat

316   abundance (df = 11, z = -2.186, $p = 0.028$) but were also lower in sites with coqui (1.92 vs.

317   2.21/100 trap nights), though this effect was not significant ($p = 0.262$; Fig. 2).

318   While the directions of the estimated relationships were consistent with the presence or

319   absence results, mongoose and rat abundance indices were not significantly correlated with coqui

320   density estimates (mongooses, r = 0.05, $p = 0.87$; black rats, r = -0.25, $p = 0.43$; Pacific rats, r = -

321   0.25, $p = 0.42$; Supplemental material B).

322

323   Rat and mongoose diet

324   Trapping efforts yielded 194 mongoose stomach samples, of which 72 were empty and

325   16 contained >50% by volume intestinal parasites or bait. There was a total of 262 black rat

326   stomachs, of which 63 were empty and 33 were >50% parasites or bait. Finally, out of 209

327   Pacific rat stomachs, 54 were empty and 14 contained >50% parasites or bait. In total, there were

328   413 stomachs (106 mongoose, 166 black rat, and 141 Pacific rat) included in analyses.

329   Coqui frogs were found only in stomach contents from mammals trapped in coqui plots.

330   The frequency of stomachs from coqui plots (n=216) containing coquis was low for all species:

331   five out of 69 (7.2%) mongoose stomachs, two out of 87 (2.3%) black rat stomachs, and one out

332   of 60 (1.7%) Pacific rat stomachs. The abundance of coqui frogs relative to all stomach contents

333   of individuals trapped in coqui plots was also low for all species: 3.7% of mongoose diet, 0.1%

334   of black rat diet, and 1.3% of Pacific rat diet on average.

335   Relative abundance of each food type was calculated from stomachs of 106 mongooses,

336   141 Pacific rats, and 166 black rats regardless of the plot type in which they were caught.

337   Mongoose diets contained all recorded food types, and the composition of all food types differed

338   significantly from those of black rats and Pacific rats ($p = 0.001$; Fig. 3). When we compared

339   black rat and Pacific rat diets, we found a higher percent of plant material in black rat stomachs

340   ($p = 0.005$), and a higher percent of arthropods in Pacific rat stomachs ($p = 0.002$; Fig. 3). The

341   remaining food type categories had low percentages and were not compared.

342   For mongoose, only the mean percent of fruit differed between coqui and non-coqui plots

343   ($p = 0.045$), with a greater percent of fruit found in stomachs in coqui plots. Similarly, for black

344   rats, there was a greater percent of fruit ($p = 0.003$) and other plant material ($p = 0.027$) in

345   stomachs in coqui plots. Results also suggest a greater percent of invertebrates in rat stomachs in

346   non-coqui than coqui plots (black rat: $p = 0.099$), most notably more caterpillars in Pacific rat

347   diets ($p = 0.068$; Table 2).

348

349   Coqui scavengers

350   Of the 384 dead frogs placed in study plots, 267 (70%) were removed. Of those

351   scavenging events, we could determine the scavenger in 228 cases (85.4%). In the remaining

352   cases, the camera failed to capture an image of the scavenger. Average time to removal was 56

353   hours (SD = 36.8 hours). We observed six species scavenging coquis. Mongooses were the most

354   frequently observed scavengers (60.5% of 228 confirmed events), followed by rats (34.2%), pigs

355   (*Sus scrofa*, 3.1%), ants (species unidentified, 1.3%), one domestic cat (*Felis catus*, 0.4%) and

356   one northern cardinal (*Cardinalis cardinalis*, 0.4%). In 2017, there were more images recorded

357 of potential scavengers at coqui carcass-baited cameras (84.2% recorded images, n = 57) than at

358 unbaited control cameras (50% recorded images, n = 58) (z = 2.145, p = 0.03).

359

360 Nest predation

361   We observed 564 artificial nests for nest predation (n = 283 in coqui plots and 281 in

362 non-coqui plots, Supplemental material C). In total, 40.6% of the nests were depredated; there

363 was no difference in the percentage of nests depredated in coqui versus non-coqui plots. On

364 average 56.7% of nests were confirmed to be depredated by rats, 28.9% by mongooses, and 14.4

365 % were depredated by unidentified predators (cameras failed to capture an image). Neither of the

366 nest predation rates for rats nor mongooses differed between coqui or non-coqui plots (z = 0.754,

367 p = 0.45 and z = 0.858, p = 0.39, respectively).

368

Discussion

370   We set out to address the hypothesis originally proposed by Kraus et al. (1999) that

371 mongoose and rats depredate coqui frogs, which in turn increases mongoose and rat abundance,

372 and subsequently increases bird nest predation. In support of this hypothesis, we found 30%

373 more mongoose where coquis were present on the island of Hawaii and mongoose were also the

374 most important scavengers of coqui. In contrast, we found 17% fewer Pacific rats where coquis

375 were present, which suggests they are not important predators of coqui, and provides support for

376 both the apparent competition or resource competition hypotheses for coquis and rats. We found

377 more support for the resource competition hypothesis than the apparent competition hypothesis,

378 primarily because coquis were in the top model for Pacific rat abundance, were a better

379 explanatory variable than mongoose, and because rat diets shifted towards more fruit and less

380   invertebrates in the presence of coquis. Perhaps because mongoose increased and rats decreased

381   in abundance in the presence of coquis, we found no support for the hypothesis that coquis

382   indirectly increase bird-nest predation rates.

383   Where coqui frogs occur, we found, on average, 30% more mongooses than in areas

384   without frogs. Other studies have shown the importance of interactions between frogs and

385   mongooses by showing that frog species decline where mongooses invade (Barbour 1930; Barun

386   et al. 2010; Gorman 1975; Watari et al. 2008). We are not aware of other studies showing that

387   frogs increase mongoose abundance, although we might expect this relationship more frequently

388   at the beginning of an invasion or at an invasion front (Simberloff and Gibbons 2004). In our

389   study, mongooses were the most common predators and scavengers of coquis. While direct

390   predation likely contributed to the increased abundance of mongooses we observed, the relative

391   abundance (4%) and frequency (7%) of coquis in the stomachs we investigated from coqui plots

392   seems low to explain the increase entirely.

393   Previous research in Hawaii has shown an individual mongoose can consume a high

394   number of coquis (remains of 15 frogs in one stomach) (Beard and Pitt 2006). We did not find

395   that to be the case in our study; rather we found at most four frogs in one mongoose stomach. We

396   offer several potential explanations for this pattern. First, perhaps mongoose consumed more

397   coquis than we observed, but they were digested quickly. Second, mongoose may only

398   opportunistically consume coquis, such as at particular times of year or life stages (Barun et al.

399   2010; Yamada 2002) that were not captured in our sampling. Finally, our results could reflect

400   that coquis indirectly increase mongooses, such as by altering available forage (e.g. by increasing

401   non-native fruit as discussed below; Sin et al. 2008).

402   In general, we found both rat species had lower indices of relative abundance in coqui

403   than in non-coqui plots, but only Pacific rats were significantly lower, on average by 17%. A

404   possible explanation for this pattern is apparent competition between coquis and rats, or more

405   specifically, that greater mongoose abundance in coqui plots resulted in greater mongoose

406   predation on rats or rat avoidance of coqui plots (Barnum 1930; Barun et al. 2011; Doty 1945;

407   Pimentel 1955; Seaman and Randall 1962; Walker 1945). We expected greater potential for

408   apparent competition with the less-arboreal Pacific rats because they are more likely to interact

409   with mongooses (Pimentel 1955; Shiels 2010; Walker 1945). Our results support this because

410   Pacific rat abundances were lower in coqui plots. Further, we found that rodents made up 27% of

411   mongoose diets. However, the top models for predicting either rat species' relative abundance

412   did not include mongoose. Therefore, while apparent competition may play a role in reducing

413   rats where coquis are present, it is likely not the only factor.

414   We expected that coquis may compete with less-arboreal Pacific rat, in particular, for

415   invertebrate prey. Coquis are, after all, insectivores, and most directly impact and reduce leaf

416   litter invertebrates (Beard 2007; Choi and Beard 2012). In support of the resource competition

417   hypothesis, coquis were in the top model and were a better explanatory variable of Pacific rat

418   abundance than mongooses. Further, Pacific rats consumed more arthropods than black rats in

419   our study, so we would expect to observe a greater reduction in Pacific than black rats if

420   competition for invertebrates was important. Finally, we found a greater relative abundance of

421   arthropods (in general or some type) in rat diets from non-coqui plots than coqui plots.

422   Therefore, competition for invertebrate resources appears to be another, at least partial,

423   explanation for the lower Pacific rat abundance in coqui plots.

424   There seems to be a dietary shift for mongooses and rats across the coqui invasion front,

425   in which both mongooses and black rats, in particular, were consuming more fruit in areas with

426   frogs compared to areas without frogs. Previous research suggests that the growth rate of

427   strawberry guava, *Psidium cattleianum*, in particular, a dominant non-native plant in many of

428   these sites, is greater in areas with coqui frogs (Sin et al. 2008). We did not measure the number

429   of fruits produced per plot, but future research should determine if fruit availability differs

430   between coqui and non-coqui plots. Our results are consistent with greater frugivory by

431   mongooses and rats in areas invaded by coqui than in areas not invaded.

432   Our study shows that other invasive species, most frequently mongooses, scavenge on

433   coquis. Abernethy et al. (2016) found that vertebrates scavenge 22% of the frogs placed in the

434   field, while we found vertebrates scavenge them 84% of the time. This difference may be due to

435   the fact that coquis were not established in the native-dominated sites used by Abernethy et al.

436   (2016) and the fauna present were not conditioned to search for such small-bodied amphibians.

437   We also observed a much lower rate of frogs removed by invertebrates. Abernethy et al. (2016)

438   observed 78% of frog carcasses removed by invertebrates. The only invertebrates we observed

439   scavenging frogs were ants, 6.3% of the time (invertebrates were only evaluated in 2017 field

440   season, but 86% of our predation events were accounted for in the 2016 field season). Our results

441   suggest that in non-native dominated sites with established coqui populations, vertebrates are

442   more important scavengers than invertebrates, and that they consume a high percentage of dead

443   coqui frogs if they are readily available.

444   Even though we found differences in the abundance of mongooses and rats where coquis

445   occur, we were unable to detect any difference in the percent of depredated artificial nests for

446   mongoose or rats in coqui invaded and uninvaded areas. We observed a greater number of rats

447 (56.7%) depredating nests compared to mongooses (28.9%), which was expected because we

448 placed nests 0.25-2 m off the ground, and black rats, in particular, are more arboreal than

449 mongooses (Shiels 2010). However, of note, we frequently observed mongooses climbing to

450 remove eggs from relatively high nests; 64% of the nests that mongooses depredated were

451 between 0.75 m and 1.75 m (Supplemental material C). Studies have found that rat control can

452 increase nest success for native birds; we can infer that areas with less rats would have lower

453 nest predation (VanderWerf 2001; VanderWerf and Smith 2002). However, because coquis were

454 associated with increased mongoose abundance, decreased Pacific rat abundance, and no

455 difference in black rat abundance, we might expect a similar risk of nest depredation in both

456 coqui invaded and uninvaded areas.

457 We were simultaneously studying the effects of coquis on predators with differing life

458 histories. Our methods may have been adequate to capture the data we wanted for one species

459 while failing to do so for another. For example, the size of our plots remained constant despite

460 the difference in home ranges between mongooses and rats (Lindsey et al. 1999; Pitt et al. 2015).

461 A study on the effects of coquis on mongoose maybe should accommodate the large home

462 ranges (8.6 to 70.2 ha) of mongooses (Pitt et al. 2015). Also, most empirical evidence suggests

463 that mongooses are a larger threat to ground foraging and nesting birds (Hoshide et al. 1990;

464 Morley and Winder 2013) while rats can depredate nests higher in the canopy (Shiels 2010;

465 VanderWerf 2001; VanderWerf and Smith 2002). Future studies focused solely on mongooses or

466 rats may capture more robust data on the target species.

467 Our results suggest that either: 1) coquis are either directly or indirectly influencing the

468 abundance and dietary behavior of mongooses and rats, or 2) mongooses and rats are responding

469 to some other factor, independent of coquis, that varies between coqui and non-coqui plots. The

470 similarities in vegetation structure across the invasion fronts as assessed by the current and past

471 studies suggests that vegetation structure and composition did not drive the differences we found

472 in mammal abundance and diets across the fronts (Choi and Beard 2012; Smith et al. 2018).

473 While we cannot rule out that some other factor contributed to the differences we found, we

474 think our study design is adequate to test relationships between coquis and mammals, and to

475 develop hypotheses that can be tested using more targeted experimental designs.

476   In conclusion, the results of our research partially support the hypothesis proposed by

477 Kraus et al. (1999) that coquis may increase populations of invasive small mammals in Hawaii.

478 The presence of coquis is associated with greater mongoose abundance, probably through direct

479 consumption of a novel prey. The association of increased mongoose abundances in areas with

480 coqui frogs should concern managers interested in conserving or restoring birds that mongooses

481 negatively affect. On the other hand, rat abundances seem to be lower in coqui-invaded plots,

482 possibly through both competition for resources and apparent competition. With the ever-

483 growing likelihood of future introductions of invasive species to Hawaii, coquis could facilitate

484 the successful establishment of other invasive predators. We recommend that managers continue

485 to monitor and prevent coqui movement across the island of Hawaii and to other locations, such

486 as Kauai and Oahu, which presently have no coquis.

487

493   approved as journal paper number 9102. This research was conducted under access permits from

494   the Hawaii Division of Forestry and Wildlife, Natural Area Reserves System, State Parks

495   Department, and Injurious Wildlife Export Permit #16-05 and was conducted in compliance with

496   USU's IACUC guidelines as protocols #2519 and #2753.

497

498   **Author Contributions**

499   Conceived and designed the research: Karen Beard and Aaron Shiels. Performed the research:

500   Shane Hill. Analyzed the data: Shane Hill and Shane Siers. Wrote the paper: Shane Hill and

501   Karen Beard. Helped revise the paper: all authors.

502

503   **Compliance with ethical standards**

504

505   **Conflict of interest**

506   The authors have declared that no competing interests exist.

507

508   **References**

24

509 Abernethy E, Turner K, Beasley J, DeVault TL, Pitt WC, Rhodes OEJ (2016) Carcasses of

510   invasive species are predominantly utilized by invasive scavengers in an island

511   ecosystem Ecosphere 7:e01496 doi:10.1002/ecs2.1496

512 Atkinson IAE (1977) A reassessment of factors, particularly *Rattus rattus* L., that influenced the

513   decline of endemic forest birds in the Hawaiian Islands Pac Sci 31:109-133

514 Atkinson IAE (1985) The spread of commensal species of *Rattus* to oceanic islands and their

515   effects on island avifaunas ICPB Tech Publ 3:35–81

516 Baldwin P, Schwartz C, Schwartz E (1952) Life history and economic status of the mongoose in

517   Hawaii J Mammal 33:335-356 doi:10.2307/1375771

518 Barbour T (1930) Some faunistic changes in the Lesser Antilles Proc New Engl Xool Club

519   11:73–85

520 Barnum C (1930) Rat control in Hawaii Hawaii Plant Rec 34:421–443

521 Barun A, Simberloff D, Budinski I (2010) Impact of the small Indian mongoose on native

522   amphibians and reptiles of the Adriatic islands, Croatia Anim Conserv 13:549–555

523   doi:10.1111/j.1469-1795.2010.00374.x

524 Barun A, Simberloff D, Tvrtković T, Pascal M (2011) Impact of the introduced small Indian

525   mongoose (*Herpestes auropunctatus*) on abundance and activity time of the introduced

526   ship rat (*Rattus rattus*) and the small mammal community on Adriatic islands, Croatia

527   NeoBiota 11:51-61 doi:10.1111/j.1469-1795.2010.00374.x

528 Beard KH (2007) Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii Diet of the

529   invasive frog, *Eleutherodactylus coqui*, in Hawaii 2007:281-291

530 Beard KH, Pitt WC (2006) Potential predators of an invasive frog (*Eleutherodactylus coqui*) in

531   Hawaiian forests J Trop Ecol 22:345-347 doi:10.1017/S0266467406003154

532   Beard KH, Price EA, Pitt WC (2009) Biology and impacts of Pacific Island invasive species. 5.

533   *Eleutherodactylus coqui*, the coqui frog (Anura: Leptodactylidae) Pac Sci 63:297-316

534   doi:10.2984/049.063.0301

535   Beckmann C, Shine R (2011) Toad's tongue for breakfast: Exploitation of a novel prey type, the

536   invasive cane toad, by scavenging raptors in tropical Australia Biol Invasions 13:1447–

537   1455 doi:10.1007/s10530-010-9903-8

538   Bernard RF, Mautz WJ (2016) Dietary overlap between the invasive coquí frog

539   (*Eleutherodactylus coqui*) and the Hawaiian hoary bat (*Lasiurus cinereus semotus*) on the

540   Island of Hawai'i Biol Invasions 18:3409-3418 doi:10.1007/s10530-016-1232-0

541   Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001)

542   Introduction to distance sampling: Estimating abundance of biological populations.

543   Oxford University Press, Oxford

544   Choi RT (2011) Invertebrate community changes along coqui invasion fronts in Hawai'i. M.S.

545   Thesis, Utah State University

546   Choi RT, Beard KH (2012) Coqui frog invasions change invertebrate communities in Hawaii

547   Biol Invasions 14:938–948 doi:10.1007/s10530-011-0127-3

548   Davis M (2003) Biotic globalization: Does competition from introduced species threaten

549   biodiversity? Bioscience 53:481–489 doi:10.1641/0006-

550   3568(2003)053[0481:bgdcfi]2.0.co;2

551   Doty RE (1945) Rat control on Hawaiian sugar cane plantations. Hawaii Plant Rec 49:71-239

552   Fiske I, Chandler R (2011) Unmarked: An R package for fitting hierarchical models of wildlife

553   occurrence and abundance.

554 Gangoso L, Zar JAD, Scholz S, Palacios CJ, Hiraldo F (2006) Contradiction in conservation of

555   island ecosystems: plants, introduced herbivores and avian scavengers in the Canary

556   Islands Biodivers Conserv 15:2231–2248 doi:10.1007/s10531-004-7181-4

557 Gorman ML (1975) The diet of feral *Herpestes auropunctatus* (Carnivora: Viverridae) in the

558   Fijian Islands J Zool 175:273-278 doi:10.1111/j.1469-7998.1975.tb01401.x

559 Grosholz ED (2005) Recent biological invasion may hasten invasional meltdown by accelerating

560   historical introductions Recent biological invasion may hasten invasional meltdown by

561   accelerating historical introductions 102:1088-1091

562 Hadfield MG, Miller SE, Carwile AH (1993) The decimation of endemic Hawai'ian tree snails

563   by alien predators Am Zoo 33:610-622 doi:10.1093/icb/33.6.610

564 Holmes RT, Schultz JC (1988) Food availability for forest birds: effects of prey distribution and

565   abundance on bird foraging Can J Zool 66:720–728

566 Holt RD (1977) Predation, apparent competition, and the structure of prey communities Theor

567   Popul Biol 12:197-229 doi:10.1016/0040-5809(77)90042-9

568 Hoshide H, Price A, Katahira L (1990) A progress report on Nene, *Branta sandvicensis*, in

569   Hawaii Volcanoes National Park from 1974-89 Wildfowl 41:152–155

570 Kaiser B, Burnett K (2006) Economic impacts of *E. coqui* frogs in Hawaii Economic impacts of

571   *E. coqui* frogs in Hawaii 8:1-11 doi:10.1504/IER.2006.053951

572 Kalnicky E, Brunson M, Beard K (2014) A social–ecological systems approach to non-native

573   species: Habituation and its effect on management of coqui frogs in Hawaii Biol Conserv

574   180:187–195 doi:10.1016/J.BIOCON.2014.09.044

575 Kalnicky EA, Beard KH, Brunson MW (2013) Community-level response to habitat structure

576   manipulations: An experimental case study in a tropical ecosystem For Ecol Manage

577   307:313-321 doi:10.1016/J.FORECO.2013.07.015

578 Kraus F, Campbell EW (2002) Human-mediated escalation of a formerly eradicable problem: the

579   invasion of Caribbean frogs in the Hawaiian Islands Biol Invasions 4:327-332

580   doi:10.1023/A:1020909205908

581 Kraus F, Campbell EW, Allison A, Pratt T (1999) *Eleutherodactylus* frog introductions to

582   Hawaii Herpetol Rev 30:21-25

583 Lindsey G, Mosher S, Fancy S, Smucker T (1999) Population structure and movements of

584   introduced rats in an Hawaiian rainforest. Pacific Conserv Biol 5:94-102

585   doi:10.1071/PC990094

586 Loope LL, Mueller-Dombois D (1989) Characteristics of invaded islands, with special reference

587   to Hawaii. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M,

588   Willaimson M (eds) Biological Invasions: A Global Perspective. John Wiley & Sons,

589   Chichester, pp 257-280

590 Mielke PW, Berry KJ, Brier GW (1981) Application of multi-response permutation procedures

591   for examining seasonal changes in monthly mean sea-level pressure patterns Mon

592   Weather Rev 109:120-126 doi:10.1175/1520-0493(1981)109<0120:AOMRPP>2.0.CO;2

593 O'Dowd DJ, Green PT, Lake PS (2003) Invasional 'meltdown' on an oceanic island Ecol Lett

594   6:812-817 doi:10.1046/j.1461-0248.2003.00512.x

595 O'Loughlin LS, Green PT (2017) Secondary invasion: When invasion success is contingent on

596   other invaders altering the properties of recipient ecosystems Ecol Evol 7:7628–7637

597   doi:10.1002/ece3.3315

598 Oksanen J et al. (2017) vegan: Community Ecology Package.

599 Olson CA, Beard KH, Koons DN, Pitt WC (2012) Detection probabilities of two introduced

600   frogs in Hawaii: implications for assessing non-native species distributions Biol

601   Invasions 14:889-900 doi:10.1007/s10530-011-0125-5

602 Pimentel D (1955) Biology of the Indian mongoose in Puerto Rico J Mammal 36:62-68

603   doi:10.2307/1375723

604 Pitt W, Sugihara R, Berentsen A (2015) Effect of travel distance, home range, and bait on the

605   management of small Indian mongooses, *Herpestes auropunctatus* Biol Invasions

606   17:1743–1759 doi:10.1007/s10530-014-0831-x

607 Puan CL, Goldizen AW, Zakaria M, Hafidzi MN, Baxter GS (2011) Relationships among rat

608   numbers, abundance of oil palm fruit and damage levels to fruit in an oil palm plantation

609   Integr Zool 6:130-139 doi:10.1111/j.1749-4877.2010.00231.x

610 R Core Team (2016) R: A language and environment for statistical computing.

611 Reed J, DesRochers D, VanderWerf E, Scott J (2012) Long-term persistence of Hawaii's

612   endangered avifauna through conservation-reliant management Bioscience 62:881–892

613   doi:10.1525/bio.2012.62.10.8

614 Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and

615   why these impacts occur Biol Invasions 8:927-939 doi:10.1007/s10530-005-5103-3

616 Savidge JA (1987) Extinction of an island forest avifauna by an introduced snake Ecology

617   68:660–668 doi:10.2307/1938471

618 Sax D, Gaines S, Brown J (2002) Species invasions exceed extinctions on islands worldwide: a

619   comparative study of plants and birds Am Nat 160:766–783 doi:10.1086/343877

620 Seaman G, Randall J (1962) The mongoose as a predator in the Virgin Islands J Mammal

621   43:544–546 doi:10.2307/1376922

622 Shiels A (2010) Ecology and impacts of introduced rodents (*Rattus* spp. and *Mus musculus*) in

623   the Hawaiian islands. PhD Dissertation, University of Hawai'i

624 Shiels AB, Flores CA, Khamsing A, Krushelnycky PD, Mosher SM, Drake DR (2013) Dietary

625   niche differentiation among three species of invasive rodents (*Rattus rattus, R. exulans,*

626   *Mus musculus*) Biol Invasions 15:1037-1048 doi:10.1007/s10530-012-0348-0

627 Simberloff D, Gibbons L (2004) Now you see them, now you don't! – population crashes of

628   established introduced species Biol Invasions 6:161-172

629 Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional

630   meltdown? Biol Invasions 1:21-32 doi:10.1023/A:1010086329619

631 Sin H, Beard KH, Pitt WC (2008) An invasive frog, *Eleutherodactylus coqui*, increases new leaf

632   production and leaf litter decomposition rates through nutrient cycling in Hawaii Biol

633   Invasions 10:335-345 doi:10.1007/s10530-007-9133-x

634 Smith RL, Beard KH, Koons DN (2018) Invasive coqui frogs are associated with greater

635   abundances of non-native birds in Hawaii Condor 120:16-29 doi:10.1650/CONDOR-17-

636   109.1

637 Sugihara R (1997) Abundance and diets of rats in two native Hawaiian forests Pacific Sci

638   51:189–198

639 Tuttle NC, Beard KH, Pitt WC (2009) Invasive litter, not an invasive insectivore, determine

640   invertebrate communities in Hawaiian forests Biol Invasions 11:845-855

641   doi:10.1007/s10530-008-9298-y

642 VanderWerf EA (2001) Rodent control decreases predation on artificial nests in O'ahu 'elepaio

643   habitat J Field Ornithol 72:448-457 doi:10.1648/0273-8570-72.3.448

644 VanderWerf EA, Smith DG (2002) Effects of alien rodent control on demography of the O'ahu

645   'Elepaio, an endangered Hawaiian forest bird Pacific Conserv Biol 8:73–81

646   doi:10.1071/PC020073

647 Vitousek P, Loope L, Stone C (1987) Introduced species in Hawaii: biological effects and

648   opportunities for ecological research Trends Ecol Evol 2:224–227 doi:10.1016/0169-

649   5347(87)90026-7

650 Walker L (1945) The Hawaiian mongoose - friend or foe Nat Hist 54:396–400

651 Wallis A, Smith R, Beard K (2016) Temporal foraging patterns of non-native Coqui Frogs

652   (*Eleutherodacytlus coqui*) in Hawaii J Herpetol 50:582-588 doi:10.1670/15-170

653 Watari Y, Takatsuki S, Miyashita T (2008) Effects of exotic mongoose (*Herpestes javanicus*) on

654   the native fauna of Amami-Oshima Island, southern Japan, estimated by distribution

655   patterns along the historical gradient of mongoose invasion Biol Invasions 10:7-17

656   doi:10.1007/s10530-007-9100-6

657 Weller S et al. (2018) The effects of introduced ungulates on native and alien plant species in an

658   island ecosystem: Implications for change in a diverse mesic forest in the Hawaiian

659   Islands For Ecol Manage 409:518–526 doi:10.1016/j.foreco.2017.11.023

660 Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quanitfying threats to imperiled

661   species in the United States Bioscience 48:607-615 doi:10.2307/1313420

662 Woolbright LL (1985) Patterns of nocturnal movement and calling by the tropical frog

663   *Eleutherodactylus coqui* Herpetologica 14:1-9

664   Yamada F (2002) Impacts and control of introduced small Indian mongoose on Amami Island,

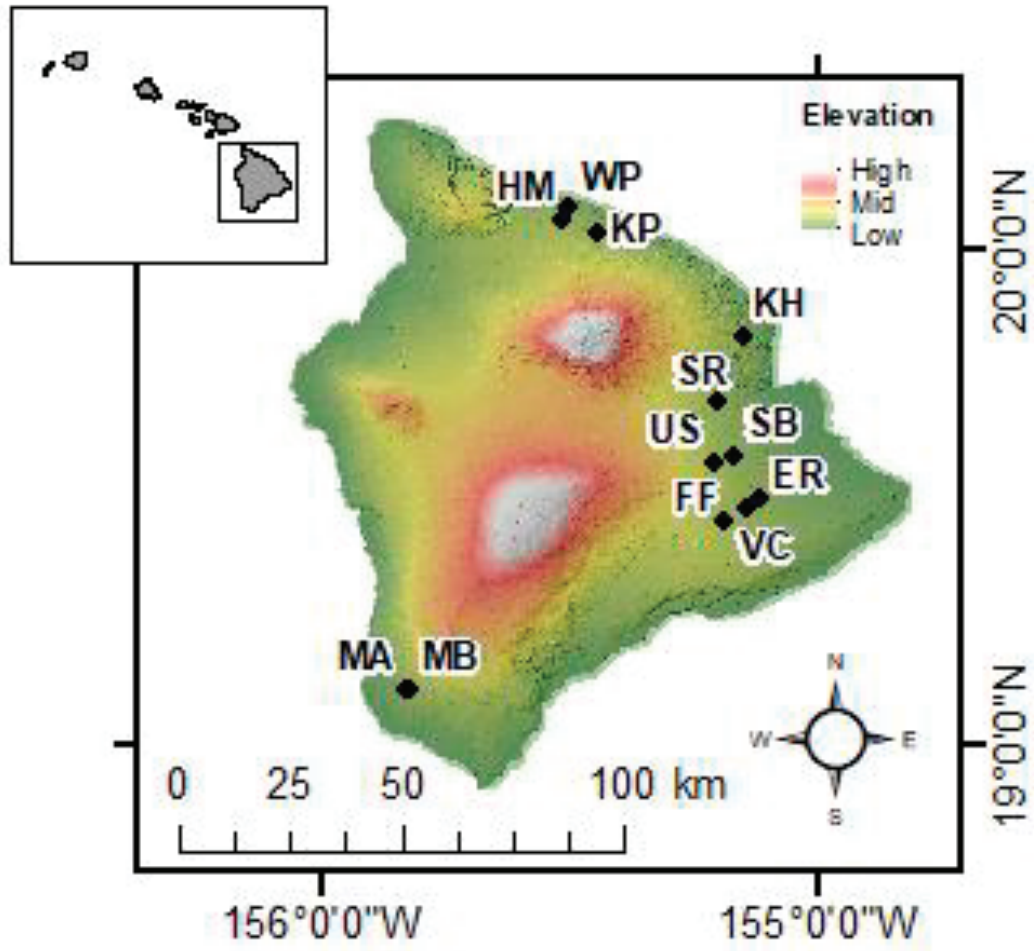665   Japan IUCN SSC Invasive Species Spec Gr:389–392

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).
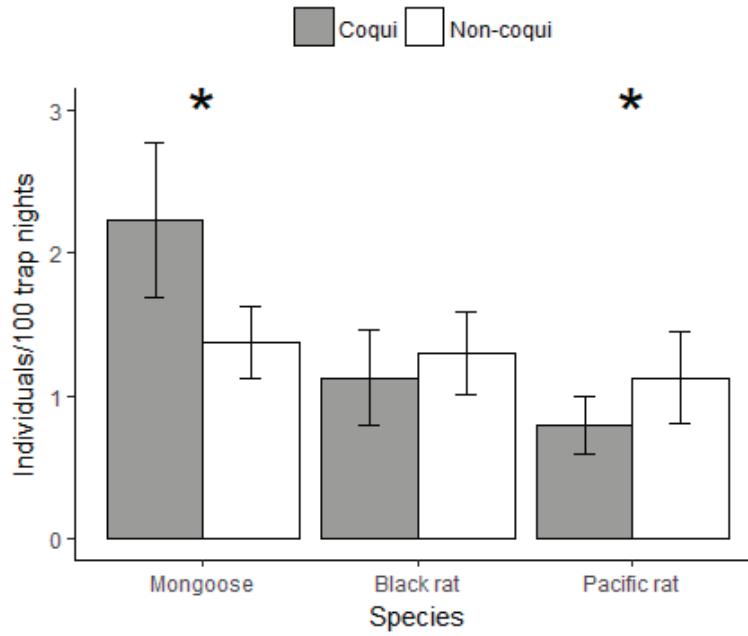
Fig. 2 Mean relative abundance indices (individuals/100 trap nights) with standard error bars for small mammals across 12 coqui and non-coqui sites. Significance based on GLMMs: * p < 0.05
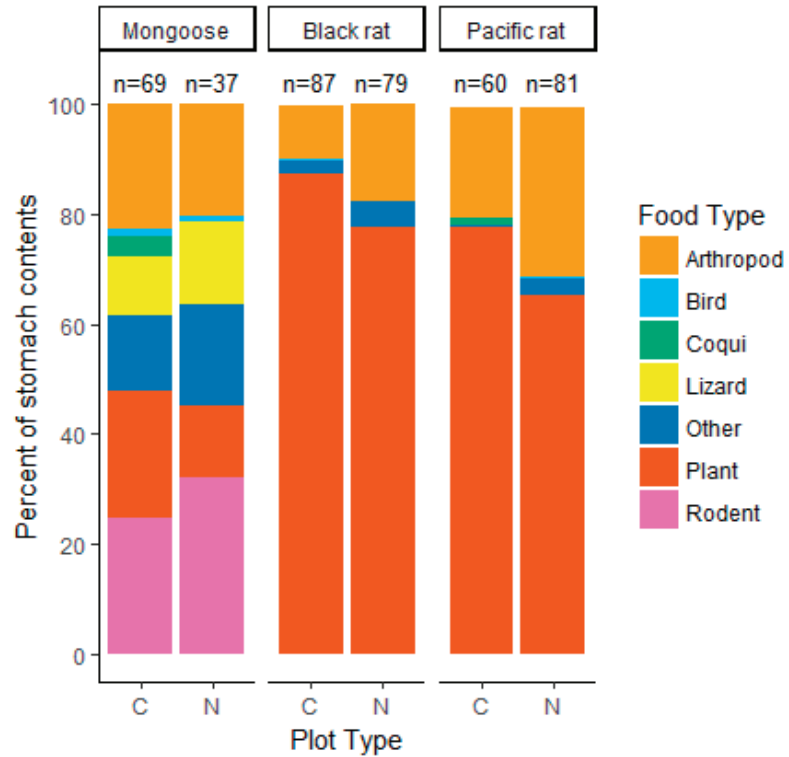
Fig. 3 Mean percent (%) of major food types found in the stomachs of mongooses, black rats, and Pacific rats compared by plot type. Differences in percent of coqui in stomach contents between coqui plots and non-coqui plots were statistically non-significant for all three species. C=coqui plots N=non-coqui plots. *n does not include empty stomachs

Table

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 ΔAIC <2 criteria.

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