

THESIS

INVASIVE PREDATOR-PREY DYNAMICS AND MONITORING IN GUAM FORESTS

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ABSTRACT

INVASIVE PREDATOR-PREY DYNAMICS AND MONITORING IN GUAM FORESTS

Managing invasive predators on islands is a global conservation priority because they are causally linked to the extinction and endangerment of hundreds of insular species. Sympatric invasive prey species further threaten native biota and complicate invasive predator management; top-down and bottom-up trophic forces following invasive predator management can negate costly control efforts and worsen invasive predator impacts. The growing possibility of landscape-scale suppression of the invasive brown treesnake (*Boiga irregularis*) on the island of Guam created the needs for 1) a cost-effective tool for monitoring brown treesnakes' invasive endothermic prey, and 2) improved understanding of the trophic dynamics between brown treesnakes and invasive small mammals. To address the first need, we tested the accuracy of chew-cards as a rat density index. Chew-card counts were correlated with rat capture-mark-recapture density estimates across a range of rat densities found in the region, and we thus consider chew-cards a suitable tool for indexing invasive rat density in these tropical island forests. To address the second need, we conducted systematic visual surveys targeting brown treesnakes and small mammals for up to three years during and after predator (snake) control treatments. There was strong support for site-specific treatment effects of predator control, but consistent top-down and bottom-up trophic effects on average small mammal and snake counts, respectively. This work adds to our growing understanding of invasive predator-prey dynamics on islands and has direct management implications for predator control and ecological restoration on Guam. Specifically, small mammal monitoring and control are likely critical

components of a management strategy for long-term snake suppression to allow reintroduction of native vertebrates on Guam.

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PREFACE

Both chapters in this thesis are intended for publication in a peer-reviewed journal. Therefore, formatting, language and tense may differ between chapters. Both articles have at least one co-author, thus I use the plural pronouns “we”, “us”, and “our” throughout. The titles and full authorship for both chapters/manuscripts are listed below.

Chapter 1: Chew-cards may provide an accurate index of invasive rat densities in Mariana Island forests

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Chapter 2: Predator-prey dynamics following invasive predator control in tropical island forests

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CHAPTER ONE

CHEW-CARDS MAY PROVIDE AN ACCURATE INDEX OF INVASIVE RAT DENSITIES IN MARIANA ISLAND FORESTS

Introduction

Invasive species jeopardize worldwide biodiversity (Chornesky and Randall 2003), economies (Pimentel et al. 2005), and human health (Duraiappah et al. 2005) and cost trillions of dollars annually in ecological damages, economic losses, and management efforts (Pimental et al. 2001). Minimizing costs to control invasive species can make combatting this problem more feasible on a global scale (Buhle et al. 2004). Primary ways invasive species management costs can be reduced are via effective pathway and vector management (e.g., screening protocols), early detection and rapid response, and improved approaches to mitigation and restoration (Pyšek and Richardson 2010).

Islands are often the focus of invasive species research and control efforts. Housing an estimated quarter of Earth's plant and animal species, islands are biodiversity hotspots and targeting them can maximize conservation funds (Myers et al. 2000). However, isolation—the same feature that supports high endemism and richness (MacArthur and Wilson 1967)—makes islands remarkably susceptible to biological invasions (Whittaker and Fernández-Palacios 2007). In particular, introduced predators can easily exploit native species that have evolved under limited predation pressure (Doherty et al. 2016).

Rats (*Rattus* spp.) are difficult to detect, easily transportable, highly fecund, and adaptable. These anthropogenic commensal generalists have become established on over 80% of the world's islands (Towns et al. 2006) and now represent one of the most damaging and expensive biological invaders (Courchamp et al. 2003; Harper and Bunbury 2014). Invasive rats

have a myriad of impacts on island ecosystems. As direct predators of many small vertebrates, rats have caused extinctions or severe declines in birds (Atkinson 1985), reptiles (Case and Bolger 1991), and mammals (Harris 2009; Hanna and Cardillo 2014). Cascading effects shift interspecific dynamics, further deteriorating island communities and exacerbating destruction caused by rats (Campbell and Atkinson 2002; Kurle et al. 2008). On some islands, rats are a prey source for other invasive predators at higher trophic levels (e.g., cats, stoats, snakes; Savidge 1986, 1987; Murphy and Bradfield 1992; Bonnaud et al. 2007) and serve as vectors for novel pathogens to highly susceptible insular faunas (Pickering and Norris 1996).

Trapping (Carter et al. 2016) and rodenticides (Broome et al. 2014; Keitt et al. 2015) can reduce rat densities, and rodenticides are credited with rodent eradications on over 300 islands (Howald et al. 2007). However, cost-effective rodenticide treatments or other control efforts first require accurate target population density estimates to inform treatment timing and effort and to assess treatment efficacy (Kim et al. 2020). Capture-mark-recapture data are frequently used to produce robust density estimates (Otis et al. 1978; Kendall 1999; Williams et al. 2002; Wiewel et al. 2009a; Yackel Adams et al. 2011), but this method is notoriously expensive, time-consuming, and labor-intensive (Wiewel et al. 2009b). Developing cheaper and easier techniques for indexing density (i.e., count-based indices) is thus a priority. An effective count-based density index enumerates animal evidence and strongly correlates with true density across all possible densities and assumes detection is constant (Anderson 2003). Such indices should also be inexpensive, user-friendly, and applicable at large spatial scales (Williams et al. 2002; Engeman 2005; Engeman and Whisson 2006). Counts of animal observations (Fagerstone and Biggins 1986), automated camera photos (Engeman et al. 2006), tracks (Brown et al. 1996), chew-marks (NPCA 2010), bait-take rates (Byers 1975), hair deposition (Zielinski et al. 2006), physical

captures (Village and Myhal 1990), and feces detections (Mills et al. 2005) have all been used to index diverse small mammal populations across the globe with varying successes and limitations.

Chew-track-cards, a tool for indexing rodents, are baited pieces of plastic that retain animal tooth impressions and footprints. Seminal work conducted in Australia and New Zealand determined that chew-track-cards are a cost-effective means of accurately indexing small mammal abundance across multiple species, including rats (Caughley et al. 1998; Sweetapple and Nugent 2011; Kavermann et al. 2013; Ruffell et al. 2015; Burge et al. 2017; Forsyth et al. 2018). However, no study since Caughley et al. (1998) has validated chew-card counts against measured density estimates; latter studies simply document relationships among multiple small mammal abundance indices (Sweetapple and Nugent 2011; Kavermann et al. 2013; Ruffell et al. 2015; Forsyth et al. 2018; Nottingham et al. 2020). Further, indices should be tested and calibrated in other ecosystems, regions, and climates before they are used to approximate population sizes beyond the range of existing studies. For example, rats on temperate islands (e.g., New Zealand) respond differently to baits than rats on tropical islands (Keitt et al. 2015). Regionally based differences in foraging behavior may affect chew-track-card interaction frequencies and influence chew-track-card effectiveness in the tropics. Consequently, evaluating chew-track-cards on tropical islands informs the ability to apply a detection tool developed in temperate environments to other ecosystems.

The Mariana Islands are optimal locations for field validating chew-track-cards in the tropics, as they have a range of rat densities and are considered islands of high global conservation concern. We tested the accuracy of chew-track-cards as a count-based index of invasive rat density on two Mariana Islands with low and high rat densities by comparing chew-

track-card counts to capture-mark-recapture density estimates and manipulated densities to test whether the relationship was retained. Our methods allowed us to identify caveats to their use in tropical systems, described herein. Our study informs future management efforts by testing a rat index that, if effective, should reduce costs and improve efficiency for monitoring invasive rat populations in the Marianas and potentially similar tropical islands.

Methods

Study area

Three rat species, Pacific rat (*Rattus exulans*), brown rat (*Rattus norvegicus*), and black rat (*Rattus rattus*), have been established in the Mariana Islands—where bats are the only native mammals—for centuries (Kuroda 1938; Baker 1946; Steadman 1999; Freycinet 2003; Musser and Carleton 2005). Despite their proliferation, rats have had minimal direct impacts on native plants and animals in the Marianas compared to other oceanic islands (Fritts and Rodda 1998). Rats did not become a major conservation concern in the Mariana Islands until they became key prey for a novel apex invader, the brown treesnake (*Boiga irregularis*; Fritts and Rodda 1998).

The brown treesnake was accidentally introduced from its native range in the South Pacific (Shine 1991) to the naturally snake-free island of Guam, the southernmost and largest of the Mariana Islands, shortly after World War II (Fritts 1988; Rodda et al. 1999). By the 1980s the snakes were widespread and abundant across Guam (Savidge 1987) and caused ecological destruction in their wake (Rodda and Savidge 2007). Most notably, brown treesnakes extirpated most of Guam's forest birds (Savidge 1987; Rodda et al. 1997; Fritts and Rodda 1998; Wiles et al. 2003). Decades of research and adaptive management have culminated in the potential for landscape-scale brown treesnake suppression in Guam forests (Clark et al. 2018; Siers et al.

2019, 2020). Due to their importance as a prey base for snakes on Guam and the potential effects they have on snake control tool efficacy (Gragg et al. 2010; Siers et al. 2018), synchronous monitoring and control of rats is likely to be important.

Our work on Guam occurred during 2018 within a 55-ha plot of homogenous disturbed limestone forest located on Andersen Air Force Base, termed the Habitat Management Unit. An extensive, interagency restoration plan including removal of non-native animals, constructing barriers, native plant recovery, and bird reintroductions exists for the Habitat Management Unit (Siers and Savidge 2017). A fence surrounding the entire site was erected in 2010 to prevent brown treesnake immigration and exclude nonnative deer (*Rusa Marianna*) and pigs (*Sus scrofa*; Siers and Savidge 2017). The Habitat Management Unit has undergone two major periods of experimental lethal snake treatments involving aerial deployment of toxic baits (dead neonatal mice laced with acetaminophen; Clark and Savarie 2012; Dorr et al. 2016; Siers et al. 2019). The first occurred during 2013 and 2014, and the second started during our study in 2018 and is ongoing. We expected rat densities to increase following snake treatments via prey release (Ritchie and Johnson 2009), thereby providing a gradient of rat densities to test chew-track-cards on Guam. However, rat populations remained low, so in 2019, we conducted additional fieldwork on Rota to test our index method on an island with higher rat densities (Savidge 1987; Wiles et al. 2003; Wiewel et al. 2009a, b). Rota lacks brown treesnakes and, consequently, its forests are more ecologically intact with abundant native birds and fruit bats that represent what successfully restored forests may resemble on Guam.

Field methods

Grid selection and setup

We sampled nine forest grids on Guam ($n = 4$ grids) and Rota ($n = 5$ grids; Figure 1.1). All four grids on Guam were located within the Habitat Management Unit, hereafter G1, G2, G3, and G4, with selection, in part, designed to avoid threatened and endangered plant species. Of the five grids sampled on Rota, three were part of a concurrent rat study where high populations were anticipated (Page 2020), hereafter R1, R2, and R3 (corresponding to grids 1, 2, and 5 in Page 2020). The other two grids had historically high rat densities, hereafter R4 and R5 (mixed and *Leucaena* forest habitats, respectively, in Wiewel et al. 2009a, b). After sampling each grid once, we manipulated rat densities in G2, G3, and R4 before resampling to increase our sample size without having to establish new grids. We resampled G3 and G2 three months after lethal snake treatments that we anticipated would increase rat density via predator reduction. At R4, we humanely euthanized rats to manually reduce the population size before resampling with chew-track-cards. To denote this, we appended .1 and .2 to the codes of grids we sampled twice (e.g., first sampling period in G2 = G2.1, second sampling period in G2 = G2.2).

All Guam grids and Rota grids R4 and R5 consisted of 11×11 trap stations with 12.5-m intervals between each station (grid area = 1.56 ha). The remaining three grids on Rota (R1 – 3) were part of a concurrent study (Page et al. 2020) and consisted of 10×10 trap stations with 10-m intervals between each station (grid area = 0.81 ha). For the larger grids, we placed one large folding Sherman® live trap (H.B. Sherman Traps, Inc., Tallahassee, FL, USA) at each trap station ($n = 121$; spacing = 12.5 m) and one wire basket trap (Haguruma® and Uni-King®, Standard Trading Co., Honolulu, HI, USA) at every other station ($n = 36$; spacing = 25 m) for a total of 157 live traps per grid (every other station had two traps). We baited traps with a mixture of peanut butter, oats, and food-grade paraffin wax (to help keep the bait ball solid in the tropical heat) and live-trapped for 10 consecutive nights. For the smaller grids (R1, R2, and R3), we

placed one basket trap at every station ($n = 100$; spacing = 10 m) and baited traps with a combination of coconut and peanut butter. We live-trapped at these grids for four consecutive nights. Both grid sizes were at least four times the target species' home range estimates (Bondrup-Nielson 1983), and spacing between stations was less than twice the target species' daily mean maximum distances moved (MMDM) in accordance with best practices (Otis et al. 1978; Wilson and Anderson 1985; Sun et al. 2014). Further, both trap and bait types are proven to be effective in this system (Baker 1946; Wiewel et al. 2009a, b; Page 2020). We accounted for trapping duration and all other sampling differences in our analyses.

Data collection

We conducted capture-mark-recapture trapping of rats within two days of a five-day card deployment so the cards would reflect the same rat densities estimated with mark-recapture methods. We did not deploy live-traps and cards simultaneously to avoid competing baits on the landscape. We set baited, fixed-open traps two days prior to the start of live-trapping to allow the rats to acclimate to their presence (Wiewel et al. 2009a, b) and placed traps on flat ground beneath or adjacent to cover (e.g., vegetation, debris, rocks) to provide shelter from sun and rain. We checked traps every morning and recorded the trap station, the lowest possible taxonomic classification (e.g., *Rattus* spp.), and marked status (new or recaptured) for each captured individual. For newly captured rats, we determined sex and age via the external genitalia (imperforate vagina = juvenile female; perforated vagina = adult female; undescended testes = juvenile male; descended testes = adult male) and measured mass and head-body length. We double marked each individual by inserting a numbered, metal ear tag (Style #1005-1, National Band and Tag Company, Newport, KY, USA) into each ear in the distal one-third of the pinna (Wang 2005) before releasing at the capture location. We closed traps after the morning check to

prevent mid-day captures when temperatures were highest to minimize heat-related trap mortalities. In the late afternoon/evening, we set and re-baited all traps and repaired and replaced them as necessary.

We constructed rat indexing cards by cutting 4-mm thick, twin-walled polypropylene sheeting into 90×180 -mm rectangles and aligned the flutes parallel to the short sides of the cards (Figure 1.2). We folded cards in half crosswise, cut a shallow slit lengthwise along the center of one half to prevent flutes from pressurizing when baited, and filled flutes with bait (peanut butter-paraffin mixture) to 2 – 3 cm from each edge (Figure 1.2). On a subset of cards (i.e., chew-track-cards), we placed 60×75 mm of contact paper in the center of the bottom halves of the cards and applied a 2 – 3-cm wide strip of black ink onto the plastic surrounding the contact paper (Figure 1.2b). We placed additional bait (~ 1 oz) at the top of the contact paper (Figure 1.2b). This design was intended to lure rats to walk through the ink and step on the contact paper, leaving visible tracks that could be identified to order (Rodentia [rats], Decapoda [crabs], Squamata [lizards], or Carnivora [cats]). However, we found this use of tracking ineffective due to the Marianas' wet climate (ink ran or faded) and the inability to distinguish rat tracks from those of non-target species. We therefore stopped deploying chew-track-cards (Figure 1.2b) and instead deployed only chew-cards (Figure 1.2a) after completing our fourth grid (G4) in August 2018.

At each station, we stapled the cards to trees approximately one meter off the ground with the baited half up (Figure 1.2). We checked the cards each morning and recorded if a card had chews from rats. To identify species chews, we cross-referenced our cards with published reference photos and guides (Sweetapple and Nugent 2001; Manaaki Whenua Landcare Research 2020) and cards we placed in captive rat enclosures on Guam. We did not replace,

repair, or re-bait cards during the five-day deployment to simulate the cards being left in the field without maintenance, as they would likely be in practice (Sweetapple and Nugent 2011). We removed the cards and all associated materials at the conclusion of the five-day card deployment.

To confirm or refute rat chew identification, we deployed a RECONYX® PC900 HyperFire Professional Covert Camera Trap (RECONYX®, Holmen, WI, USA) at six randomly selected cards from each grid, except R2 and R3, for the duration of the five-day card deployment. We initially programmed the cameras to trigger upon motion detection (for G1, G2.1, G3.1, G4, G3.2) but switched to a time-lapse setting after December 2018 (for grids G2.2, R1, R4.1, R4.2, and R5) to better capture species interactions with the cards. We reviewed all camera-trap photos and cross-referenced our field assessments of rat chews with the photos from the corresponding camera-trap night. We measured daily rainfall via rain gauges at all grids except R2 and R3.

Data analyses

We calculated individual body condition indices by dividing mass by head-body length based on the allometric relationship between the two variables (Stevenson and Woods 2006). We used two-sample, one-tailed Student's *t* tests ($\alpha = 0.05$) to assess the differences between masses, head-body lengths, and body condition indices between rats trapped on Guam versus Rota.

Density estimation

We used spatially explicit capture-recapture models (Efford 2004) executed in the R package *secr* 4.2.2 (Efford 2020; R Core Team 2020) to estimate rat density and Akaike's Information Criterion corrected for small sample size (AIC_c) to determine the best-supported models in our candidate sets (Burnham and Anderson 2002). We derive model-averaged density

estimates and standard errors from the final model set (Burnham and Anderson 2002). Rationale for all models came from a combination of results from preceding studies, the biology and life history traits of small mammals, knowledge of our system, and subject-matter area expertise, intuition, and experience, described herein.

Capture probabilities can vary by time, behavior, and individual heterogeneity (Otis et al. 1978). Small mammals tend to be wary of new objects (Temme and Jackson 1979; Inglis et al. 1996; Clapperton 2006; Yackel Adams et al. 2011) and, in the Marianas, have previously exhibited a two-day neophobic response where capture probabilities during the first two nights were lower than capture probabilities on the remaining occasions, even after a trap acclimation period (Wiewel et al. 2009a, b). Other hypothesized patterns of temporal variation included a time trend where rat capture probabilities changed linearly (on the logit-scale) over all capture occasions (Cusack 2011; Morehouse and Boyce 2016) or via daily changes in weather (e.g., rain; van Hensbergen and Martin 1993; Stokes et al. 2001; Wiewel et al. 2009a, b). Behavioral responses are also well documented across taxa and systems and occur when animals become ‘trap-happy’ or ‘trap-shy’ (Kahn 1992; Hammond and Anthony 2006) and are associated with a positive (e.g., food) or negative (e.g., stress) trap experience (Otis et al. 1978). Lastly, we based our *a priori* hypotheses regarding individual heterogeneity largely on Wiewel et al. (2009a, b) who found higher capture probabilities for reproductively active (i.e., adult) female small mammals in the Marianas. Age and size affect capture probabilities of many global species (King et al. 2003; Hiller et al. 2010; Singh et al. 2014); thus, we tested an addition hypothesis that individuals in lower body condition may be more attracted to our baits, resulting in higher capture probabilities.

We analyzed data from each grid separately. At grids with sufficient data (R4 – 5), we used a two-step approach to model capture probabilities from which we derived density estimates. First (Step 1), we accounted for all available hypothesized sources of individual heterogeneity in capture probability by including sex, age, and body condition index as predictors. We fit models with additive combinations of temporal covariates, including a two-night neophobic response (neophobia2), a time trend (Time), daily rainfall amount (rain; when available), a behavioral response (behavior), and no temporal variation (.). We did not include neophobia2 with either rain or Time in the same model. We retained the best-supported temporal variation structure(s) to test all possible additive combinations of individual covariates, including sex, age, body condition index, and no individual heterogeneity (Step 2). We failed to collect individual covariate and rain data for Rota grids R1 – 3, and thus did not have sufficient data for the two-step approach. For these grids, we simply fit all other possible additive combinations of the remaining temporal covariates. We held the spatial parameter (σ) constant (i.e., null) in all models.

Data from grids on Guam were too sparse (< 10 total captures per grid) to use spatially explicit models, so we used simpler closed-capture conditional likelihood models (Huggins 1989, 1991) from Program MARK 6.2 (White and Burnham 1999). We combined encounter histories from all Guam grids, with grids differentiated by group, and, with the sparse data, were able to fit two simple models: constant capture probability (i.e., a null model) and a model with a behavioral effect (Appendix 1). We used the derived model-averaged abundance estimates to calculate density by dividing each estimate by an effective trapping area (ETA; Wilson and Anderson 1985; Efford 2004). We used results from the spatially explicit analysis to inform our choice of boundary strip (full MMDM) for our ETA calculations (Appendix 2). For grids with no

movement metrics we used the mean MMDM of all other grids from the same island and calculated standard errors using the delta method (Seber 2002).

Chew-card density index calibration

We did not analyze tracking ink data because we deemed our tracking ink methods ineffective in this system and instead treated all cards as ‘chew-cards’ and limited our analysis to teeth impressions. We summed the cumulative number of cards with rat chews for each deployment day (1 – 5 days) for each grid and calculated the daily proportion of cards with rat chews. We used linear regression models and Pearson’s product-moment correlations, implemented in base R, to assess the relationship between card indices and capture-mark-recapture density estimates. We conducted these analyses five times, where the predictor variable in each regression analysis was the proportion of cards that detected rats after one, two, three, four, and five deployment nights, respectively, for each grid. We evaluated diagnostic plots to ensure these models met the linear regressions assumptions of homoscedasticity and normality.

Results

Capture-mark-recapture of live-trapped rats

We captured 233 individuals a total of 444 times in 10,315 corrected trap nights over the course of our study (Table 1.1), where non-functioning and falsely sprung traps represented no trapping effort or a half night of trapping effort, respectively (Nelson and Clark 1973). We trapped almost 11 times as many rats on Rota ($n = 213$ rats) as we did on Guam ($n = 20$ rats) with approximately half the trapping effort (Table 1.1). We determined sex and age for 194 captured individuals. Of those, we captured more males than females and more adults than juveniles on both islands (Table 1.1). Rats were heavier ($t = 8.92$; $df = 180$; $p < 0.0001$; Figure

1.3a), slightly longer ($t = 1.45$; $df = 180$; $p = 0.15$; Figure 1.3b), and had higher body condition indices ($t = 10.48$; $df = 180$; $p < 0.0001$; Figure 1.3c) on Guam compared to Rota.

We found that rat capture probability on both islands exhibited a behavioral effect (Figure 1.4; Appendix 1). There was little evidence of additional temporal variation in capture probability; a model with a two-night neophobic effect was the best-supported model for one grid on Rota ($R5$; $\hat{\beta} = 0.07$; $\widehat{SE}[\hat{\beta}] = 0.24$). We found no evidence of variation in capture probability among individuals (associated with body condition, age, or sex) and no evidence that capture probability varied as a function of rain (Appendix 1).

Our grids represented a wide range of rat density estimates (\widehat{D} range = 0.00 – 34.73 rats/ha) to test card indices. Rat densities on Rota (\widehat{D} range = 7.09 – 34.73 rats/ha) were much higher than those on Guam (\widehat{D} range = 0.00 – 1.93 rats/ha). At the two grids we re-sampled after lethal snake treatments on Guam, G3.2 and G2.2, rat density increased by 28% and 41%, respectively, but remained comparatively low even three months after snake control was applied ($\widehat{D} = 1.01$; $\widehat{SE}[\widehat{D}] = 9.65$ and $\widehat{D} = 1.93$; $\widehat{SE}[\widehat{D}] = 0.18$, respectively; Appendix 1).

Chew-cards

We deployed 1,389 chew-cards during 60 days of sampling on Guam ($n = 6$ deployments) and Rota ($n = 6$ deployments). The mean proportion of cards chewed after five days was 0.12 (SD = 0.09) on Guam and 0.73 (SD = 0.24) on Rota. On average, the proportion of cards with chews increased by 0.03 (SD = 0.03) a day on Guam and 0.10 (SD = 0.10) a day on Rota.

The proportion of cards chewed by rats was correlated with density estimates when cards were left in the field for at least three nights (Fig. 5). The correlation increased daily and was

highest after five nights ($R^2 = 0.74$). When chew-cards were deployed for five nights, a 10% increase in the proportion of cards chewed equated to an estimated increase in rat density of approximately 2.4 individuals per ha:

$$\widehat{\text{rat density}} = 23.51(\text{cumulative proportion of cards with rat chews}).$$

Note that an intercept (B_0) was not included in this equation because it rounded to zero.

We deployed cameras on 60 cards and processed > 24,000 photos with animals on the cards. Twenty-eight of these cards had field recordings of rat chews, and we confirmed rat identification via photos at 27/28 (96%) of the card/camera nights (e.g., Figure 1.6).

Discussion

Count-based indices are commonly used as relative measures of abundance or density (McKelvey and Pearson 2001). However, indices have been criticized because 1) assumptions are often ignored and untested (e.g., constant detection probability; Anderson 2001, 2003; Skalski 2005) and 2) are frequently used to make inferences or inform management decisions without any preceding testing or calibration (Rosenstock et al. 2002). Nevertheless, indices can represent relative differences in abundance or density for specified regions (Wilson et al. 1996; Engeman 2003) if *in situ* calibration studies show a positive monotonic relationship between the count and true abundance or density across the range of possible abundances or densities in a given region (Nichols 1992). Our study tested the above-mentioned criteria, and we conclude that chew-cards provided a valid index of rat densities in Guam and Rota forests and may be effective on similar tropical islands.

Specifically, counts from chew-cards deployed for 3 – 5 nights correlated with rat capture-mark-recapture density estimates. This relationship was retained across rat density

estimates ranging from 0 – 35 rats/ha and after management. The correlation between the proportion of cards with rat chews and capture-mark-recapture density estimates increased daily and was highest after five nights, when nearly three quarters of the variance in capture-mark-recapture density estimates was predicted by variation in chew-card proportions ($R^2 = 0.74$). Accordingly, chew-cards should be deployed for a minimum of three nights, but five nights is optimal as this duration provided the smallest standard error around the regression line. Evaluating longer chew-card deployment periods (6 + nights) may be advantageous as additional nights might have even stronger correlations with rat density. However, the proportion of cards chewed will eventually stabilize or become saturated (when all the cards are chewed), and this may occur more quickly at high rat densities (Forsyth et al. 2018).

We were confident that rat chews were correctly identified in our study and are easily distinguished from non-target chews (e.g., feral cats [*Felis catus*] and crab (*Coenobita brevimanus*; *Birgus latro*) pinches) as confirmed by our camera trap data. Specifically, rats were photographed chewing cards at nearly all cards positive for rat chews (27 of 28 [96%] card/camera nights). The single unconfirmed chew was likely not misidentified but was more likely not captured because the camera's motion detection did not trigger. We switched camera settings from motion detection to time-lapse after this occurrence to improve rat detection on cameras, and all rat chews corresponding to a camera-trap night were photographed thereafter. Our study was the first to confirm chew-card species identification with cameras, as recommended by Forsyth et al. (2018).

We encountered significant issues with tracking ink during our study. First, the Marianas' tropical climate caused the ink to run and fade. Second, a multitude of non-target species (e.g., geckos, skinks, crabs, snails/slugs, ants, worms) left unidentifiable tracks that made

distinguishing any rat tracks difficult, time-consuming, and erroneous. Similar to other studies, we found that tracking ink provides little additional information relative to chew marks alone (P. J. Sweetapple; pers. comm. 08 Sep 2018), and recent studies have discontinued its use in New Zealand (Ruffell et al. 2015; Burge et al. 2017; Forsyth et al. 2018; Nottingham et al. 2020). Protecting the tracking ink and contact paper from the elements (e.g., placing them in tunnels) may reduce these issues in the tropics. A ‘tracking tunnel’ method was successful on tropical islands in the Caribbean with a similar non-target assemblage consisting of small lizards and invertebrates (Shiels et al. 2020). However, additional tracking ink work may not be pressing, given our promising findings with chew-cards.

Non-targets may further hinder chew-card efficacy in Mariana Island forests via bait consumption and interspecific interference. We observed bait consumption by ants in the field, and reduced bait availability likely reduces chew-card attraction/effectiveness. In forests with abundant ants, chew-cards may be ineffective (pers. obs.). Use by non-targets may affect rat chew-card detection (i.e., interspecific interference); for example, two studies in New Zealand found that interspecifics were less likely to chew cards if they had already been chewed by another species (Sweetapple and Nugent 2009; Burge et al. 2017). Rats may be deterred from chew-cards if other species, especially stinging ants (e.g., little fire ants [*Wasmannia auropunctata*]) or coconut crabs, known predators of rats, are present. Further investigations of the relationships among rat chew-card detection rates, bait availability, and non-target species is warranted. Non-target exclusion methods could also be explored.

Our study results suggests that chew-cards can be appropriate for monitoring changes in rat distribution or relative density over space or time in association with invasive predator (e.g., brown treesnake) occurrence or suppression efforts in Mariana Island forests. Chew-cards have

several advantages over capture-mark-recapture density estimation, at the forefront of which is cost. Extrapolating from cost analyses conducted by Wiewel et al. (2009b) and Sweetapple and Nugent (2011), we calculated that a single 11×11 grid with 12.5-m spacing costs roughly 10 times more to employ capture-mark-recapture methods (~ US\$3,000) than chew-cards (~ US\$300). Like many indices, the reduced cost and simplified logistics of chew-cards make them more feasible for application at larger scales. Chew-cards also require less training than capture-mark-recapture sampling (e.g., no animal handling) and minimal quantitative skills to use and interpret. However, capture-mark-recapture density estimation remains vital to scientists and invasive species managers, providing measures of precision and demographic and morphological data necessary for many studies or management decisions.

Controlling invasive species on islands is a global conservation priority (Doherty et al. 2016), and cost-effective monitoring tools can stretch limited resources and enhance our understanding and management of islands with invasive species. Chew-cards can provide accurate indices of differences in rat densities in Mariana Island forests and potentially similar habitats and are a cheaper alternative to capture-mark-recapture sampling when relative differences in density are of interest and measures of precision or ancillary data are unnecessary. This is likely to be the case for many situations in the Marianas because rats are, foremost, prey for a more damaging invasive predator, the brown treesnake; chew-card based indices will likely detect the major fluctuations in prey density that we expect following effective management of invasive predators (Howald et al. 2007; Lardner and Yackel Adams, *unpublished data*). Further, with reduced costs and simplified logistics, chew-cards can be deployed more often or in more areas to gather estimates of relative rat densities and precision over time and space. These data could be used to inform invasive species control efforts, assess treatment efficacy, and

investigate invasive predator-prey dynamics, all of which improve success of invasive species management on islands.

Table 1.1) Corrected trap nights^a, number of individual rats (*Rattus* spp.) captured, and total number of captures (including recaptures), sex (M = male; F = female; U = undetermined sex), and age (A = adult; J = juvenile; U = undetermined age) for each sampling grid in Guam and Rota forest habitats during June 2018–August 2019.

Grid	Date	Corrected trap nights ^a	Number individuals	Total captures	Sex			Age		
					M	F	U	A	J	U
Guam										
G1	11–20 Jun. 2018	1,297.0	1	1	1	0	0	1	0	0
G2.1	19–28 Jul. 2018	1,155.5	4	5	2	2	0	4	0	0
G3.1	19–28 Jul. 2018	880.5	3	3	2	1	0	3	0	0
G4	04–13 Aug. 2018	1,009.5	0	0	0	0	0	0	0	0
G2.2	02–11 Feb. 2019	1,247.5	6	7	5	1	0	5	1	0
G3.2	29 Nov.–08 Dec. 2018	1,161.0	6	11	4	2	0	5	1	0
Total		6,751.0	20	27	14	6	0	18	2	0
Rota										
R1	04–07 Jun. 2019	303.5	20	35	9	5	6	5	9	6
R2	11–14 Jun. 2019	341.0	12	14	4	4	4	2	6	4
R3	11–14 Jun. 2019	325.0	17	27	3	5	9	7	1	9
R4	28 Jun.–07 Jul. 2019	1,385.0	92	196	48	44	0	51	41	0
R5	27 Jul.–05 Aug. 2019	1,209.5	72	145	40	32	0	56	16	0
Total		3,564	213	417	104	90	19	121	73	19
Total		10,315.0	233	444	118	96	19	139	75	19

^aOne corrected trap night equals one active trap night corrected for sprung (via false trips and non-targets) and non-functioning/missing traps by considering them to represent half of a night of trapping effort and no trapping effort, respectively (Nelson and Clark 1973).

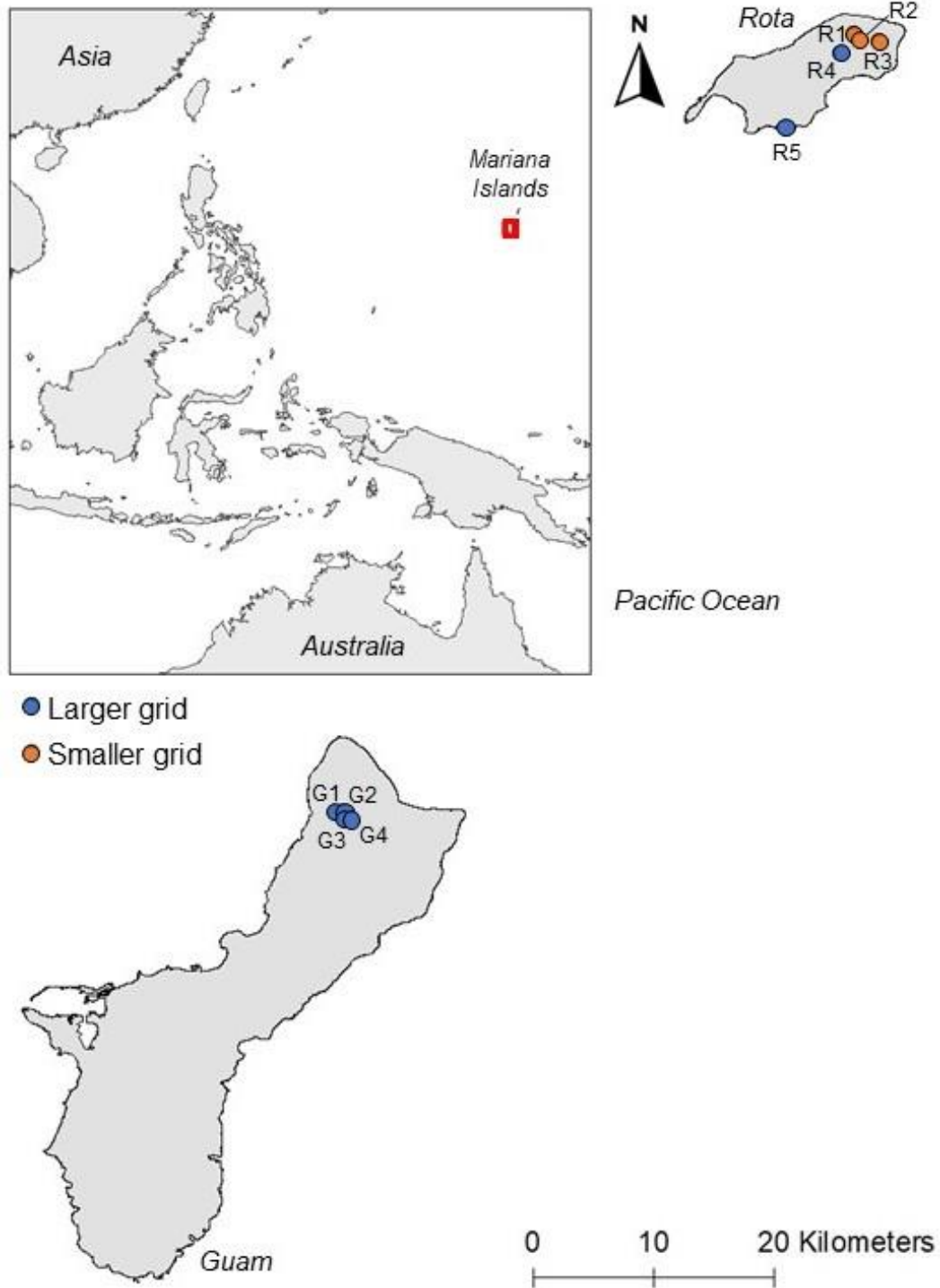


Figure 1.1) Nine forest grids sampled via chew-cards and live-trapping for rats (*Rattus* spp.) during June 2018 – August 2019 on Guam (G1 – 4) and Rota (R1 – 5) in the Mariana Islands. The blue circles indicate 11 × 11 grids with 12.5-m intervals between each station (grid area = 1.56 ha), and orange circles indicate 10 × 10 grids with 10-m intervals between each station (grid area = 0.81 ha).

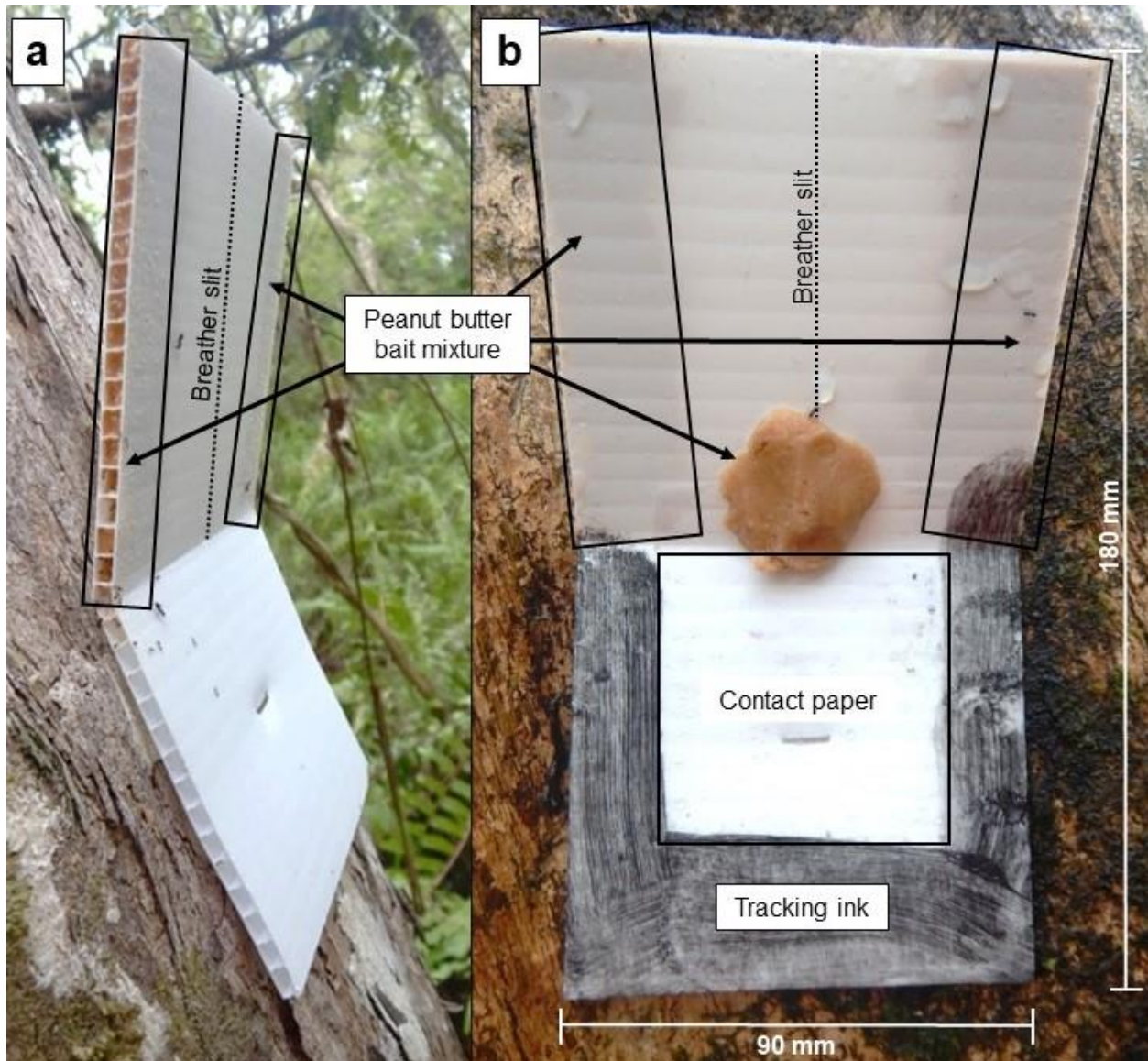


Figure 1.2) Chew-card (a) and chew-track-card (b) designs used to index rat (*Rattus* spp.) density in Guam and Rota forest habitats during June 2018 – August 2019. Designs were patterned after Sweetapple and Nugent (2011).

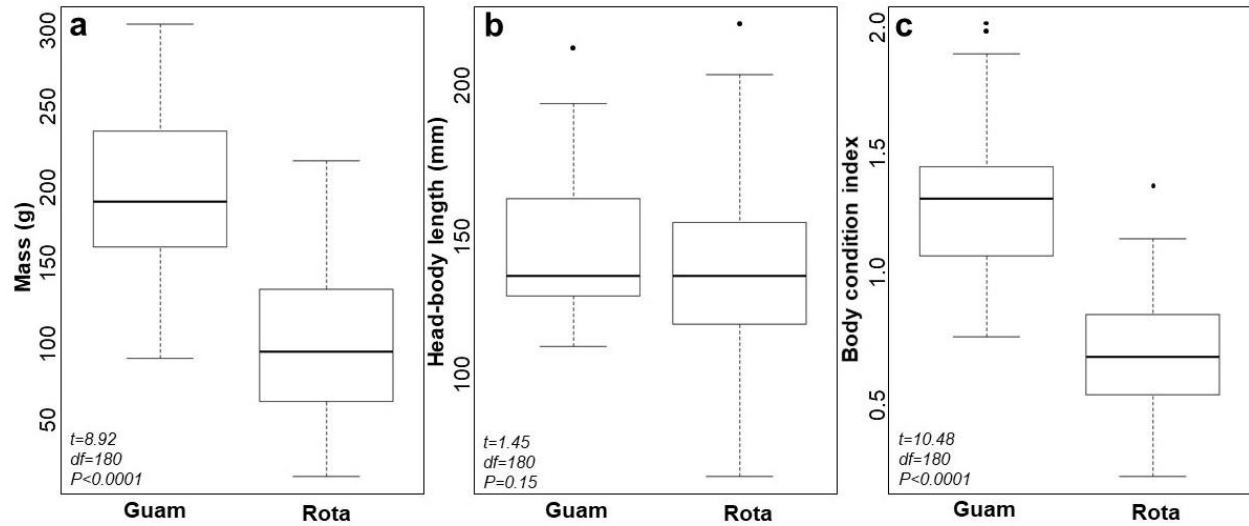


Figure 1.3) Boxplots depicting the medians (bold lines), interquartile ranges (IQRs; 25th – 75th percentiles; rectangles), minimums (first quartile-1.5*IQR) and maximums (third quartile+1.5*IQR; dashed lines), and any outliers (black dots) for mass (a), head-body length (b), and body condition index (c) for live-trapped rats (*Rattus* spp.) in Guam ($n = 19$ rats) and Rota ($n = 163$ rats) forest habitats during June 2018 – August 2019

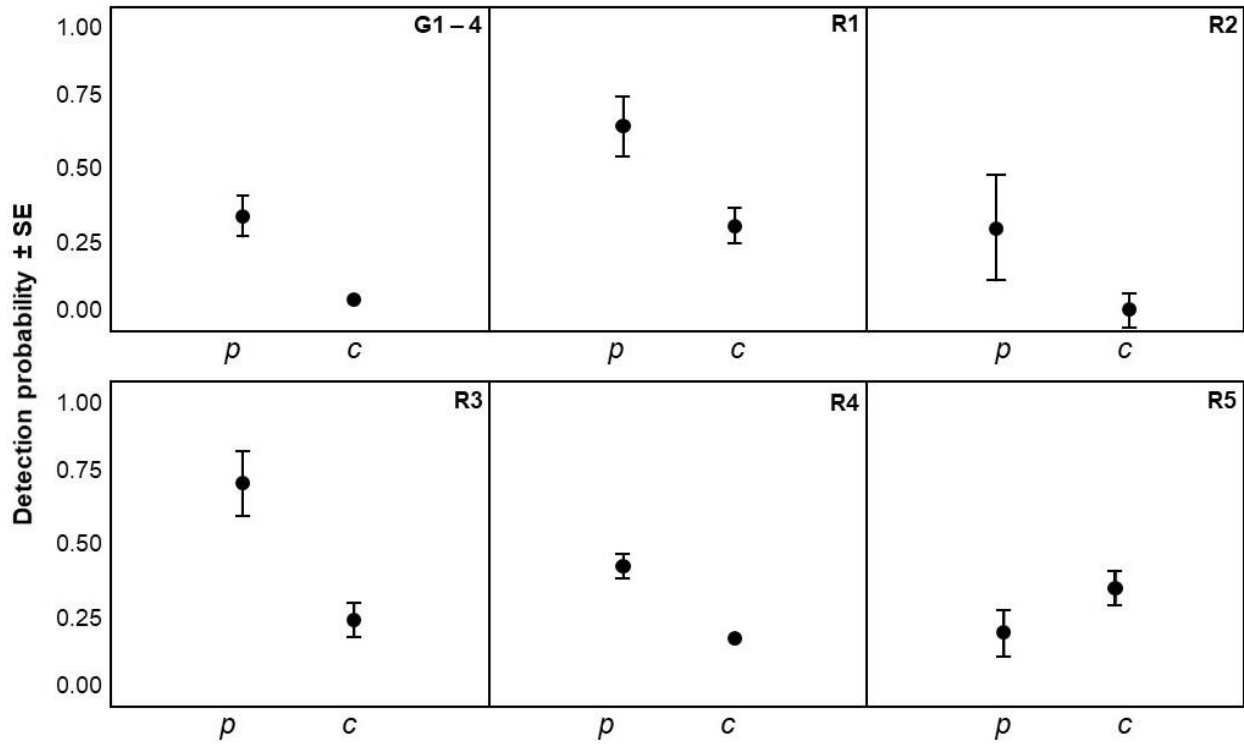


Figure 1.4) Capture (p) and recapture (c) probabilities from closed-capture conditional likelihood models for rats (*Rattus* spp.) in Guam (G1 – 4) and Rota (R1 – 5) forest habitats during June 2018 – August 2019.

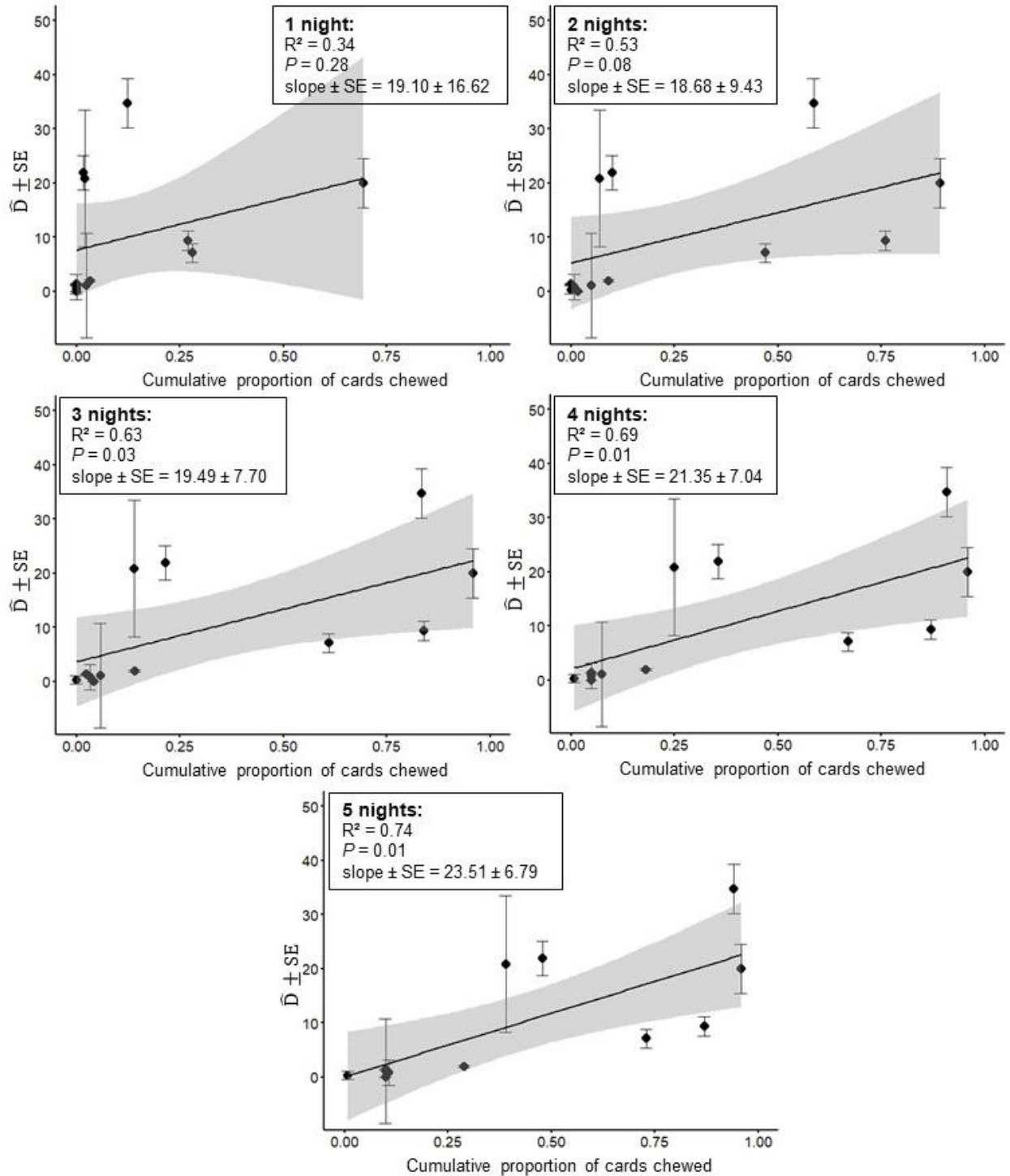


Figure 1.5) Linear regressions and Pearson’s product-moment correlations to assess the relationship between the cumulative proportion of cards with rat (*Rattus* spp.) chews after one, two, three, four, and five nights (x -axis) and capture-mark-recapture density estimates plus/minus standard error ($\hat{D} \pm SE$; y -axis) in Guam and Rota forest habitats during June 2018 – August 2019.

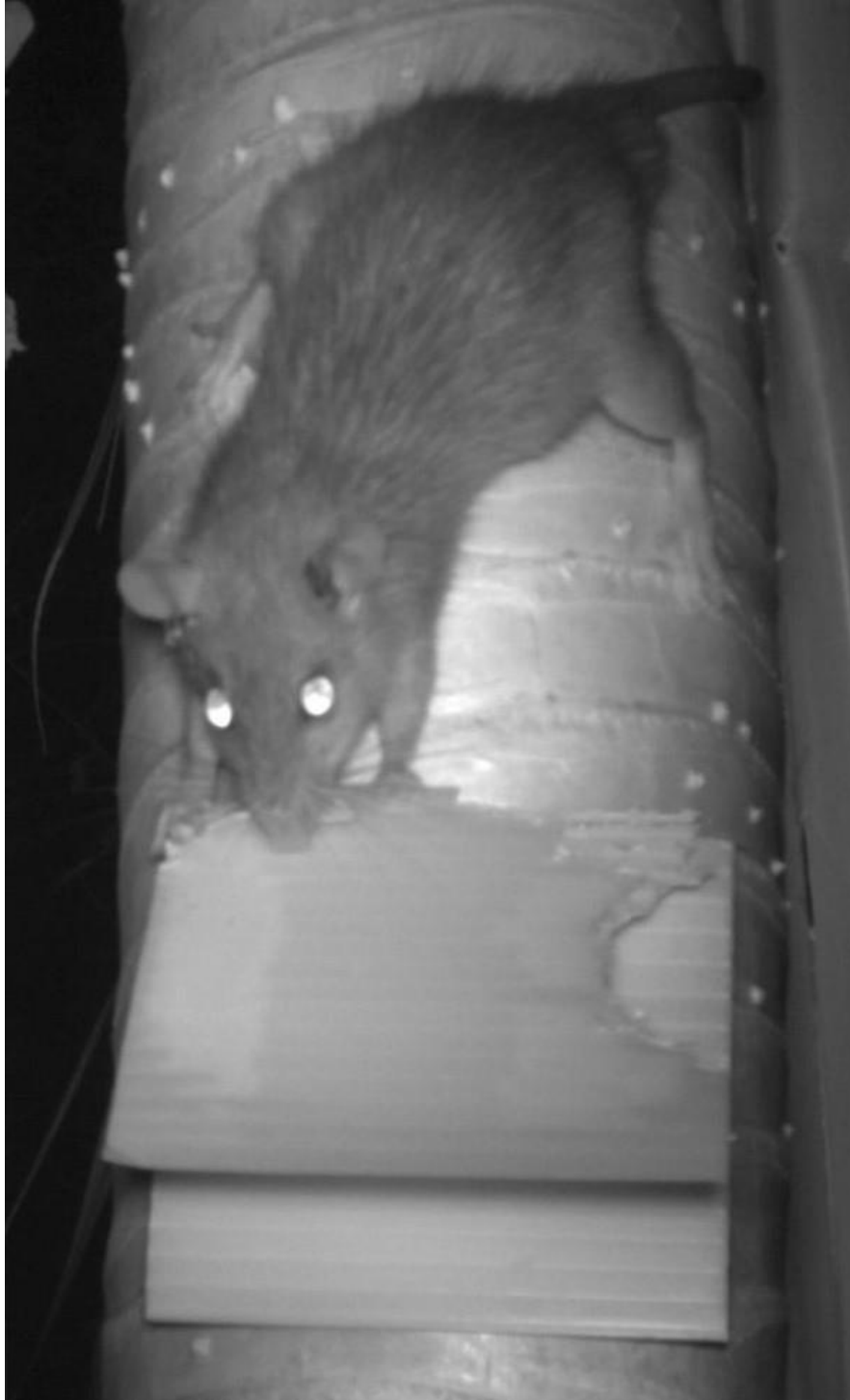


Figure 1.6) Trail camera photo of a rat (*Rattus* spp.) leaving visible chews on a chew-card. We used trail cameras to confirm or refute rat chew identification at randomly selected cards from each grid.

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CHAPTER TWO

PREDATOR-PREY DYNAMICS FOLLOWING INVASIVE PREDATOR CONTROL IN TWO ENCLOSED FORESTS ON A TROPICAL ISLAND

Introduction

Biotic interactions catalyze evolution and shape complex ecosystem dynamics (Wootton 1994; Abrams 2000). Predation is one of five main types of biotic relationships (in addition to competition, parasitism, mutualism, and commensalism) and occurs when energy transfers up a trophic level, from prey to predator, via the predator killing and consuming the prey (Stevens 2010). Coevolution of predator and prey species has led to a diversity of predator tactics and prey defenses, resulting in highly variable predator-prey population dynamics within and among ecological communities (McGhee et al. 2013). Disturbances (Ruiz-Capillas et al. 2013; DeMars and Boutin 2018) and seasonal variability (Rudolf 2012; Tyson et al. 2016) further muddle top-down (predator-driven) and bottom-up (resource/prey-driven) processes that affect vital rates, movement, behavior, and densities of both predator and prey species (de Roos et al. 1991; McCauley et al. 1993). In addition, ecosystems invaded by multiple vertebrate species across multiple trophic levels foster unpredictable predator-prey relationships and pose challenges to management (Murphy and Bradfield 1992; Courchamp et al. 2000; Ruscoe et al. 2011).

Multitrophic invasive vertebrate assemblages are well documented on islands because insular ecosystems are highly susceptible to biological invasions (Whittaker and Fernández-Palacios 2007). Historically, management of these assemblages on islands has prioritized invasive predators over invasive prey due to the disproportionate impact of novel predators on insular fauna (Doherty et al. 2016). However, trophic interactions among invasive predators and prey can negate predator control efforts or worsen their impacts via predator release of prey

species (Courchamp et al. 2000). Further, invasive species are, by definition, harmful to native insular faunas and are, therefore, important to control irrespective of compounding trophic interactions (Karl and Best 1982). For example, invasive Asian house/musk shrews (*Suncus murinus*) predated several native lizard species to low abundances on the Pacific island of Guam, and these shrews also serve as a food source for a more damaging invasive predator, the brown treesnake (*Boiga irregularis*; Fritts and Rodda 1998). In this and similar cases, tandem control of both the invasive predator and the invasive prey species maximizes conservation benefits by reducing predation on native species at multiple trophic levels and controlling bottom-up energy flow to invasive predators (Lurgi et al. 2017). However, such management is not without its own challenges and requires an understanding of predator-prey relationships. Invasive predator control efforts that do not account for trophic dynamics and/or seasonal variability have resulted in numerous adverse outcomes on islands, described herein.

Top-down processes following predator removal can lead to significant changes in prey densities and subsequent ecosystem regime shifts (Paine 1980; Terborgh and Estes 2010). For example, prey release occurs when prey populations surge following predator suppression (Vance-Chalcraft et al. 2007; Fung et al. 2015), and the impacts of rapid increases in invasive prey densities are at least twofold. A boom in invasive prey can result in greater harm to native species at lower trophic levels (Crooks and Soule 1999; Zavaleta et al. 2001). In some cases, the negative impacts of increased intermediate predation on native prey can outweigh the conservation benefits of invasive top predator removal (Courchamp et al. 1999). Additionally, abundant invasive prey can increase invasive predator subsistence (Chapuis 1995a, b) and fitness (Scroggie et al. 2018), with the potential to fuel rebound in the suppressed predator population after a time lag that allows for foraging and reproduction. Interestingly, predator removal may

have bottom-up consequences, a phenomenon that highlights the complexity of multitrophic invasive vertebrate management. Overall, invasive predator control that accounts for the high fecundity and reproductive rates of their invasive prey are likely to be more successful (Moller and Craig 1987).

Bottom-up limitations restrict species abundance at higher trophic levels (Cruz et al. 2013; Russel and Kaiser-Bunbury 2019). Murphy and Bradfield (1992) and Scroggie et al. (2018) sought to exploit bottom-up forces by killing invasive prey (rats [*Rattus rattus*] and rabbits [*Oryctolagus cuniculus*]) to manage invasive predators (stoats [*Mustela erminea*] and foxes [*Vulpes vulpes*] in New Zealand and Australia, respectively). Not only were invasive predator densities unaffected in both studies, but predators also switched from diets of primarily invasive prey to native species, exacerbating impacts to native bird populations via hyperpredation. We are not aware of any successful invasive predator control efforts that have depended exclusively on invasive prey removal; this may not be a reliable method on its own, but, rather, an important component of multitrophic invasive vertebrate management as a whole.

Seasonal variability further complicates invasive predator and prey management on islands. Scroggie et al. (2018) concluded that rainfall was a better predictor of invasive fox density than changes in invasive rabbit density, and Blackwell et al. (2003) observed invasive rat population eruptions following seasonal tree seeding as opposed to predator control. The hypothesized mechanism producing these and similar results from other studies (e.g., Previtali et al. 2009) is seasonal increases in precipitation and primary production. Increased vegetation production not only prompts bottom-up processes, leading to increased predator survival and recruitment (Scroggie et al. 2018), but also serves as a direct food source for some omnivorous predators (e.g., foxes; Leckie et al. 1998).

Documentation of interacting invasive predator and prey species on islands across regional climates has increased in recent years. However, the literature on this topic is still relatively sparse, often contradictory (e.g., Norbury 2017 vs. Scroggie et al. 2018) and almost exclusively from temperate islands in the Pacific Ocean. Additionally, there is a bias in the literature towards invasive mammalian predators with few exceptions (e.g., golden eagles [*Aquila chrysaetos*] on the California Channel Islands; Morrison 2007), likely due to the disproportionate number of invasive mammalian predators on islands (Doherty et al. 2016). Nonetheless, invasive reptiles are increasingly recognized as a major threat to insular faunas (Quick et al. 2005; Cabrera-Pérez et al. 2012; Vázquez-Domínguez et al. 2012; Reynolds et al. 2013; Monzón-Argüello et al. 2015; Hanslowe et al. 2018), but there is a dearth of knowledge about invasive reptilian predator and prey dynamics on islands.

Invasive brown treesnakes on the island of Guam are responsible for eliminating and reducing local fauna (Savidge 1987; Rodda et al. 1997; Fritts and Rodda 1998; Wiles et al. 2003). Research indicates that novel snake suppression treatments may reduce the invasive predator populations (Clark and Savarie 2012; Clark et al. 2018; Siers et al. 2019; Siers et al. 2020), and suppression of the snake may support reintroduction of some native vertebrate species, depending on the levels of predation they can sustain. However, interactions with invasive small mammals, a key prey base for brown treesnakes on Guam, may complicate this prospect. Small mammals may directly predate avian nests (Sheils et al. 2014), boost brown treesnake populations (Fritts and Rodda 1998; Rodda et al. 1999), or reduce the efficacy of snake control tools (Gragg et al. 2007). We used existing monitoring data following lethal snake treatments on Guam to quantify top-down, bottom-up, and seasonal processes driving brown treesnake and small mammal counts. Specifically, we investigated the effects of predator control

efforts on snake and small mammal counts over time, across tropical seasons, and between forest sites. We tested for support of prey release, lagged bottom-up effects, and detection effects that may have influenced our predator and prey indices (i.e., counts).

Methods

Study species and sites

The brown treesnake was unintentionally introduced from its native range in the South Pacific (Shine 1991) to the naturally snake-free island of Guam in the late 1940s or early 1950s (Fritts 1988; Rodda et al. 1999). In less than 40 years following the snake's arrival, most of Guam's forest birds had disappeared due to this invasive predator (Savidge 1987). Individuals from two endemic bird populations—ko'ko' (Guam rails; *Hypotaenidia owstoni*) and sihek (Micronesian kingfishers; *Halcyon cinnamomina cinnamomina*)—were captured and placed in captivity for species preservation and breeding (Haig and Ballou 1995). Reintroduction of these species to the island of Guam is contingent on brown treesnake suppression or eradication. Five species of invasive small mammals, the black rat (*Rattus rattus*), the brown rat (*Rattus norvegicus*), the Pacific rat (*Rattus exulans*), the house mouse (*Mus musculus*), and the Asian house/musk shrew are also present on Guam (Wiewel et al. 2009) and now serve as important prey for brown treesnakes.

We conducted our fieldwork in two enclosed forest habitats on Andersen Air Force Base in northern Guam: the Closed Population (CP) and the Habitat Management Unit (HMU). The CP is a 5-ha (224 × 224 m) enclosure that has been used for experimental studies on brown treesnakes since 2004 (Tyrrell et al. 2009; Christy et al. 2010). The CP consists of primary forest habitat located atop a corraline limestone plateau and is dominated by non-native tangan-tangan

(*Leucaena leucocephala*). The CP is geographically closed to brown treesnakes (i.e., no immigration or emigration) via a 1.5-m tall double-sided chain-link bulge barrier fence overlaid with welded steel mesh on both sides that was erected in 2004 (Perry et al. 1998; Rodda et al. 2010).

The HMU is a 55-ha plot of homogenous disturbed limestone forest (NAVFACPAC 2009) dominated by invasive smallflower chasetree (*Vitex parviflora*) and native sword fern (*Nephrolepis hirsutula*) and is a proposed location for native bird reintroductions. Habitat in the HMU is overall taller, denser, and more complex than that of the CP. An extensive, interagency restoration plan exists for the HMU and includes non-native species removal and an exclusion barrier that allows brown treesnakes to leave but not enter (Siers and Savidge 2017). The barrier was erected in 2010 and consists of a 1.83-m tall chain-link fence sheathed with wire mesh hardware cloth on the interior and top and an exterior bulge (Siers and Savidge 2017).

Populations of brown treesnakes and small mammals persist in the CP and HMU. Both fences have concrete bases with wire mesh skirts that prevent snakes from going beneath the fence and are inspected regularly and immediately repaired if damaged. Vegetation is cleared within two meters on either side of the fences to eliminate tree limbs that snakes could climb to escape or enter the enclosures. Both enclosures have designated parallel transects with cleared vegetation for conducting systematic visual surveys targeting brown treesnakes and small mammals (see ‘Visual surveys’). The CP has 29 transects that cover the entire enclosure; transects are 2-m wide and 220-m long and spaced at 8-m intervals (Figure 2.1). The HMU has five sets of three 200-m long transects dispersed within subplots representative of the enclosure (Figure 2.1).

Lethal snake (predator) treatments

We conducted lethal brown treesnake treatments during April 2017 – January 2020. Both sites were treated with toxic snake bait applications consisting of ~ 120 baits/ha, where each bait consisted of a dead neonatal mouse with an 80-mg acetaminophen tablet glued to its abdomen. Baits were distributed evenly throughout each enclosure, but the method of deployment and frequency of treatments varied between the two enclosures. In the CP, we hand-placed one bait along all interior transects (i.e., all but the two edge transects, 570 baits/treatment) every 2 – 18 weeks during March 2017 – February 2019, simulating an aerial application (Nafus et al. in review; Figure 2.2; Table A3.1). We used poles to place baits in the forest canopy (70%, $n = 399$ baits), midstory (20%, $n = 114$ baits), on the ground (5%, $n = 57$), and simulated bait “failures” (where the bait capsule does not open and is unavailable for ingestion; 5%) resulting in an 8 × 10-m grid array that simulated the optimized 9 × 9-m array for aerial delivery spatial distributions (*sensu* Siers et al. 2019). We randomized vertical bait placement locations for each treatment.

The U.S. Department of Agriculture implemented all HMU snake treatments and applied series of 2 – 3 treatments via helicopter every 12 – 36 weeks during October 2018 – February 2020 (Figure 2.2; Table A3.1). Baits were dispensed automatically every 9 m along parallel transects that were 9 m apart. The entire study area was treated in several hours. Within both enclosures, baits were applied in accordance with the Environmental Protection Agency pesticide registration label (Reg. No. 56228-34-92773), allowing for up to three applications with a maximum of 120 baits/ha per 4-month period and no more than 1,080 baits/ha annually.

Visual surveys

In association with snake control treatments, we conducted repeated nighttime visual surveys targeting brown treesnakes and small mammals along the designated linear transects

within each site (Christy et al. 2010). Two trained observers slowly walked (~ 0.5 – 1.5 km/hr) side-by-side while meticulously scanning the adjacent vegetation and ground with high-lumen headlamps (Wilma RX, Lupine Lighting Systems GmbH, Neumarkt, Germany). Each observer searched one side of the transect only and recorded all snake and small mammal observations for that side. Searches were strictly passive, that is, no habitat-altering methods were used to find animals (e.g., bark peeling, rock overturning). We collected start- and end-times for each transect and stop- and resume-times if surveys were stopped for any reason.

We walked all twenty-nine 220-m transects during every visual survey night in the CP and walked twelve 200-m transects during every visual survey night in the HMU. The frequency of visual survey nights changed over the course of our 3-year study depending on labor availability, weather, and funding. Typically, we completed 1 – 2 visual survey nights per week for each site. However, some weeks ($n = 7$ weeks) had as many as six survey nights, and there were several periods ($n = 3$ periods) where over a month passed between survey nights.

Data analysis

For each survey night at each site, we summed the number of brown treesnake and small mammal observations and divided those values by the total number of person-hours searched that night to calculate the catch-per-unit effort (CPUE) for our two target taxa (snakes or mammals). To smooth short-term fluctuations and highlight longer-term trends, we calculated two-week CPUE averages (Figure 2.2) to use as the response variables in our linear models (described below).

We generated two sets of linear models (R package *MuMIn* 1.43.17; Barton 2012; R Studio Team 2019) to test hypotheses regarding snake and small mammal responses following predator suppression on Guam. Predictor variables included metrics of cumulative baits per area,

time since the last snake treatment(s), concurrent and time-lagged interspecific CPUEs, site, season, rain, and an interaction between site and cumulative baits. These variables addressed hypotheses detailed below related to treatment/top-down effects (H_{1-4}), bottom-up (H_5), seasonal (H_6), and detection effects ($H_{7,8}$) on brown treesnake and small mammal populations (Table 2.1):

Treatment/top-down effects

$H_{1A,B}$: As more baits are applied (i.e., the cumulative baits per area increases), snake CPUE decreases due to increased mortality (Clark et al. 2018; Siers et al. 2020), and small mammal CPUE increases due to decreased predation pressure (i.e., prey release). We tested two cumulative baits metrics, the sum of the total cumulative baits per area (H_{1A}) and the cumulative baits per area within the past year (H_{1B}) to determine which was best supported by the data. Both metrics do not appear in the same model, and the best supported metric was used to develop an interaction hypothesis (see H_4).

$H_{2A,B}$: The influence of toxic bait applications diminishes over time, after which snake CPUE increases because the population starts to rebound, and small mammal densities decrease concurrently (H_{2A}) or after a time lag (H_{2B}) due to increased predation pressure by snakes.

$H_{3A,B}$: As brown treesnake CPUE increases, small mammal CPUE decreases concurrently (H_{3A}) or after a time lag (H_{3B}), as higher snake density increases predation pressure on small mammal prey.

H_4 : Site differences (e.g., habitat structure, pre-treatment abundances and/or demographics, treatment delivery) affect snake treatment efficacy, cascading effects,

and/or animal detection (see H₈), thereby affecting snake and small mammal CPUEs differently in each study area.

Lagged bottom-up effects

H₅: As small mammal CPUE increases, snake CPUE increases four months later. More prey (small mammals) increases snake body condition and reproductive potential, leading to increased snake densities four months later (to account for the three-month snake gestation period and a buffer for foraging and mating).

Seasonal effects

H_{6A, B}: Snake and small mammal CPUE is higher during the wet season (H_{6A}) or with more rainfall (H_{6B}) based on previous literature (Shivik et al. 1999; Wiewel et al. 2009).

Detection effects

H₇: As small mammal CPUE increases, concurrent snake CPUE decreases because increased prey availability (i.e., more small mammals) may decrease periods of active foraging by snakes because prey is easier to find, thereby decreasing their chances of being seen.

H₈: Dense vegetation in the HMU makes both taxa harder to detect, lowering CPUEs for snakes and small mammals in the HMU.

Both the snake and small mammal model sets included all possible additive combinations of predictor variables (Doherty et al. 2012) with the following restrictions: season or rain and only one cumulative bait covariate could appear in the same model because these metrics were not independent. We used an information-theoretic model selection approach based on Akaike's Information Criterion corrected for small sample size (AIC_c) to determine the best-supported

models in our candidate sets (Burnham and Anderson 2002) and assessed directionality and strength of the effects via the estimated coefficients ($\hat{\beta}$ s) and measures of precision ($\widehat{SE}[\hat{\beta}]$) from the best-supported models. We evaluated diagnostic plots to ensure models met the assumptions of homoscedasticity and normality and calculated variance inflation factors to assess multicollinearity among predictors.

Results

We searched 3,924 km over 3,332 person-hours during 374 visual survey nights during 2017 – 2020 and had 2,054 brown treesnake detections and 137 small mammal detections. There was no evidence of collinearity among our predictor variables included in the same models (VIF range = 1.32 – 1.63). We fit 192 models to our snake and small mammal CPUE data.

There was strong support for site-specific (i.e., interactive) treatment effects of predator control (H₄; Table 2.2) but consistent top-down effects on average small mammal CPUE (H_{3A}; Figures 2.3 and 2.4). Specifically, as more baits were applied in each study area, average snake CPUE decreased in the HMU and increased in the CP (Figure 2.3a, b), and average small mammal CPUE increased in the HMU and decreased in the CP (H₄; Figure 2.3c). Furthermore, average small mammal CPUE decreased as concurrent average brown treesnake CPUE increased ($\hat{\beta} = -0.04$; $\widehat{SE}[\hat{\beta}] = 0.03$; H_{3A}; Figure 2.4). Collectively, these results suggest strong top-down effects; as predator densities increase, prey densities decline concurrently. There was no evidence that snake densities rebounded as more time passed since toxic bait applications (Table 2), and average small mammal CPUE increased slightly ($\hat{\beta} = 0.002$; $\widehat{SE}[\hat{\beta}] = 0.001$), a result that was opposite of our *a priori* predictions (H₂).

We also found strong evidence of bottom-up effects (H₅; Tables 2.1 and 2.2). As average small mammal CPUE increased, average snake CPUE increased four months later ($\hat{\beta} = 1.18$; $\widehat{SE}[\hat{\beta}] = 0.56$; Figure 2.5). Finally, there was evidence of seasonal effects for the predatory brown treesnake only (H_{6A}; Table 2.2), but direction of the effect was the opposite of what we expected. We had fewer snake observations during the wet season versus the dry season ($\hat{\beta} = -0.09$; $\widehat{SE}[\hat{\beta}] = 0.04$; Figures 2.3a, b, 2.5). There was little support for either of our two detection hypotheses (H_{7, 8}; Table 2.2).

Discussion

We found evidence of top-down and bottom-up trophic dynamics as well as seasonal effects on invasive brown treesnake and small mammal counts in forests on northern Guam. Top-down effects were supported irrespective of site. Small mammal counts decreased as brown treesnake counts increased (in the CP) and vice versa (in the HMU), indicating that brown treesnakes likely suppress small mammals in Guam forests. The top-down effects of brown treesnakes are well documented on endo- (Savidge et al. 1987) and ectothermic (Campbell et al. 2012) as well as native and invasive prey species on Guam. Most notably, brown treesnakes are responsible for extirpating most of Guam's forest birds (Savidge 1987; Rodda et al. 1997; Fritts and Rodda 1998; Wiles et al. 2003). Savidge (1987) also investigated top-down effects of brown treesnakes on Guam's invasive small mammal populations by comparing small mammal abundance estimates before (Barbehenn 1964, 1974) and after brown treesnake establishment, and found a 94% decrease in small mammal abundance in habitats where brown treesnakes were common. Wiewel et al. (2009) expanded this query to other islands in the Marianas and found far lower small mammal densities on Guam than on ecologically similar islands nearby with no snakes. In addition, a field experiment conducted on Guam showed an inverse relationship

between the abundance of several small lizard species and brown treesnakes (Campbell et al. 2012). Our data provide yet another line of evidence in support of the direct top-down effects of brown treesnakes on Guam and further document trophic dynamics following predator suppression efforts (e.g., prey release).

Knowledge of strong top-down effects can foreshadow possible prey release following predator suppression (Elmhagen and Rushton 2007; Österblom et al. 2007), the effects of which are at least threefold. First, spikes in invasive small mammals directly threaten native fauna via predation of lizards (Fritts and Rodda 1998) and birds (Sheils et al. 2014). Second, increased availability of wild rodents diminishes the efficacy of rodent baits (Gragg et al. 2007) used in most brown treesnake suppression efforts, including mouse-baited live-traps (Tyrell et al. 2009; Nafus et al. 2018; Yackel Adams et al. 2019), bait tubes (Lardner et al. 2013), and toxicants (Clark and Savarie 2012; Clark et al. 2018; Siers et al. 2019; Siers et al. 2020). Third, small mammals are an important food source for brown treesnakes that increase their fecundity (Lardner and Yackel Adams, *unpublished data*), potentially leading to bottom-up effects that increase predator populations.

Indeed, support for bottom-up effects was another of our important findings. Specifically, increased small mammal counts were associated with increased snake counts four months later, a time lag that would allow snakes to reproduce. Biologically, we postulate that bottom-up energy flows prompted by minor prey release boosted snake survival (Gragg et al. 2007), growth, fecundity (Lardner and Yackel Adams, *unpublished data*), and eventually abundance (Fritts and Rodda 1998; Rodda et al. 1999). Although we did not test these hypotheses mechanistically, we used available data to determine that these processes were, in fact, feasible in our system (i.e., were supported by the available data).

The magnitude of small mammal prey release likely correlates with the magnitude of snake removal, particularly that of large snakes whose diet consists of mainly small mammals in the absence of avian prey. For example, a study conducted in the CP six years before ours manually removed all large snakes (> 900 mm snout-vent length) via traps and recorded a prolonged eruption in small mammal counts and a subsequent boost in snake fecundity (Lardner and Yackel Adams, *unpublished data*). Other studies that monitored small mammals after successful toxicant applications observed, at most, brief spikes in small mammal captures and only when snake activity decreased by at least 60% (Siers et al. 2018). Negligible changes in small mammal capture rates occurred in treated sites with lower reductions in snake activity (< 40%; Siers et al. 2018; 2020). Effective small mammal monitoring and control will likely be important as snake treatments advance to better target the mammal-consuming individuals and intensify the removal of larger portions of the brown treesnake population.

Interestingly, we found strong evidence for an interaction between predator control efforts and site. The effect of lethal snake treatments was different between the sites; as more toxic snake baits were applied, snake counts decreased in the HMU as anticipated, but increased in the CP. This finding prompted two significant questions: 1) Is this predator control method consistently effective for invasive brown treesnakes on Guam? And, if so, 2) why did we continue seeing more snakes in the CP despite ongoing control efforts? Foremost, our findings do not discount the potential for brown treesnake suppression via toxic bait applications on Guam; extensive support exists in favor of this method (Savarie et al. 2001; Shivik et al. 2002; Clark and Savarie 2012; Clark et al. 2018; Siers et al. 2019; Siers et al. 2020). However, variation in pre-treatment population demographics could have led to different treatment outcomes in the CP and HMU. For example, size/age-based differences in brown treesnake

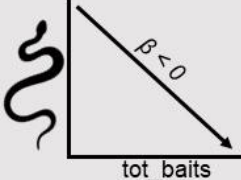
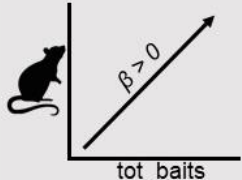
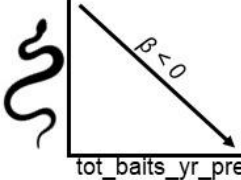
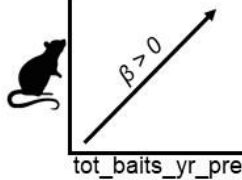
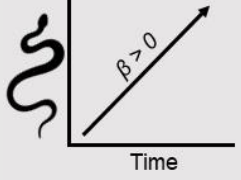
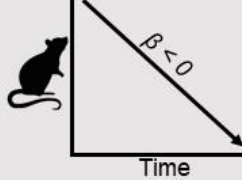
dietary preferences (Savidge 1988; Greene 1989; Mackessy et al. 2006) affect the efficacy of rodent baits for small/young snakes that eat mostly lizards and thus potential population-level effects of toxic mouse applications likely depend on the population structure (e.g., skewed smaller/younger; Siers et al. 2017).

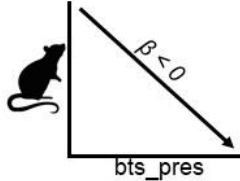

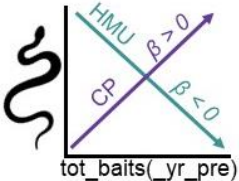
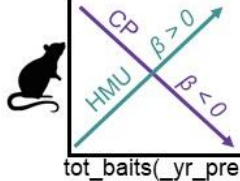
A major caveat of this study is the use of a count-based index—CPUE—to monitor snake and small mammal densities; we assume that CPUE indices correlate with true snake and small mammal densities and that detection was constant across surveys and observers (Anderson 2003). While CPUE is frequently used as an abundance index for many species and systems (Ormerod et al. 1988; Ericsson and Wallin 1999; Jessop et al. 2007; Guzzo et al. 2014), it has not been validated for either snakes or small mammals on Guam. Therefore, we cannot disentangle spatial and temporal density differences from potential differences in detection probability. Fortunately, data collection was standardized to limit variability in detection across observers and surveys: 1) observers were highly trained (at least 25 hours of training in the field before they could collect data), and 2) visual surveys were standardized across observers and time. All observers used the same high-lumen headlamps, followed a very specific protocol, and surveys were cancelled during unfavorable weather conditions (e.g., high winds, rain). Additionally, we tested two hypotheses related to detection (H₇, 8), and neither was supported by the data. Nonetheless, we recognize that our negative and/or anomalous results (treatment by site interaction and seasonal effects) could be attributed to detection differences, and we ultimately cannot disentangle what factor(s) led to different treatment outcomes in the CP and HMU as measured via brown treesnake and small mammal CPUE.

In summary, top-down and bottom-up trophic dynamics following attempted predator control play an important role in invasive brown treesnake and small mammal populations in

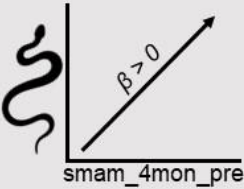
forests on Guam. Although the effect of lethal snake treatments varied by site, we detected consistent top-down and bottom-up effects that may result in prey release and subsequent predator rebound following snake suppression. As such, small mammal monitoring and control are likely critical components of any long-term invasive species management strategy focused on reintroduction of native vertebrates on Guam. Important future research includes mechanistic testing of our supported hypotheses and validating of visual survey or other count-based indices for brown treesnakes and small mammals using robust abundance/density estimation that incorporates detection probability (see Chapter 1). Here, we leveraged existing data to investigate the consistency of invasive predator-prey dynamics and predator suppression treatments on Guam and contributed to an evolving understanding of insular multitrophic invasive vertebrate dynamics.

Table 2.1) Hypotheses for models based on response variables (average 2-week visual survey catch-per-unit effort, CPUE, for invasive brown treesnake (*Boiga irregularis*) and small mammal (*Rattus* spp., *Mus musculus*, and *Suncus murinus*) as a function of predictor variables. Associated hypotheses, predictor variables, expectations, reasoning/mechanisms/citations, and results for each hypothesized predictor of invasive brown treesnake (*Boiga irregularis*) and small mammal (*Rattus* spp., *Mus musculus*, and *Suncus murinus*) average two-week visual survey catch-per-unit effort (CPUE; number of target animals observed per one-person hour of visual searching) following lethal snake treatments in the Habitat Management Unit (HMU) and the Closed Population (CP) on northern Guam during 2017 – 2020.

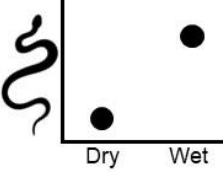
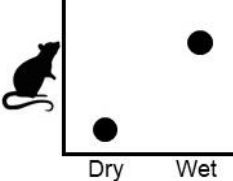
Hypothesis	Predictor variable	Response variable		Result		
		Average two-week brown treesnake CPUE	Average two-week small mammal CPUE			
		Expectation	Biological reasoning, mechanism, and/or citation(s)	Expectation	Biological reasoning, mechanism, and/or citation(s)	
Treatment/top-down effects						
H _{1A}	Sum of total baits/ha by site (tot_baits) ¹		Higher snake mortality as more toxic snake baits are applied (Clark et al. 2018; Siers et al. 2020)		Small mammal populations increase due to decreased snake predation pressure (i.e., prey release).	Not supported (see H ₄)
H _{1B}	Sum of total baits/ha by site within the past year (tot_baits_yr_pre) ¹		"		"	"
H ₂	Time (in weeks) since the last toxic snake bait application of ~120 baits/ha (time)		Without continued treatments, the snake population rebounds.		Without continued treatments, the snake population rebounds, increasing predation pressure on small mammals and reducing their densities.	Opposite expectation: A positive time effect was in the best-supported small mammal model (Fig. 3b). Time was not an important predictor of snake CPUE.

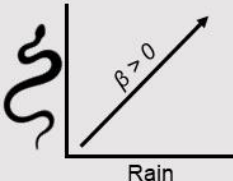
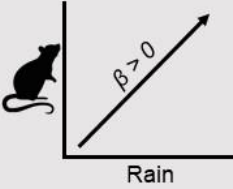
H _{3A}	Concurrent two-week average brown treesnake CPUE (bts_pres)	—	—		Higher snake density increases predation pressure, decreasing small mammal densities.	Fully supported (Fig. 3a)
H _{3B}	Two-week average brown treesnake CPUE from two weeks prior (bts_2wk_pre)	—	—		Higher snake density increases predation pressure, decreasing small mammal densities two weeks later via a delayed predation effect.	Unsupported
H ₄	Site × both cumulative bait per area covariates (tot_baits[_yr_pre]) ²		Site differences affect snake treatment efficacy and detection, thereby affecting snake CPUEs differently by site. We had no expectation for the nature of the interaction.		Site affect snake treatment efficacy, cascading effects, and detection, thereby affecting small mammal CPUEs differently by site. We had no expectation for the nature of the interaction.	Fully supported: Interactions between site and selected bait covariates were in the best-supported snake and small mammal models, respectively. As more baits were applied, snake CPUE decreased in the HMU and increased in the CP (Fig. 5a, b), and small mammal CPUE increased in the HMU and decreased in the CP (Fig. 5c).

Lagged bottom-up effects

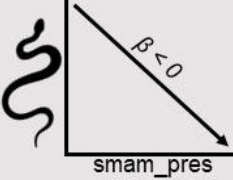
H ₅	Two-week average small mammal CPUE from four months prior (smam_4mon_pre)		More prey increases snake reproductive potential, leading to increased snake densities four months later.	—	—	Fully supported (Fig. 4)
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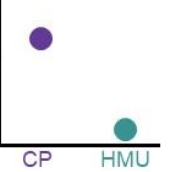

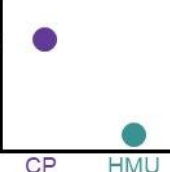
Seasonal effects

H _{6A}	Wet (July–October) or dry (November–June) season (season) ³		Shivik et al. 1999		Wiewel et al. 2009	Opposite expectation: An effect of season was retained in the best-supported snake model but not the best-supported small mammal model. However, the direction of the effect of season on snake CPUE was the opposite of what we expected (Fig. 4; Fig. 5a, b).
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H _{6B}	Total rain over the two-week period (rain) ³		Shivik et al. 1999		Wiewel et al. 2009	Unsupported
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Detection effects

H ₇	Concurrent two-week average small mammal CPUE (smam_pres)		Increased prey availability may decrease prolonged periods of active foraging by snakes because prey is easier to find,	—	—	Unsupported
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thereby decreasing their chances of being seen.								
H ₈	Closed Population (CP) or Habitat Management Unit (HMU)			Dense vegetation in the HMU (versus the CP) may decrease snake detection.			Dense vegetation in the HMU (versus the CP) may decrease small mammal detection.	Unsupported (see H ₄)

¹While our hypotheses and expectations for both cumulative baits metrics were the same, we wanted to determine which was best supported by the data for inclusion in interactions (see H₆). Both metrics do not appear in the same model.

²We used the cumulative bait covariate that was best supported by the data (see H₁) for each species for this interaction.

³Season and rain do not appear in the same model.

Table 2.2) Linear model results of best-supported models ($w_i > 0.05$) for 2-week average catch-per-unit effort (CPUE; number of target animals observed per 1-person visual-survey hour) on Guam during 2017 – 2020 for brown treesnake (*Boiga irregularis*) and small mammal (*Rattus* spp., *Mus musculus*, and *Suncus murinus*) count data on Guam. We ranked models using Akaike’s Information Criterion with a small sample size correction (AIC_c), used cumulative weights (w_i) to identify important covariates, and assessed relative model fit with log-likelihood (log L). Covariates included in the best-supported models ($w_i > 0.05$) were: site (Habitat Management Unit or Closed Population), total snake baits applied per ha throughout the respective site (tot_baits), total snake baits applied per ha within the previous year (tot_baits_yr_pre), season (wet [July – October] or dry [November – June]), small mammal CPUE from four months prior (smam_4mon_pre), simultaneous small mammal and brown treesnake CPUEs (smam_pres and bts_pres, respectively), and weeks since the last application of at least 120 baits per ha (time).

Species	Model	AIC_c	w_i	log L
Brown treesnakes	site + tot_baits + site*tot_baits + season + smam_4mon_pre	-60.53	0.14	38.15
	site + tot_baits + site*tot_baits + season + smam_4mon_pre + smam_pres	-59.86	0.10	39.09
	site + tot_baits + site*tot_baits + season + smam_4mon_pre + time	-59.29	0.07	38.81
	site + tot_baits + site*tot_baits + season + smam_4mon_pre + smam_pres + time	-59.06	0.07	40.01
	site + tot_baits + site*tot_baits	-58.77	0.06	34.84
	site + tot_baits + site*tot_baits + smam_4mon_pre + smam_pres	-58.70	0.06	37.23
	site + tot_baits + site*tot_baits + smam_pres	-58.55	0.05	35.93
Small mammals	site + tot_baits_yr_pre + site*tot_baits_yr_pre + time + bts_pres	-268.38	0.16	142.00
	site + tot_baits_yr_pre + site*tot_baits_yr_pre + time	-268.24	0.15	140.72
	site + tot_baits_yr_pre + site*tot_baits_yr_pre	-266.82	0.07	138.83
	site + tot_baits_yr_pre + site*tot_baits_yr_pre + time + season	-266.56	0.06	141.09
	site + tot_baits_yr_pre + site*tot_baits_yr_pre + season	-266.30	0.06	139.75
	site + tot_baits_yr_pre + site*tot_baits_yr_pre + time + season + bts_pres	-266.09	0.05	142.10

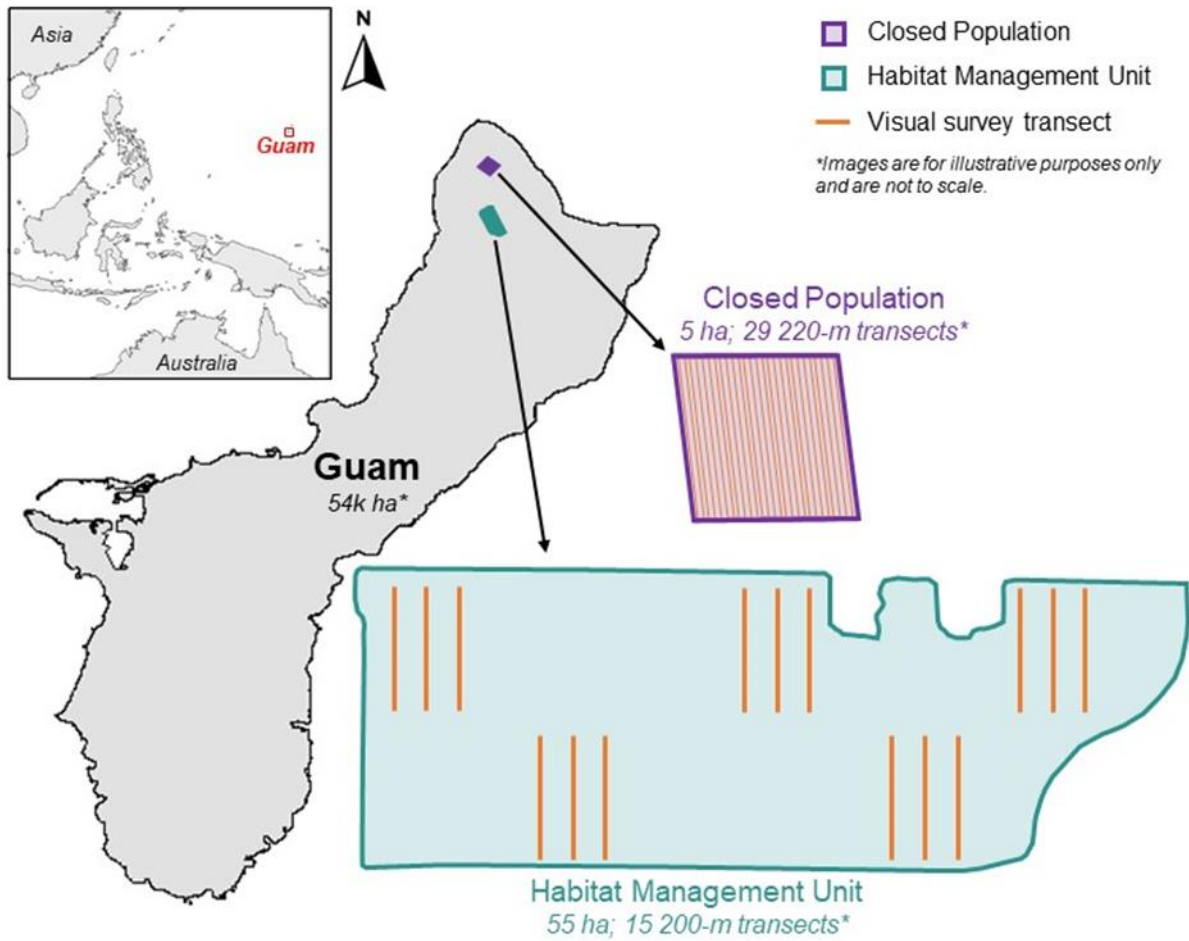


Figure 2.1) Two snake-enclosed forest habitat sites on Andersen Air Force Base in northern Guam. The Closed Population (CP; purple) and the Habitat Management Unit (HMU; teal). The CP is five ha and has 29 transects that cover the entire study area; transects are 2-m wide and 220-m long and spaced at 8-m intervals. The HMU is 55 ha with five sets of three 200-m long transects dispersed throughout the study area. Both sites are surrounded by a snake-proof fence and have undergone repeated lethal brown treesnake treatments via toxicant baits during 2017 – 2020.

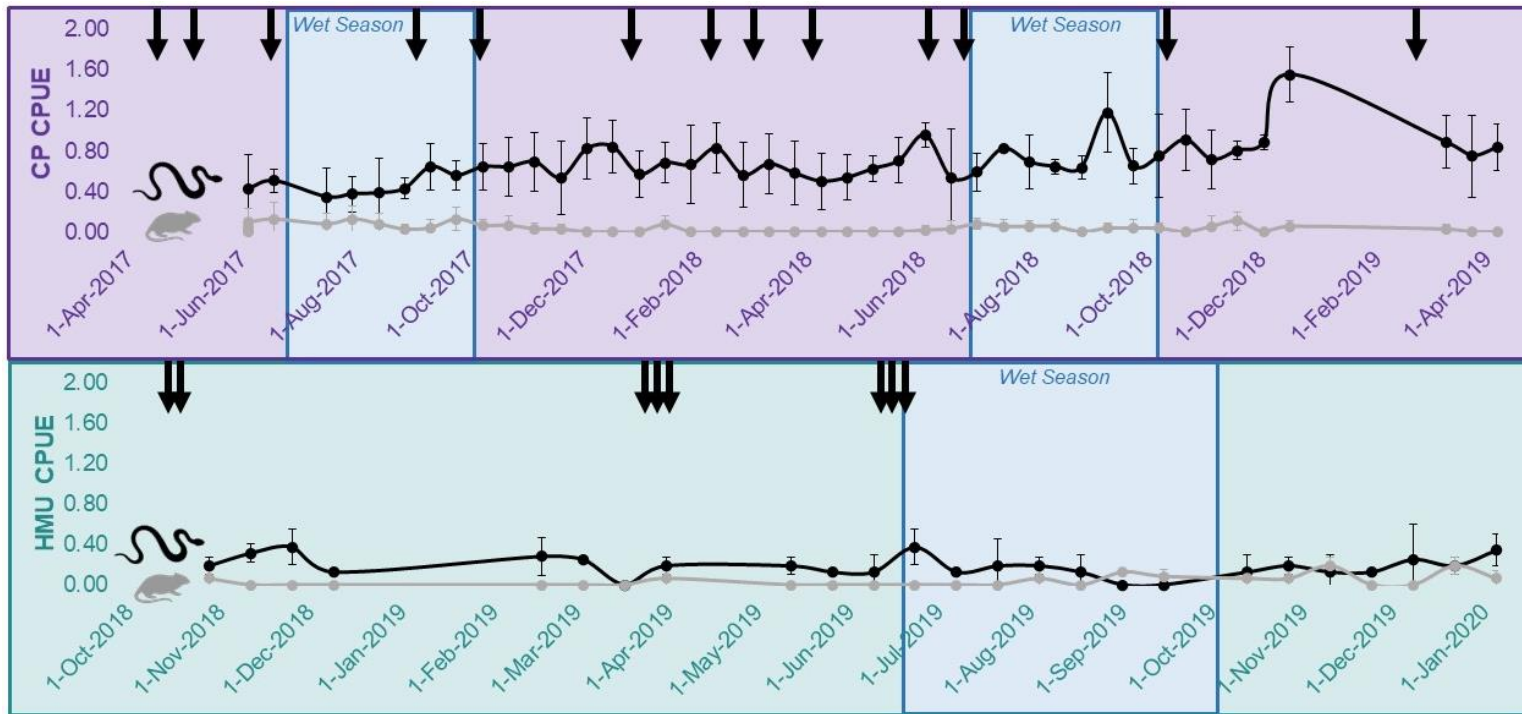


Figure 2.2) Average brown treesnake (*Boiga irregularis*) and small mammal (*Rattus* spp., *Mus musculus*, and *Suncus murinus*) visual survey catch-per-unit effort after lethal snake (predator) treatments at both study sites. Invasive brown treesnake (black) and small mammal (gray) average two-week catch-per-unit efforts (CPUE; number of animals observed per one-person hour of visual searching) and standard deviations for the Closed Population (CP; top; purple) and Habitat Management Unit (HMU; bottom; teal) on Guam during 2017 – 2020. No error bars indicate that either only one survey occurred during that two-week period or that average CPUE equaled zero. Arrows represent an application of up to 120 toxic baits (acetaminophen-laced dead neonatal mice) per hectare throughout the respective study areas. Blue rectangles differentiate the wet season (July – October).

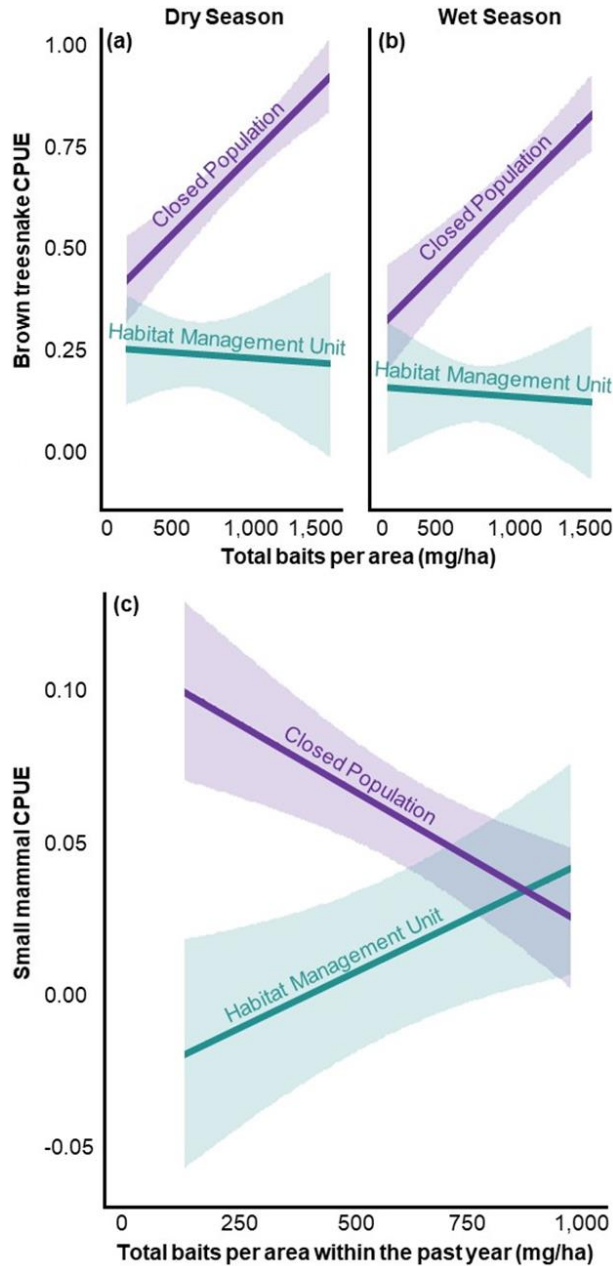


Figure 2.3) Interaction between study sites and lethal brown treesnake (*Boiga irregularis*; predator) treatments on snake and small mammal (*Rattus* spp., *Mus musculus*, and *Suncus murinus*) counts. Taxa-specific average bi-weekly visual survey catch-per-unit effort (CPUE; number of animals observed per one-person hour of visual searching) modeled as an interaction between study area (the Habitat Management Unit [teal lines] or the Closed Population [purple lines]) and the total baits per area covariates included in the best-supported models for invasive brown treesnakes (a; b) and small mammals (c) on Guam during 2017 – 2020. Interactive relationships for brown treesnakes are given for the dry (a) and wet (b) seasons. We held predictors included in the best-supported models that are not specified in this figure at their mean effects (time and *bts_pres*). Shaded regions are 95% confidence intervals.

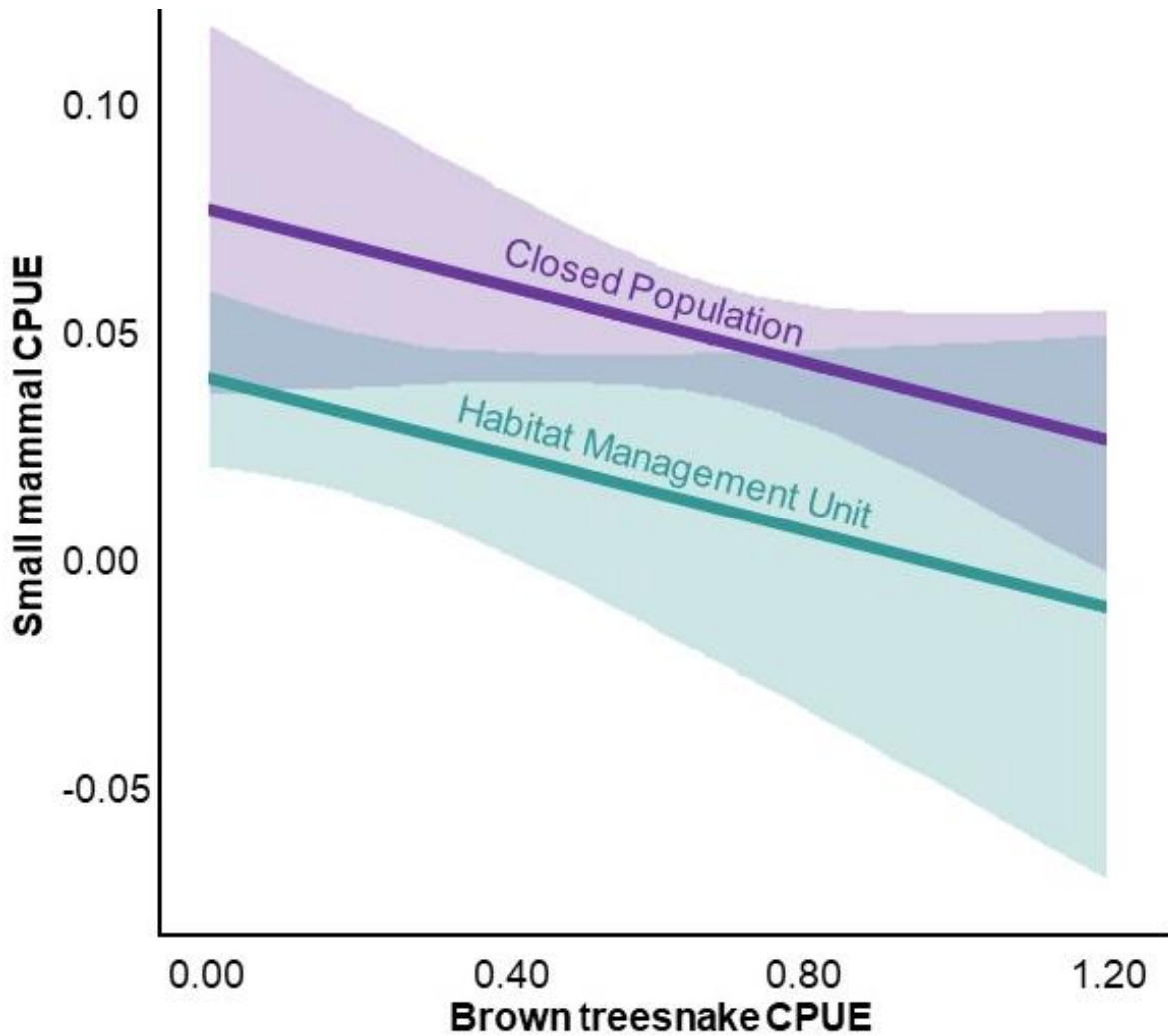


Figure 2.4) Effect of brown treesnake (*Boiga irregularis*) counts on small mammal (*Rattus* spp., *Mus musculus*, and *Suncus murinus*) counts. Invasive small mammal average 2-week visual survey catch-per-unit effort (CPUE; number of mammals observed per one-person hour of visual searching) modeled as a function of invasive brown treesnake average 2-week visual survey CPUE for the Closed Population (purple) and Habitat Management Unit (teal) on Guam during 2017 – 2020. We held total baits per area from the past year at its mean effect, and shaded regions are 95% confidence intervals.

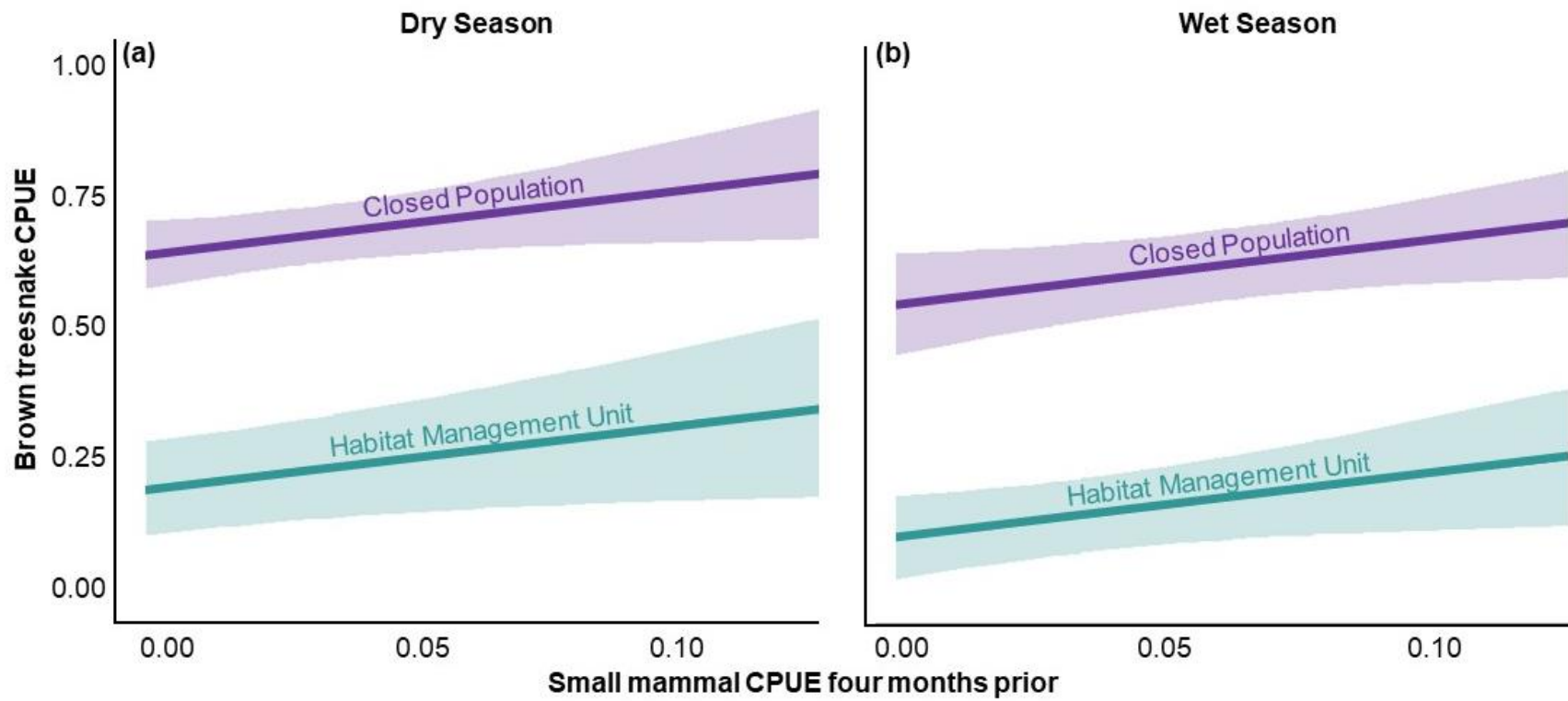


Figure 2.5) Time-lagged effect of small mammal (*Rattus* spp., *Mus musculus*, and *Suncus murinus*) counts on brown treesnake (*Boiga irregularis*) counts by site and season. Invasive brown treesnake average two-week visual survey catch-per-unit effort (CPUE; number of snakes observed per one-person hour of visual searching) modeled as a function of invasive small mammal average two-week visual survey CPUE from four months prior (to account for the three-month snake gestation period and a buffer for foraging and mating) for the dry (a) and wet (b) seasons and the Closed Population (purple) and Habitat Management Unit (teal) on Guam during 2017 – 2020. We held total baits per area at its mean effect, and shaded regions are 95% confidence intervals.

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APPENDICES

Appendix 1

We modeled potential heterogeneity in capture probabilities (p) among sampling occasions and/or individuals in our spatially explicit Huggins' closed-capture conditional likelihood analyses of live-trapped rats (*Rattus* spp.) in Guam (G1 – 4) and Rota (R1 – 5) forest habitats during June 2018 – August 2019. For Rota grids with higher rat captures (R4 – 5) we used spatially explicit models and a two-step approach. First (Step 1), we accounted for all hypothesized sources of individual variation in capture probability by including sex, body condition index (BCI), and age (juvenile or adult) while exploring models with additive combinations of temporal covariates, including daily rainfall amount (when available; rain), a two-night neophobic response (neophobia2), a behavioral response (behavior), a time trend (Time), and no temporal variation (.). We did not include neophobia2 with either rain or Time in the same model. We retained the best-supported temporal variation structure(s) in Step 2 where we tested all possible additive combinations of individual covariates (sex, BCI, age, and no individual heterogeneity). For Rota grids R1 – 3 we used a single-step approach to compare models with temporal covariates only, excluding rainfall. For all Guam grids, data were too sparse (< 10 total captures per grid) to use spatially explicit models or support covariates. We modeled all Guam data together (with grids differentiated by group) using Huggins' closed-capture conditional likelihood models and compared a null model (constant capture probability) to a model with a behavioral effect, as this was all these data could support. We ranked models using Akaike's Information Criterion with a small sample size correction (AIC_c) and used cumulative variable weights (w) to identify important covariates within each step. We also

include the number of parameters (**K**) and log-likelihood (**logLik**) for each model (Tables A1.1 – 4).

Table A1.1) Guam: Huggins’ closed-capture conditional likelihood model selection results for combined Guam grids sampled during June 2018 – February 2019.

Guam model structures	AIC_c	w	K	logLik
<i>p</i> (behavior)	132.371	0.995	2	-64.154
<i>p</i> (.)	143.079	0.005	1	-70.014

Table A1.2) R1 – 3: Model selection results for spatially explicit models fit to data collected during June 2019 from grids for which we did not collect individual covariates. Results from the temporal models only (Step 1) are provided by grid.

R1 model structures	AIC_c	w	K	logLik
<i>p</i> (behavior)	310.710	0.587	3	-151.605
<i>p</i> (behavior + Time)	312.293	0.266	4	-150.813
<i>p</i> (behavior + neophobia2)	313.543	0.142	4	-151.438
<i>p</i> (Time)	320.225	0.005	3	-156.362
<i>p</i> (neophobia2)	321.498	0.000	3	-156.999
<i>p</i> (.)	322.631	0.000	2	-158.963
R2 model structures	AIC_c	w	K	logLik
<i>p</i> (behavior)	132.464	0.415	3	-61.732
<i>p</i> (.)	132.845	0.343	2	-63.756
<i>p</i> (Time)	135.440	0.094	3	-63.220
<i>p</i> (neophobia2)	136.175	0.065	3	-63.587
<i>p</i> (neophobia2 + behavior)	137.026	0.042	4	-61.656
<i>p</i> (Time + behavior)	137.112	0.041	4	-61.699
R3 model structures	AIC_c	w	K	logLik
<i>p</i> (behavior)	236.974	0.592	3	-114.564
<i>p</i> (Time + behavior)	238.413	0.288	4	-113.540
<i>p</i> (neophobia2 + behavior)	240.378	0.108	4	-114.522
<i>p</i> (Time)	246.079	0.006	3	-119.116
<i>p</i> (neophobia2)	246.123	0.006	3	-119.139
<i>p</i> (.)	249.898	0.000	2	-122.521

Table A1.3) R4: Spatially explicit model selection for rats sampled during June – July 2019. Step 1 models include all hypothesized sources of individual variation in capture probability (sex + age + BCI + *temporal structures*) listed below. We retained the best-supported temporal structure (behavior) when testing all possible additive combinations of individual covariates in Step 2 (sex, BCI, age, and no individual heterogeneity)

Step 1: Temporal model structures	AIC_c	w	K	logLik
<i>p</i> (... + behavior)	1596.626	0.452	6	-791.819
<i>p</i> (... + behavior + neophobia2)	1598.623	0.167	7	-791.645
<i>p</i> (... + behavior + rain)	1598.646	0.165	7	-791.656
<i>p</i> (... + behavior + Time)	1598.666	0.163	7	-791.666
<i>p</i> (... + behavior + Time + rain)	1600.875	0.054	8	-791.570
<i>p</i> (... + Time + rain)	1630.401	0.000	7	-807.534
<i>p</i> (... + neophobia2)	1630.653	0.000	6	-808.832
<i>p</i> (... + Time)	1633.905	0.000	6	-810.459
<i>p</i> (... + rain)	1653.401	0.000	6	-820.206
<i>p</i> (...)	1655.074	0.000	5	-822.188
Step 2: Individual covariates model structures	AIC_c	w	K	logLik
<i>p</i> (behavior)	1588.893	0.760	3	-791.310
<i>p</i> (BCI + behavior)	1592.397	0.132	4	-791.968
<i>p</i> (BCI + sex + behavior)	1594.427	0.048	5	-791.865
<i>p</i> (BCI + age + behavior)	1594.560	0.045	5	-791.931
<i>p</i> (BCI + age + sex + behavior)	1596.626	0.016	6	-791.819
<i>p</i> (age + behavior)	1599.041	0.000	4	-795.291
<i>p</i> (sex + age + behavior)	1601.083	0.000	5	-795.193
<i>p</i> (sex + behavior)	1601.617	0.000	4	-796.579

Table A1.4) R5: Spatially explicit model selection for rats sampled during July – August 2019. Step 1 models include all hypothesized sources of individual variation in capture probability (sex + age + BCI + *temporal structures*) listed below. We retained the best-supported temporal structure (behavior + neophobia2) when testing all possible additive combinations of individual covariates in Step 2 (sex, BCI, age, and no individual heterogeneity)

Step 1: Temporal model structures	AIC_c	w	K	logLik
<i>p</i> (... + behavior + neophobia2)	1445.445	0.341	7	-714.847
<i>p</i> (... + behavior)	1445.487	0.334	6	-716.097
<i>p</i> (... + behavior + Time)	1447.621	0.115	7	-715.936
<i>p</i> (... + behavior + rain)	1447.932	0.098	7	-716.091
<i>p</i> (... + neophobia2)	1448.358	0.080	6	-717.533
<i>p</i> (... + behavior + rain + Time)	1450.156	0.032	8	-715.935
<i>p</i> (... + Time)	1456.471	0.000	6	-721.589
<i>p</i> (...)	1457.712	0.000	5	-723.401
<i>p</i> (... + Time + rain)	1458.743	0.000	7	-721.497
<i>p</i> (... + rain)	1460.068	0.000	6	-723.388
Step 2: Individual covariates model structures	AIC_c	w	K	logLik
<i>p</i> (neophobia2 + behavior)	1426.892	1.000	4	-709.147
<i>p</i> (age + neophobia2 + behavior)	1440.812	0.000	5	-714.952
<i>p</i> (BCI + neophobia2 + behavior)	1442.040	0.000	5	-715.565
<i>p</i> (age + sex + neophobia2 + behavior)	1443.069	0.000	6	-714.888
<i>p</i> (age + BCI + neophobia2 + behavior)	1443.134	0.000	6	-714.921
<i>p</i> (sex + neophobia2 + behavior)	1444.407	0.000	6	-715.558
<i>p</i> (sex + BCI + neophobia2 + behavior)	1444.407	0.000	6	-715.558
<i>p</i> (sex + age + BCI + neophobia2 + behavior)	1445.445	0.000	7	-714.847

Appendix 2

We compared three density estimators for rats (*Rattus* spp.) using capture-mark-recapture data from nine grids sampled a total of 11 times in Guam (G1 – 4) and Rota (R1 – 5) forest habitats during June 2018 – August 2019. Specifically, for each grid we report: 1) model-averaged Huggins' closed-capture conditional likelihood model abundance estimates (\hat{N} s) divided by effective trapping areas (ETAs) calculated as the grid area plus half of the mean maximum distances moved by rats captured more than once (0.5MMDM; $\hat{N}/ETA_{0.5MMDM}$), 2) \hat{N} s divided by ETAs equaling the grid area plus a boundary equal to the full MMDM (\hat{N}/ETA_{MMDM}), and 3) the model-averaged spatially explicit capture-mark-recapture (SECR) density estimates (SECR \hat{D}) for Rota grids only. We followed the same modeling steps across density estimators for each grid as described in our methods and Appendix 1 (e.g., one step for R1 – 3, two steps for R4 – 5).

For grids with enough data to test all three density estimators (i.e., Rota grids), SECR models always produced the lowest, most precise estimates of density, and these estimates were always contained within the confidence intervals of the non-spatial estimates. Density estimates produced using the full MMDM buffers, \hat{N}/ETA_{MMDM} , were closer to SECR \hat{D} s than those obtained using 0.5MMDM (Fig. A2.1). Accordingly, we reported density estimates using effective trapping areas calculated using the full MMDM (\hat{N}/ETA_{MMDM}) for Guam grids and used these estimates in our regression analyses used for index calibration.

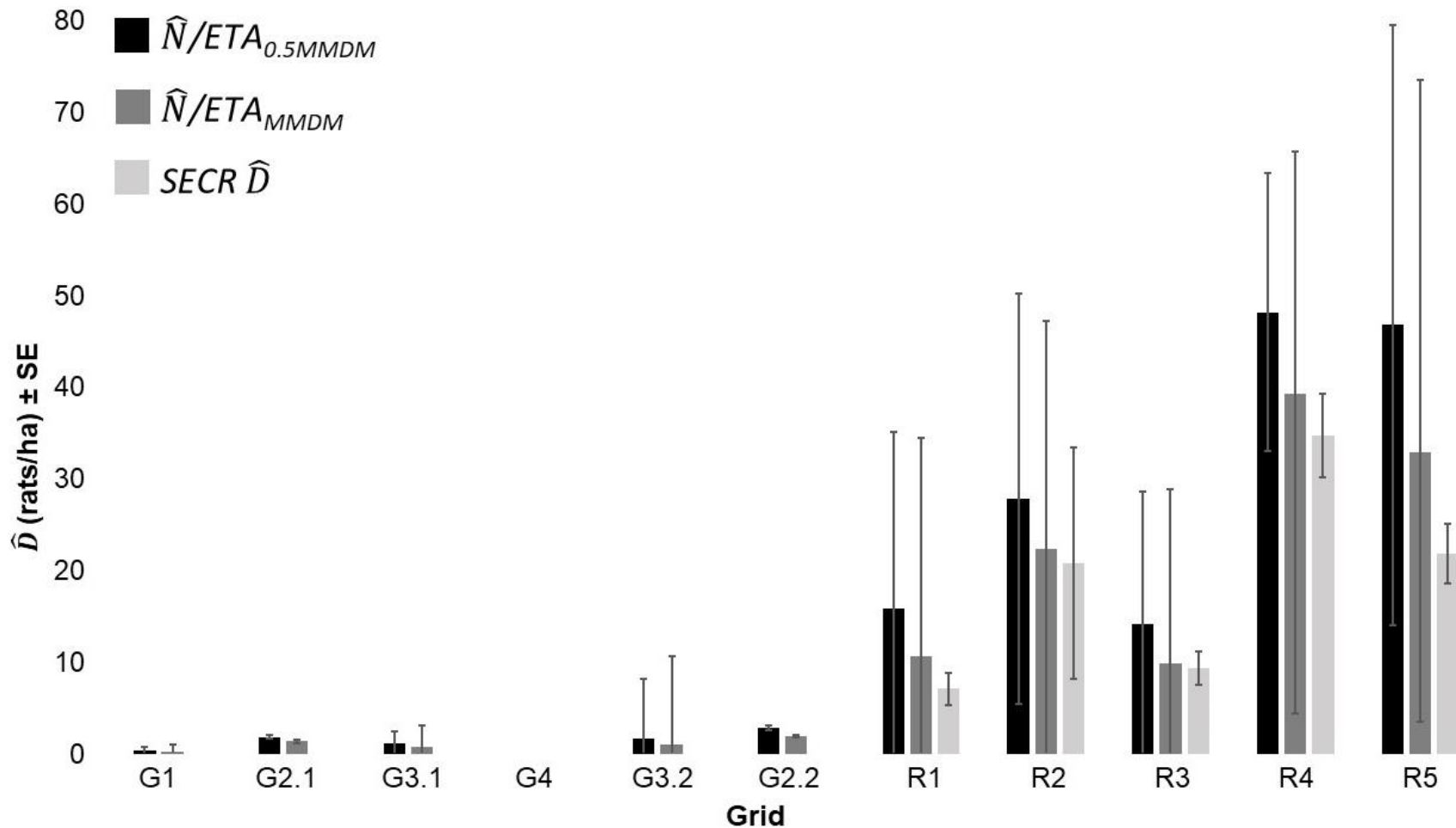


Figure A2.1) Comparison of three density estimation approaches for rats (*Rattus* spp.) using capture-mark-recapture data from Guam (G1 – 4) and Rota (R1 – 5) forest grids during June 2018 – August 2019. Black and dark gray bars represent density estimates ($\hat{D}s$) calculated from model-averaged abundance estimates ($\hat{N}s$) divided by effective trapping areas (ETAs) calculated by adding boundary strips equaling half of the mean maximum distances moved by rats captured more than once (0.5MMDM) and the full MMDM, respectively. Light gray bars represent $\hat{D}s$ from spatially explicit capture-recapture (SECR) models for sites on Rota only.

Appendix 3

Table A3.1) Toxicant application quantities and dates for brown treesnake (*Boiga irregularis*; predator) within forested enclosures on Guam. Invasive brown treesnake treatment application dates, weeks since the last application, baits/ha, and cumulative baits/ha for the Closed Population and Habitat Management Unit on Anderson Air Force Base in northern Guam during 2017 – 2020. One toxicant bait consists of one dead mouse with an 80-mg acetaminophen tablet glued to its abdomen.

Closed Population (area = 5 ha; method = hand-placement)			
Application date	Weeks since last application	Baits/ha	Cumulative baits/ha
31 March 2017	—	120	120
14 April 2017	2	120	240
02 June 2017	7	120	360
04 August 2017	9	120	480
22 September 2017	7	120	600
01 December 2017	10	120	720
26 January 2018	8	120	840
09 February 2018	2	120	960
26 March 2018	6	120	1080
21 May 2018	8	120	1200
04 June 2018	2	120	1320
01 October 2018	17	120	1440
04 February 2019	18	120	1560
Habitat Management Unit (area = 55 ha; method = helicopter)			
Application date	Weeks since last application	Baits/ha	Cumulative baits/ha
01 October 2018	—	117	117
04 October 2018	—	110	226
09 March 2019	22	120	346
12 March 2019	—	120	466
15 March 2019	—	120	586
07 June 2019	12	120	706
10 June 2019	—	120	826
14 June 2019	—	120	946
19 February 2020	36	117	1063
22 February 2020	—	120	1183
25 February 2020	—	120	1303