

THE EFFECTS OF FERAL CAT REMOVAL ON RAT ABUNDANCE IN AN
INSULAR, TROPICAL ECOSYSTEM

By

Douglas A. Page

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

Committee Membership

Dr. Richard Brown, Committee Chair

Dr. Daniel Barton, Committee Member

David Garcelon, Committee Member

Dr. Erin Kelly, Graduate Coordinator

December 2020

ABSTRACT

THE EFFECTS OF FERAL CAT REMOVAL ON RAT ABUNDANCE IN AN INSULAR, TROPICAL ECOSYSTEM

Douglas A. Page

The colonization by rats (*Rattus* spp.) and cats (*Felis catus*) on islands are known to contribute to the decline of native birds. On the island of Rota, Commonwealth of the Northern Mariana Islands, cats are being lethally removed to conserve two endangered bird species. Although cats are controlled to reduce impacts on birds, they can also prey heavily on sympatric rats. Of euthanized feral cats on Rota, 60% had ≥ 1 rat in the stomach. Predation by cats could be a mechanism of top-down control of rats. Removing feral cats may reduce the magnitude of that control, leading to increased rat abundance and, in turn, predation on native birds. To determine if the level of cat control being conducted on Rota is positively influencing rat abundance, I conducted a robust design capture-mark-recapture of rats, using a before-after-control-impact design, in two areas where the ongoing cat removal was not being conducted. Between primary rat trapping occasions, feral cats were removed from one of the two rat trapping areas. Using program MARK to model the data and Akaike information criterion to rank the models I determined that there was no effect of cat removal on the apparent survival of rats and that the estimated abundance did not change significantly in either the control or treatment groups after cat removal.

ACKNOWLEDGEMENTS

This project was made possible by funding from the US Fish and Wildlife Service (USFWS) to the Guam Department of Agriculture, Division of Aquatic and Wildlife Resources (DAWR). Permitting for the project was graciously awarded by the Commonwealth of the Northern Mariana Islands Division of Fish and Wildlife. An enormous thanks goes to Suzanne Medina of DAWR for all her extensive efforts and commitment to seeing this project get off the ground. I greatly appreciate the hard work and dedicated assistance provided by technicians Hannah Phares, Derald Apatang, and especially Nalani Ludington for her dedication and continued support. I would also like to thank my committee members Dr. Richard Brown, Dr. Daniel Barton, and David Garcelon as well as colleagues Dr. Brian Hudgens and Matthew Brinkman for their guidance and input on the design and analysis of this project.

Most importantly, I would like to thank the people of Rota for their support of and inspiration for this project, and I hope that they ultimately benefit from these findings. Malago' yo' para bai hu nã'i i manaotao Luta un dãnko na si Yu'os Mã'ãse' nu i goftao-ñiha yan i suppotasion-ñiha gi i estudio-hu. Hu tatanga na i estudio-hu gaibali-ña para i komunidãt guini giya Luta yan i mamamaila na henerasion siha.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iii
LIST OF TABLES.....	v
LIST OF FIGURES.....	vi
INTRODUCTION.....	1
STUDY AREA.....	4
MATERIALS AND METHODS.....	5
Treatment.....	5
Trapping.....	7
Analysis.....	9
RESULTS.....	11
Treatment.....	11
Rat Trapping.....	11
Mark-Recapture Analysis.....	12
Parameter Estimates.....	15
Abundance and Recruitment.....	16
DISCUSSION.....	20
SUMMARY AND RECOMMENDATIONS.....	25
LITERATURE CITED.....	26
APPENDIX.....	31

LIST OF TABLES

Table 1. Dates on which rat trapping occurred and the number of days of feral cat removal treatment between trapping sessions, by grid number, on Rota, Commonwealth of the Northern Mariana Islands, USA. Grids which received no treatment were in the control group.	6
Table 2. Candidate set of robust design Huggins' p and c models for <i>Rattus</i> spp. on Rota, Commonwealth of the Northern Mariana Islands, USA, ranked by Akaike's Information Criterion corrected for sample size (AIC _c). Model parameters included apparent survival (<i>S</i>), initial capture probability (<i>p</i>), and recapture probability (<i>c</i>). Covariates included control and treatment group (treatment), primary occasion (session), and days since the first trapping day within a session (time). The operators + and * represent additive and interactive terms, respectively, between covariates. Model parameters held constant across groups are denoted with a (1). Gamma' and Gamma'' were fixed at zero and are not included in the model descriptions.	14
Table 3. Abundance estimates for each session, combined by experimental group, for <i>Rattus</i> spp. on Rota, Commonwealth of the Northern Mariana Islands, USA. between sampling periods in control and treatment (feral cat removal) trapping grids. Trapping occurred between November 2016 and March 2017. Recruitment refers to the estimated number of individuals that were in addition to the expected number of individuals to have survived and remained on the plot from sessions 1 to 2.	18
Table 4. Mean maximum distance moved (MMDM) between captures for <i>Rattus</i> spp. sorted by grid and trapping session on Rota, Commonwealth of the Northern Mariana Islands, USA. Only individuals with >1 capture within a session were used to calculate MMDM (n). Density was calculated using the abundance estimates from the capture-mark-recapture model and effective trapping area of each grid (see Methods).	19

LIST OF FIGURES

Figure 1. Rota, Commonwealth of the Northern Mariana Islands, USA and the locations of capture-mark-recapture grids set for <i>Rattus</i> spp., sorted by control and treatment (feral cat removal) groups.....	7
Figure 2. Initial capture (p) and recapture (c) probability estimates, with confidence interval, from a robust design Huggins' p and c model, by time and experimental group for <i>Rattus</i> spp. on Rota, Commonwealth of the Northern Mariana Islands, USA. Trapping occurred between November 2016 and March 2017.	15
Figure 3. Model estimates of abundance, with confidence intervals, before and after cat removal treatment for each grid in both the control and treatment group for <i>Rattus</i> spp. on Rota, Commonwealth of the Northern Mariana Islands, USA. Trapping occurred between November 2016 and March 2017.	17

INTRODUCTION

Feral cats (*Felis catus*) have been implicated in the extinction or as a major threat to insular native bird species around the globe (Medina et al. 2011). For this reason, controlling or eradicating cat populations from islands may be an effective strategy to aid in the recovery of bird species (Côté and Sutherland 1997, Keitt and Tershy 2003, Nogales et al. 2004, Bonnaud et al. 2010). On Rota, Commonwealth of the Mariana Islands, USA, feral cat removal is employed to protect two endangered bird species endemic to the Mariana Islands, the Guam rail (*Gallirallus owstoni*) and the Mariana crow (*Corvus kubaryi*; Leo et al. 2018, Faegre et al. 2019).

There is concern, however, that feral cat removal may have unintended negative consequences to the native fauna of Rota through the increase in abundance of invasive rats. The mechanism of this possible consequence is known as the “mesopredator release” (Soulé et al. 1988), in which the reduction or removal of an apex predator leads to the explosion of a lesser predator or omnivore, leading to increased predation on a shared prey. A major assumption of this hypothesis is the control of a secondary predator by the apex predator through predation or direct competition, or what could be generalized as “top-down control” (Terborgh 1988).

Feral cats are often found to prey more heavily on mammals than birds (Kutt 2012, Loss et al. 2013), and on some islands rats can account for as much as a 95% occurrence in feral cat diets (Zavaleta et al. 2001). On Rota, we found that 60% (n = 299) of stomachs from euthanized feral cats contained at least one rat (D. A. Page, Institute for

Wildlife Studies, unpublished data). Ranchers on Rota claim (D. A. Page, personal observation) to have observed more crop damage from rats since feral cat removal began, suggesting a system of top-down control of rats by feral cats. If predation by feral cats does limit rat population density in areas targeted for feral cat removal, the resulting increase in rat density could lead to greater predation pressure on native prey species. Examples of prey declines following mesopredator release have been documented in a variety of habitats and ecosystems (Courchamp et al. 1999a, Rayner et al. 2007, Russell et al. 2009). Rats are particularly problematic for nesting birds because they consume both the eggs and nestlings of many bird species (Amarasekare 1993, Innes et al. 1999, Vanderwerf 2009) and have been directly observed taking nests of native forest birds on Rota (Nietmann and Ha 2018). Moreover, rats can also contribute to land mollusk declines (Hadfield et al. 1993, Chiba 2010, St Clair 2011) and are voracious seed predators that can interrupt natural seed dispersal and germination of native forests (Shiels et al. 2014, Harper and Bunbury 2015).

According to data collected between 1982 and 2012, five of the eight native forest birds on Rota are in decline (Camp et al. 2014). Two endangered species of tree snail, the fragile tree snail (*Samoana fragilis*) and humped tree snail (*Partula gibba*), also occur on Rota. All of these native fauna may be at risk to the presence of either or both feral cats and rats. Feral cat control is a desirable conservation strategy for Rota (Zarones et al. 2015). However, it seems wise to investigate the consequences of cat removal because of the mixed results of such efforts (Campbell et al. 2011). If invasive species management

is aimed at reducing feral cat predation of native forest birds, but is causing an increase in the rat population, the benefits may be offset by an increase in predation by rats.

The purpose of this study is to inform wildlife managers by testing the hypothesis that feral cat removal on Rota, as it has been previously conducted, leads to an increase in rat abundance or greater rat survival.

STUDY AREA

Rota is the second southernmost island in the Mariana Island Archipelago (hereafter, Marianas) located in the northwestern Pacific Ocean (14°09'13" north 145°12'11" east). The average high temperatures range from 27–31°C throughout the year, and average monthly rainfall ranges from 8.9–36.6 cm with most rain accumulating between July and November (Weather Atlas 2019). The habitat of interest to this study was the native limestone forest, which canopy and subcanopy consists primarily of *Intsia bijuga*, *Hibiscus tiliaceus*, *Pandanus* spp., *Ochrosia oppositifolia*, *Guamia mariannae*, *Artocarpus* spp., *Ficus* spp., *Elaeocarpus joga*, *Hernandia sonora*, and *Pisonia grandis* (Falanruw et al. 1989, J. C. Bamba, Commonwealth of the Northern Mariana Islands Department of Lands and Natural Resources, personal communication). Two species of rats inhabit Rota; the black rat (*Rattus rattus*) and Pacific rat (*Rattus exulans*; Wiewel et al. 2009). Unlike Guam, Rota has not been infested by the invasive brown treesnake (*Boiga irregularis*), which is responsible for the extirpation of most of Guam's indigenous avifauna and also suppresses small mammal populations (Savidge 1987, Wiles et al. 2003).

MATERIALS AND METHODS

To infer the effects of feral cat removal on rat populations, I estimated rat abundance, apparent survival, and calculated recruitment on trapping grids in three control plots and three treatment plots in which feral cats were lethally removed. Two areas northeast of the airport, the control (14°11'06.5" north 145°15'16.3" east) and the treatment (14°10'49.6" north 145°16'07.8" east), were chosen for this study because of their representative native forest composition and accessibility (Figure 1). I employed a before-after-control-impact design so that I could separate the effects of feral cat control from other time-varying factors impacting rat abundance and demographic rates. Rat abundance and apparent survival rates were estimated from a mark-recapture sampling conducted on each grid before and after feral cat removal treatments were imposed. Rat recruitment between pre- and post-treatment trapping sessions was calculated from the estimated changes in abundances and apparent survival rates. The experiment ran from November 2016 through March 2017.

Treatment

The feral cat removal treatment was implemented by the Institute for Wildlife Studies (IWS). Feral cat home ranges on Rota were 0.13–0.58 km² for females and 0.11–3.35 km² for males (Leo et al. 2016, D. A. Page, unpublished data). Removal and control plots were spaced ≥ 1 km apart to ensure that most feral cats eliminated from the removal plots would not have also ranged into the control plots.

Feral cats were removed by trapping and nighttime hunting. There was a maintained level of effort consistent with previous feral cat removal work conducted by IWS in other areas of the island, during which effort averaged 29.8 traps set per night and 39.5 kilometers driven per night (Page and Garcelon 2016). Each plot in the treatment group received 71–96 days of feral cat removal between pre- and post-treatment assessments of rat abundance and demographic rates (Table 1). Some plots received longer periods of feral cat control, because rat trapping on all plots was completed prior to cat removal.

Table 1. Dates on which rat trapping occurred and the number of days of feral cat removal treatment between trapping sessions, by grid number, on Rota, Commonwealth of the Northern Mariana Islands, USA. Grids which received no treatment were in the control group.

Grid	Session 1	Session 2	Treatment days
1	16–20 Nov, 2016	24–28 Feb, 2017	0
2	26–30 Nov, 2016	10–14 Mar, 2017	0
3	10–14 Dec, 2016	21–25 Mar, 2017	0
4	15–19 Nov, 2016	24–28 Feb, 2017	71
5	26–30 Nov, 2016	10–14 Mar, 2017	85
6	10–14 Dec, 2016	21–25 Mar, 2017	96

Once rat trapping began for the post-treatment session, trapping plots that had not yet been opened were still receiving the cat removal treatment. However, the time between the pre- and post-treatment sessions was similar for any given plot (96–100 days). Cat removal thus occurred over a period approximately twice the average time between litters of black rats in Oceania (27–38 days; Innes 2005) to allow rat populations

to respond to the change in predator density. No prolonged removal of feral cats was done in the study area for >10 months prior to the experiment.

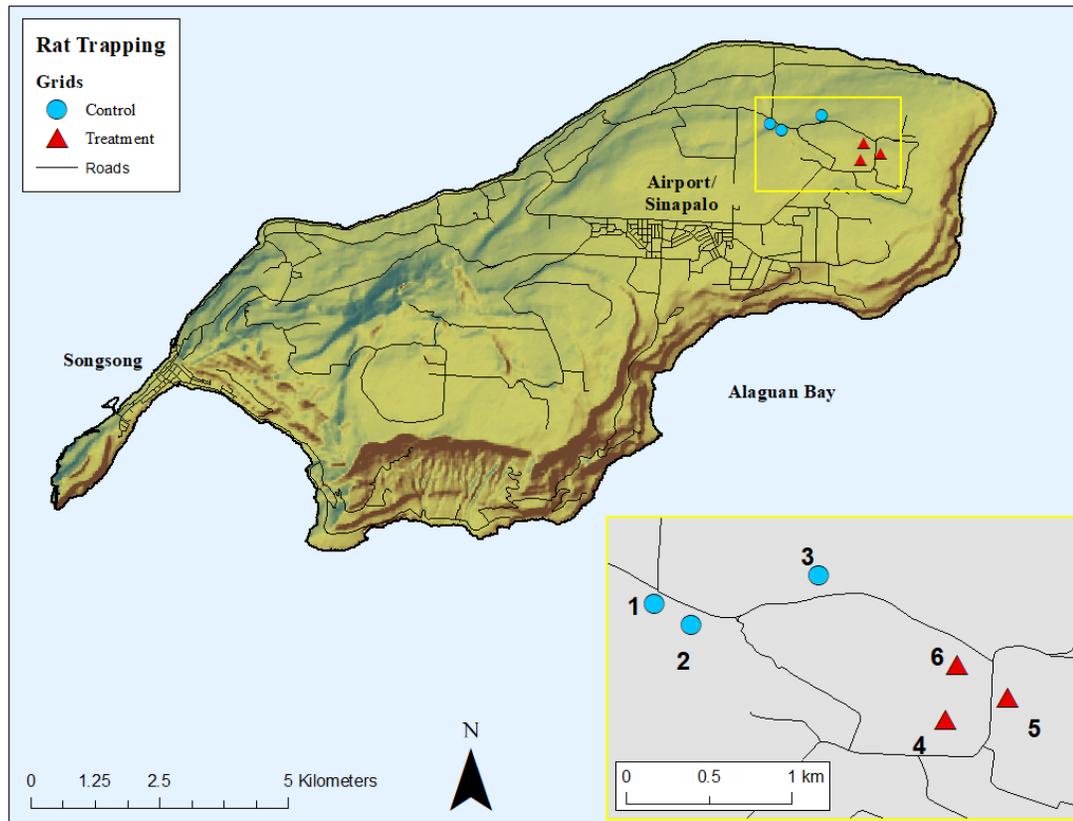


Figure 1. Rota, Commonwealth of the Northern Mariana Islands, USA and the locations of capture-mark-recapture grids set for *Rattus* spp., sorted by control and treatment (feral cat removal) groups.

Trapping

Within each study plot, traps were arranged in a 10×10 grid with traps spaced 10 m apart. Wiewel et al. (2009a) reported a mean maximum distance traveled between traps of 14.5 m for rats, therefore the spatial arrangement of our traps was expected to

result in multiple traps within most rat home ranges. Each grid was oriented to be completely within forest cover and not bordering roads or agricultural lands. Haguruma live-traps (285 × 210 × 140 mm; Uni-King, Honolulu, HI) were used because they are more effective at capturing rats than other live-trap types previously used in the Marianas, and lethal trapping methods provide less precise abundance estimates (Wiewel et al. 2009b). Traps were placed on the ground, tethered to a secure object with wire, marked by tying flagging on the nearest tree, and baited with a combination of mature coconut meat and peanut butter. Rats are naturally sensitive to new structures in their environments (Cowan 1977), therefore traps were baited and the doors were wired open for two days prior to initiating trapping to help the rats acclimate to the presence of the traps. Traps remained set and were checked daily for five consecutive nights. Two plots were trapped at a time; one from the treatment and one from the control. These plot pairings were trapped in the same order for each session. I monitored the weather daily to assess the risk of captured animals becoming hypothermic due to storm events, but was never forced to interrupt a trapping session once it had started. The trapping protocol was approved by the Humboldt State University Institutional Animal Care and Use Committee on 19 October, 2016 (No. 16/17.W.44-A).

The initial rat trapping session began 15 November and concluded 14 December 2016, and the second rat trapping session began 24 February and concluded 25 March 2017. The first time each rat was captured I applied numbered, metal ear tags (Style 1005-1; National Band & Tag Company, Newport, KY) in both ears, and recorded trap location, ear length, hind foot length, sex, and reproductive maturity (i.e., descended

testes or perforated vagina). For each recaptured rat, I recorded the ear tag combination and immediately released the animal. Metal ear tags were chosen over passive integrated transponder (PIT) tags because PIT tags are more expensive and have shown no significant advantage in retention over metal ear tags in several species (Morley 2002, Fokidis et al. 2006). When a rat was recaptured with an ear tag missing in one ear, a replacement tag was applied to that ear and the new number was recorded. I tracked changes in ear tag combinations when organizing individual capture histories to create a unique encounter history for each individual.

Analysis

All mark-recapture analysis was done in program MARK (White and Burnham 1999) using program R (R Core Team 2019) and the package RMARK (Laake 2013) as an interface. I used a robust design Huggins' closed captures p and c model to estimate abundance (N) at each pre- and post-treatment trapping session, apparent survival between pre- and post-treatment trapping sessions (S), and nightly probabilities of initial capture (p) and recapture (c) during each trapping session (Pollock 1982, Huggins 1989, 1991, Kendall et al. 1995). This model also estimates temporary immigration and emigration, however since our study design only includes two primary occasions, these were effectively inestimable parameters and were fixed to zero.

I fit several models to the data to evaluate different hypotheses about what variables influenced capture and recapture probabilities, and apparent survival. The model set included a null model which assumed that each of these parameters was

constant across all grids and all trapping sessions. The only covariate I included for capture and recapture parameters was days since the first trap day within a session as a continuous variable (time). Covariates for the apparent survival parameter included treatment or control group (treatment), trapping session (session), and plot pairings that were trapped concurrently (pair).

I used Akaike's Information Criterion corrected for sample size (AIC_c) to evaluate relative support for alternative models (Burnham and Anderson 1998), and report the parameter estimates from this model. I calculated recruitment between pre- and post-treatment periods in each field season as the number of animals expected to have survived and remain on the study plot during the treatment period, subtracted from the abundance estimate of the primary occasion after the treatment. I calculated this as the abundance estimate post-treatment (\widehat{N}_{t+1}) minus the product of the abundance estimate prior to treatment (\widehat{N}_t) and apparent survival estimate for that interval (S):

$$recruitment = \widehat{N}_{t+1} - \widehat{N}_t S$$

I used package SECR (Efford 2019) in program R to calculate mean maximum distance moved between captures for each grid within each trapping session. To calculate the effective trapping area for each grid, I buffered the grid dimensions by half the mean maximum distance moved to mitigate overestimation of density (Wilson and Anderson 1985). These calculated areas were then used with each abundance estimate to calculate rat densities at each grid within each trapping session.

RESULTS

Treatment

Seventeen feral cats were removed by hunting and trapping between the end of the first rat trapping session to the end of the second rat trapping session. The Institute for Wildlife Studies set an average of 41.7 feral cat traps set per night of effort, and drove an average of 36.2 kilometers driven per night. These efforts totaled 868.7 kilometers driven, and 3,672 trapnights. Cats removed from the grids were dissected and their gastrointestinal tract searched for rat remains and metal ear tags. Nearly all cats had rats in their stomachs, however, only one ear tag was recovered (D. A. Page, Institute for Wildlife Studies, unpublished data).

Rat Trapping

I captured and marked a total of 565 individual rats in 6000 trap-nights. Because of the morphological similarities between *R. rattus* and *R. exulans* (A. S. Wiewel, University of Adelaide, personal communication), I did not attempt to differentiate them in the field and both rat species were combined for analysis. Sex ratios of captured rats were slightly male-biased with 271 males to 254 females. An additional 40 captured rats were not sexed due to human error. All individuals were included in the analysis regardless of having their sex confirmed. Although present on Rota, no *Mus musculus* were captured.

I averaged 0.29 rat captures per adjusted trap-night. Adjusted trap-nights is defined as the number of traps that captured a rat or were still set and baited when checked, plus one half of the number of traps that were not available to capture a rat (e.g., tripped without a capture, robbed of bait, or captured bycatch). This assumes that, on average, these traps were available to capture a rat for half of the time they were deployed. Bycatch of hermit crabs (*Coenobita* spp.) and coconut crabs (*Birgus latro*) accounted for 29.6% of trap disturbance. Crabs were likely also responsible for other types of trap disturbance, as evidenced by the nature of damage to tripped traps. Although I did not keep records of trap damage, a substantial amount of time was devoted to repairing traps damaged by coconut crabs.

Mark-Recapture Analysis

The robust design model that had the lowest AIC_c held apparent survival constant across all groups and included an interactive term between days since trapping began (time) and experimental group on capture and recapture, and the model with the next lowest AIC_c only differed in that it included treatment as a covariate for apparent survival (Table 2). The models only differed by 0.87 AIC units and together held almost all the model weight. There was no effect of the order in which plots were trapped (pair) on apparent survival in any of the top competing models.

Since some individuals were not sexed ($n = 40$) and inclusion of these would likely result in any model with sex as a covariate ranking highly by virtue of the small sample size of that group, I conducted a preliminary analysis of the effect of sex. I began

by removing those unsexed individuals and using a dataset that included only known sex individuals, then ranking models with and without sex as a covariate (Appendix A).

Models without sex had lower AIC_c than models which included sex as a covariate for apparent survival and/or capture and recapture probabilities, thus I determined that differences in males and females for any parameter were not substantial. All individuals – males, females, and unknown sex – were included in the final dataset and sex was not included as a factor in the final model set.

Table 2. Candidate set of robust design Huggins' p and c models for *Rattus* spp. on Rota, Commonwealth of the Northern Mariana Islands, USA, ranked by Akaike's Information Criterion corrected for sample size (AIC_c). Model parameters included apparent survival (S), initial capture probability (p), and recapture probability (c). Covariates included control and treatment group (treatment), primary occasion (session), and days since the first trapping day within a session (time). The operators + and * represent additive and interactive terms, respectively, between covariates. Model parameters held constant across groups are denoted with a (1). Gamma' and Gamma'' were fixed at zero and are not included in the model descriptions.

Model description	Parameter count	AIC_c	Delta AIC	Model weight	Deviance
S(1)p(time * treatment)c(time * treatment)	9	5028.94	0.00	0.61	5354.06
S(treatment)p(time * treatment)c(time * treatment)	10	5029.81	0.87	0.39	5352.90
S(treatment)p(time * session)c(time * session)	10	5079.48	50.54	0	5402.57
S(1)p(time * session)c(time * session)	9	5084.29	55.35	0	5409.41
S(treatment)p(time)c(time)	6	5107.21	78.27	0	5438.39
S(1)p(time)c(time)	5	5112.03	83.09	0	5445.23
S(treatment * pair)p(time)c(time)	10	5112.83	83.89	0	5435.92
S(pair)p(time)c(time)	7	5115.76	86.82	0	5444.93
S(1)p(treatment * session)c(treatment * session)	9	5134.81	105.87	0	5459.93
S(treatment)p(treatment * session)c(treatment * session)	10	5135.44	106.50	0	5458.53
S(treatment)p(1)c(1)	4	5243.62	214.68	0	5578.83
S(1)p(1)c(1)	3	5248.45	219.51	0	5585.67

Parameter Estimates

Capture and recapture probability estimates ranged from 0.09 to 0.60. Both capture and recapture probabilities declined through each trapping session and were lower overall in the treatment group (Figure 2). Recapture estimates were slightly higher than capture estimates within each group. Apparent survival between trapping occasions was 0.50 (SE = 0.056) and constant across all groups.

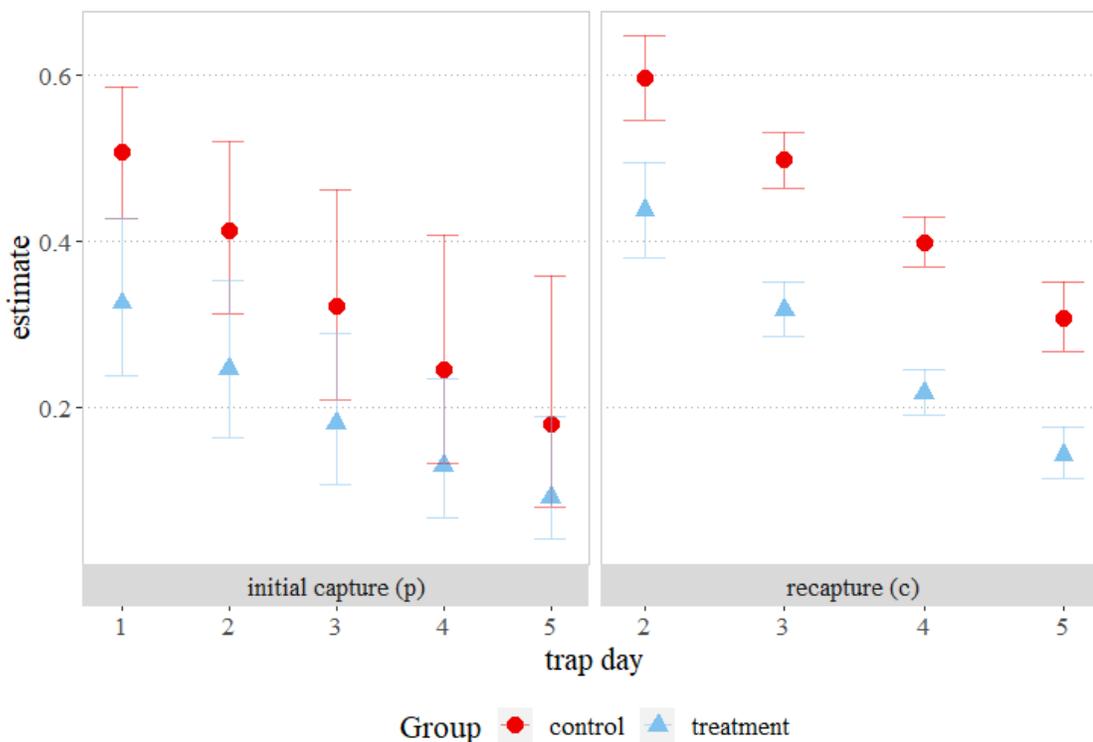


Figure 2. Initial capture (p) and recapture (c) probability estimates, with confidence interval, from a robust design Huggins' p and c model, by time and experimental group for *Rattus* spp. on Rota, Commonwealth of the Northern Mariana Islands, USA. Trapping occurred between November 2016 and March 2017.

Abundance and Recruitment

Abundance estimates declined from before to after the treatment period on all grids, though these declines were not significant based on overlapping confidence intervals from first to second session estimates (Figure 3). Second session individual grid abundances were estimated to be composed of 30–46% new individuals, or 41% and 38% overall for the control and treatment groups, respectively (Table 3).

Mean maximum distance moved between captures for individuals with >1 capture per session ranged from 14.6–19.7 m across all grids and sessions (Table 4). Every grid saw an increase in the mean maximum distance moved from the first to second session. The greatest distance moved between captures was 92.2 m and several individuals moved a maximum of 0 m between captures (returned to the same trap for any subsequent captures). There was a negative linear relationship between the mean maximum distance moved and rat density on each grid ($F_{1,9} = 13.35$, $P = 0.005$).

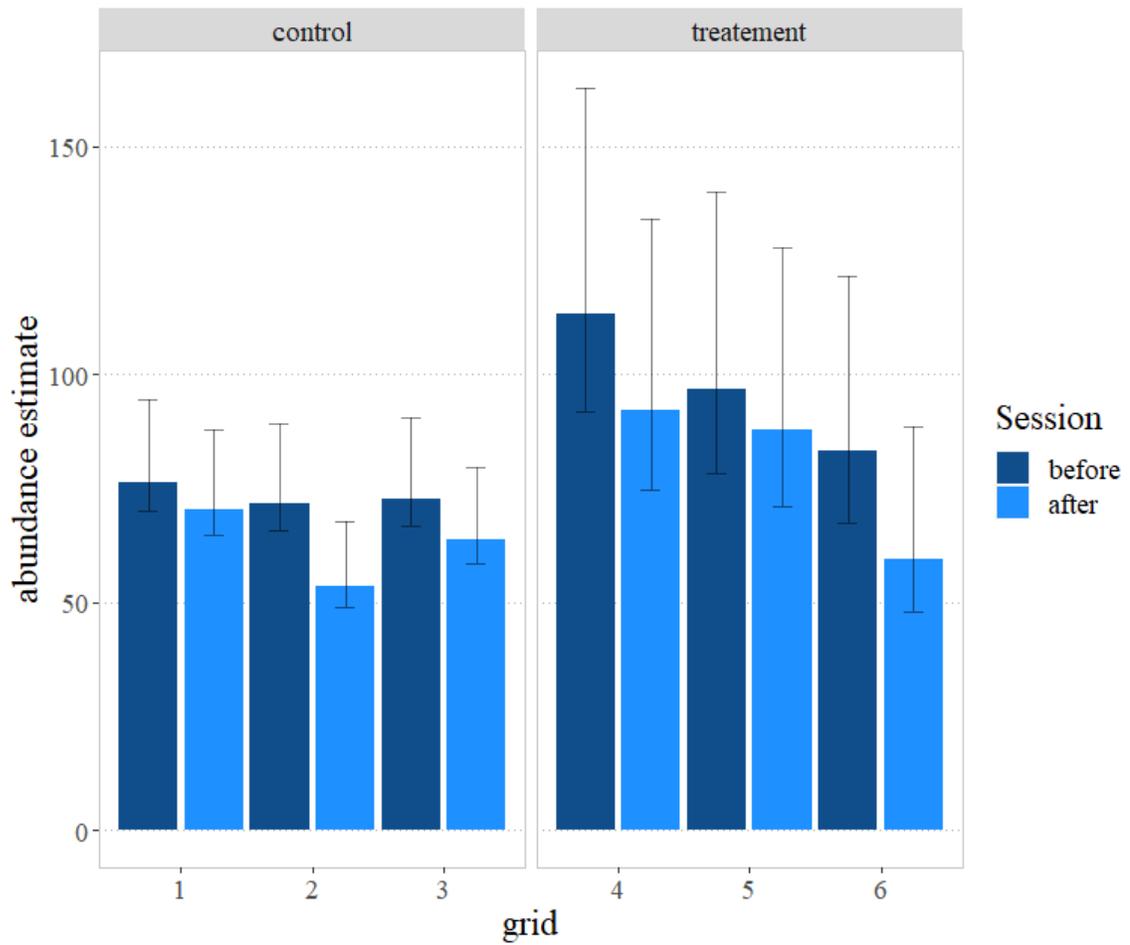


Figure 3. Model estimates of abundance, with confidence intervals, before and after cat removal treatment for each grid in both the control and treatment group for *Rattus* spp. on Rota, Commonwealth of the Northern Mariana Islands, USA. Trapping occurred between November 2016 and March 2017.

Table 3. Abundance estimates for each session, combined by experimental group, for *Rattus* spp. on Rota, Commonwealth of the Northern Mariana Islands, USA. between sampling periods in control and treatment (feral cat removal) trapping grids. Trapping occurred between November 2016 and March 2017. Recruitment refers to the estimated number of individuals that were in addition to the expected number of individuals to have survived and remained on the plot from sessions 1 to 2.

Group	Session	Abundance estimate	Standard error	Lower confidence interval	Upper confidence interval	Change in abundance	Recruitment
Control	1	221	14.27	202.92	274.30	–	–
Control	2	188	12.29	172.38	235.23	-14.95%	76.63
Treatment	1	293	41.01	237.85	424.64	–	–
Treatment	2	240	33.83	193.78	350.56	-18.27%	92.09

Table 4. Mean maximum distance moved (MMDM) between captures for *Rattus* spp. sorted by grid and trapping session on Rota, Commonwealth of the Northern Mariana Islands, USA. Only individuals with >1 capture within a session were used to calculate MMDM (n). Density was calculated using the abundance estimates from the capture-mark-recapture model and effective trapping area of each grid (see Methods).

Group	Grid	Session	n	MMDM (m)	Standard error	Density (rats/ha)
Control	1	1	34	16.5	1.81	54
Control	1	2	40	18.5	1.99	49
Control	2	1	33	18.0	1.85	50
Control	2	2	28	20.5	2.60	35
Control	3	1	51	19.7	1.98	49
Control	3	2	39	21.3	2.73	42
Treatment	4	1	41	16.3	1.38	81
Treatment	4	2	26	16.8	2.55	66
Treatment	5	1	24	14.6	1.89	72
Treatment	5	2	26	23.7	3.41	55
Treatment	6	1	34	16.5	1.81	60
Treatment	6	2	40	18.5	1.99	41

DISCUSSION

The results of this study do not support the hypothesis that feral cat removal, as it has historically been done on Rota, positively affects rat abundance in native limestone forests. Rat abundance declined in all plots between pre- and post-treatment trapping sessions. This result suggests that rat population growth did not show a positive response to feral cat removal. Had that been the case, rat population size estimates at removal sites would have displayed greater growth (or smaller decline) than control sites. Additionally, apparent survival estimates should have been higher at sites with feral cat removal, even if both groups declined in abundance. However, there was no difference in apparent survival between the sites where cats were removed and those from which cats were not removed. Even when considering the second-ranked model that included experimental group as a covariate of the apparent survival parameter, apparent survival was lower where feral cats were being removed compared to the control (0.41 vs. 0.53) and there was no significant difference among the groups based on overlapping confidence intervals. This, again, suggests that removing feral cats from the landscape does not release rat population dynamics from top-down control, at least over the time interval during which this study was performed.

Rat densities were high compared to other studies of *R. rattus* (Dowding and Murphy 1994, Whisson et al. 2007, Harper 2016), including the last abundance estimates of this habitat type on Rota (Wiewel et al. 2009a). However, other habitat types from that

same study saw similar densities, as did a study of *R. exulans* on nearby Aguiquan (Yackel Adams et al. 2011).

I suggest two possible reasons why feral cat removal does not appear to influence rat abundance. First, current feral cat removal strategies may not reduce local cat abundance sufficiently to affect detectable changes in rat abundance when employed at the temporal and spatial scales of this project. Second, rat abundances may be resource-limited and not controlled by feral cat predation. Of course, these are not mutually exclusive and may be density dependent.

Because feral cat abundance was not measured independently of the removal effort, we do not know the scale of the change in feral cat population during the treatment period. There is evidence that intermittent removal of feral cats can actually increase their local abundance immediately following a cull (Lazenby et al. 2015). Lazenby et al. (2015) hypothesized that higher feral cat densities following a cull were caused by greater home range overlap by immigrant feral cats moving into the newly vacant territories. Given that rat survival appeared not to differ between control and treatment plots, it is unlikely that culling led to increased feral cat predation pressure on rats in my study. However, feral cat immigration may have maintained similar cat densities across treatments with no change in the predation pressure on rats. If so, a longer period of feral cat control over a wider area buffering our study plots would be necessary to determine if rat abundance and apparent survival are tied to local feral cat abundance.

Given the largest feral cat home range recorded on Rota was 3.35 km², focusing removal effort on an area that buffers treatment grids by at least 2.1 km (the diameter of a

3.35 km² circle) may reduce the amount of immigrant feral cats that are able to impact the treatment plot. This strategy, however, would require a greater hunting and trapping effort to achieve the same level of removal intensity and would require the control group of rat trapping grids to be similarly buffered from removal activities, approximately 4.2 km between the two nearest grids from the control and treatment groups. It would be difficult to select two areas that are far enough from each other but are also similar in habitat. Additionally, land ownership may be a limiting factor.

This study was conducted at the start of the dry season, which may have consequently lead to the observation of overall lower rat abundance in the second trapping session. A decline in rat abundance with the progression of the dry season would be consistent with other rodent studies in areas of seasonal food availability (Bunn and Craig 1989, Tristiani and Murakami 2003, White 2008, Letnic et al. 2011). Trees such as breadfruit (*Artocarpus* spp.) and pandanus (*Pandanus tectorius*), which were very common on the grids, produce a crop of fruit only once or twice per year (Atchley and Cox 1985, Thomson et al. 2006). Rats in Oceania primarily feed on fruit (Shiels et al. 2014), and when these trees are fruiting the jungle may be rich in easily-found calories in the surrounding area for a short time. The rapid reproductive capabilities of rats (Shiels et al. 2014) could allow the population to expand during this time, especially if fruiting is staggered among plant species. The onset of the dry season and slowed or ceased fruit production would reduce food and water resources. This follows the premise of “bottom-up control” in which the carrying capacity of a species is limited by resource density (e.g., food or space) rather than by predator density (Hunter and Price 1992, Power 1992,

Terborgh and Estes 2010). The increased movement of individuals (mean maximum distance moved) as the population decreased from the first to the second session is another possible indicator that food limitation, rather than predation, was affecting abundance (Cameron and Spencer 1985, Endries and Adler 2005).

By definition, bottom-up control should equally apply to predators, meaning limited growth of rats should in turn limit the growth of feral cats. Therefore, it is possible that the lethal control of rats may have the additional benefit of reducing feral cat abundance whereby providing a two-fold benefit to native forest birds. This indirect link between rats and forest birds, where both are prey to feral cats, is known as “predator mediated competition” in which an increase in a primary prey species (e.g., rats) increases predator abundance (e.g., feral cats) which in turn increases predation rates on a secondary prey (e.g. native forest birds; Holt 1977, Courchamp et al. 2000). In this case, since rats are also nest predators of forest birds, controlling rats may have both direct and indirect benefits to forest birds (Courchamp et al. 1999b, Norbury 2017).

Feral cats may not be completely dependent on rats as a food source, and therefore could switch to alternative prey (i.e., forest birds) if rats became more scarce. This prey-switching behavior has been observed in feral cats and stoats (*Mustela erminea*) primarily feeding on introduced rabbits (*Oryctolagus cuniculus*) and rats, respectively (Murphy and Bradfield 1992, Doherty et al. 2015). However, Mutze (2017) found that prey-switching by feral cats was more common after natural declines in the rabbit population rather than after rapid declines from control effort. Regardless, concurrent feral cat removal would be advised — at least during the initial reduction of

rats — to mitigate the impacts of potential prey switching on native forest birds. Leo et al. (2018) estimated that previous spotlight hunting of feral cats may have only reduced cat abundance by 15% island-wide after 17 months of hunting, suggesting the need for more effective strategies for controlling feral cats on Rota. The addition of bottom-up control of feral cats by reducing one of their primary food sources may have a compounding benefit by greatly increasing the effectiveness of feral cat control efforts when combined with traditional techniques (McGregor et al. 2020).

SUMMARY AND RECOMMENDATIONS

Based on this study, the effects of predation by feral cats on rats in the forests of Rota do not appear to be strong enough to be controlling the rat population. This finding is contrary to the commonly purported repercussions of feral cat removal programs on Rota, where community members believe removing cats results in increasing rat numbers, and is contrary to the mesopredator release hypothesis.

Further exploration of the dynamics between cats and rats on Rota and how to most effectively control them would be merited. I suggest two ways of doing this. First, by expanding on this study in time and space while incorporating an accurate measure of feral cat abundance. This would increase the precision of the analyses and address some data gaps regarding the efficacy of feral cat removal. It would also be advantageous to conduct the experiment over an entire calendar year to better understand how rodent populations vary seasonally. Second, conducting a study to track the abundance and movement patterns of feral cats before and after a period of lethal rat control over a larger area would help to elucidate any dependence cats may have on rats as a food source. The results of one or both such studies might create a clearer picture of feral cat and rat interactions on Rota and pave a path for better, more informed management.

LITERATURE CITED

- Amarasekare, P. 1993. Potential impact of mammalian nest predators on endemic forest birds of Western Mauna Kea, Hawaii. *Conservation Biology* 7:316–324.
- Atchley, J., and P. A. Cox. 1985. Breadfruit fermentation in Micronesia. *Economic Botany* 39:326–335.
- Bonnaud, E., D. Zarzoso-Lacoste, K. Bourgeois, L. Ruffino, J. Legrand, and E. Vidal. 2010. Top-predator control on islands boosts endemic prey but not mesopredator. *Animal Conservation* 13:556–567.
- Bunn, T. J., and J. L. Craig. 1989. Population cycles of *Rattus exulans*: Population changes, diet, and food availability. *New Zealand Journal of Zoology* 16:409–418.
- Burnham, K. P., and D. R. Anderson. 1998. Practical Use of the Information-Theoretic Approach. Pages 75–117 in K. P. Burnham and D. R. Anderson, editors. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, New York, New York, USA.
- Cameron, G. N., and S. R. Spencer. 1985. Assessment of space-use patterns in the hispid cotton rat (*Sigmodon hispidus*). *Oecologia* 68:133–139.
- Camp, R. J., K. W. Brinck, P. M. Gorresen, F. A. Amidon, P. M. Radley, S. P. Berkowitz, and P. C. Banko. 2014. Status of forest birds on Rota, Mariana Islands. Hawai'i Cooperative Studies Unit University of Hawai'i at Hilo, Hilo, Hawai'i, USA.
- Campbell, K. J., G. Harper, D. Algar, C. C. Hanson, B. S. Keitt, and S. Robinson. 2011. Review of feral cat eradications on islands. Pages 37–46 in C. R. Veitch, M. N. Clout, and D. R. Towns, editors. *Proceedings of the International Conference on Island Invasives*, 8–12 February 2010. IUCN, Auckland, New Zealand.
- Chiba, S. 2010. Invasive rats alter assemblage characteristics of land snails in the Ogasawara Islands. *Biological Conservation* 143:1558–1563.
- Côté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. *Conservation Biology* 11:395–405.
- Courchamp, F., M. Langlais, and G. Sugihara. 1999a. Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology* 68:282–292.
- Courchamp, F., M. Langlais, and G. Sugihara. 1999b. Control of rabbits to protect island birds from cat predation. *Biological Conservation* 89:219–225.
- Courchamp, F., M. Langlais, and G. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* 69:154–164.
- Cowan, P. E. 1977. Neophobia and neophilia: new-object and new-place reactions of three *Rattus* species. *Journal of Comparative and Physiological Psychology* 91:63–71.

- Doherty, T. S., R. A. Davis, E. J. B. van Etten, D. Algar, N. Collier, C. R. Dickman, G. Edwards, P. Masters, R. Palmer, and S. Robinson. 2015. A continental-scale analysis of feral cat diet in Australia. *Journal of Biogeography* 42:964–975.
- Dowding, J. E., and E. C. Murphy. 1994. Ecology of ship rats (*Rattus rattus*) in a kauri (*Agathis australis*) forest in Northland, New Zealand. *New Zealand Journal of Ecology* 18:19–28.
- Endries, M. J., and G. H. Adler. 2005. Spacing patterns of a tropical forest rodent, the spiny rat (*Proechimys semispinosus*), in Panama. *Journal of Zoology* 265:147–155.
- Faegre, S. K., L. Nietmann, D. Hubl, J. C. Ha, and R. R. Ha. 2019. Spatial ecology of the Mariana Crow *Corvus kubaryi*: Implications for management strategies. *Bird Conservation International* 29:527–541.
- Falanruw, M. C., T. G. Cole, and A. H. Ambacher. 1989. Vegetation survey of Rota, Tinian, and Saipan, Commonwealth of the Northern Mariana Islands. Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.
- Fokidis, H. B., C. Robertson, and T. S. Risch. 2006. Keeping tabs: are redundant marking systems needed for rodents? *Wildlife Society Bulletin* 34:764–771.
- Hadfield, M. G., S. E. Miller, and A. H. Carwile. 1993. The decimation of endemic Hawai’ian tree snails by alien predators. *American Zoologist* 33:610–622.
- Harper, G. 2016. Home range and population density of black rats (*Rattus rattus*) on a seabird island: a case for a marine subsidised effect? *New Zealand Journal of Ecology* 40:219–228.
- Harper, G. A., and N. Bunbury. 2015. Invasive rats on tropical islands: Their population biology and impacts on native species. *Global Ecology and Conservation* 3:607–627.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Huggins, R. M. 1989. On the Statistical Analysis of Capture Experiments. *Biometrika* 76:133–140.
- Huggins, R. M. 1991. Some Practical Aspects of a Conditional Likelihood Approach to Capture Experiments. *Biometrics* 47:725–732.
- Hunter, M. D., and P. W. Price. 1992. Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities. *Ecological Society of America* 73:724–732.
- Innes, J. G. 2005. Ship rat. Pages 187–203 in C. M. King, editor. *The Handbook of New Zealand Mammals*. Second. Oxford University Press, South Melbourne, Victoria, Australia.
- Innes, J., R. Hay, I. Flux, P. Bradfield, H. Speed, and P. Jansen. 1999. Successful recovery of North Island kokako *Callaeas cinerea wilsoni* populations, by adaptive management. *Biological Conservation* 87:201–214.
- Keitt, B. S., and B. R. Tershy. 2003. Cat eradication significantly decreases shearwater mortality. *Animal Conservation* 6:307–308.

- Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A Likelihood-Based Approach to Capture-Recapture Estimation of Demographic Parameters under the Robust Design. *Biometrics* 51:293–308.
- Kutt, A. S. 2012. Feral cat (*Felis catus*) prey size and selectivity in north-eastern Australia: implications for mammal conservation: Feral cat prey size and selection. *Journal of Zoology* 287:292–300.
- Lazenby, B. T., N. J. Mooney, and C. R. Dickman. 2015. Effects of low-level culling of feral cats in open populations: a case study from the forests of southern Tasmania. *Wildlife Research* 41:407–420.
- Leo, B. T., J. J. Anderson, R. Brand Phillips, and R. R. Ha. 2016. Home Range Estimates of Feral Cats (*Felis catus*) on Rota Island and Determining Asymptotic Convergence. *Pacific Science* 70:323–331.
- Leo, B. T., J. J. Anderson, J. Ha, R. B. Phillips, and R. R. Ha. 2018. Modeling Impacts of Hunting on Control of an Insular Feral Cat Population. *Pacific Science* 72:57–68.
- Letnic, M., P. Story, G. Story, J. Field, O. Brown, and C. R. Dickman. 2011. Resource pulses, switching trophic control, and the dynamics of small mammal assemblages in arid Australia. *Journal of Mammalogy* 92:1210–1222.
- Loss, S. R., T. Will, and P. P. Marra. 2013. The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications* 4:1396.
- McGregor, H., K. Moseby, C. N. Johnson, and S. Legge. 2020. The short-term response of feral cats to rabbit population decline: Are alternative native prey more at risk? *Biological Invasions* 22:799–811.
- Medina, F. M., E. Bonnaud, E. Vidal, B. R. Tershy, E. S. Zavaleta, C. J. Donlan, B. S. Keitt, M. Le Corre, S. V. Horwath, and M. Nogales. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology* 17:3503–3510.
- Morley, C. G. 2002. Evaluating the performance of PIT tags and ear tags in a capture-recapture experiment. *New Zealand Journal of Zoology* 29:143–148.
- Murphy, E., and P. Bradfield. 1992. Change in diet of stoats following poisoning of rats in a New Zealand forest. *New Zealand Journal of Ecology* 16:137–140.
- Mutze, G. 2017. Continental-scale analysis of feral cat diet in Australia, prey-switching and the risk: benefit of rabbit control. *Journal of Biogeography* 44:1679–1981.
- Nietmann, L., and R. R. Ha. 2018. Variation in age-dependent nest predation between island and continental Rufous Fantail (*Rhipidura rufifrons*) subspecies. *The Auk: Ornithological Advances* 135:1064–1075.
- Nogales, M., A. Martín, B. R. Tershy, C. J. Donlan, D. Veitch, N. Puerta, B. Wood, and J. Alonso. 2004. A review of feral cat eradication on islands. *Conservation Biology* 18:310–319.
- Norbury, G. 2017. The case for ‘bottom-up’ pest management. *New Zealand Journal of Ecology* 41:271–277.
- Pollock, K. H. 1982. A Capture-Recapture Design Robust to Unequal Probability of Capture. *The Journal of Wildlife Management* 46:752–757.

- Power, M. E. 1992. Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy. *Ecology* 73:733–746.
- Rayner, M. J., M. E. Hauber, M. J. Imber, R. K. Stamp, and M. N. Clout. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences* 104:20862–20865.
- Russell, J. C., V. Lecomte, Y. Dumont, and M. Le Corre. 2009. Intraguild predation and mesopredator release effect on long-lived prey. *Ecological Modelling* 220:1098–1104.
- Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68:660–668.
- Shiels, A. B., W. C. Pitt, R. T. Sugihara, and G. W. Witmer. 2014. Biology and impacts of Pacific island invasive Species. 11. *Rattus rattus*, the black rat (Rodentia: Muridae). *Pacific Science* 68:145–184.
- Soulé, M. E., D. T. Bolger, A. C. Alberts, J. Wrights, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2:75–92.
- St Clair, J. J. H. 2011. The impacts of invasive rodents on island invertebrates. *Biological Conservation* 144:68–81.
- Terborgh, J. 1988. The Big Things that Run The World — A Sequel to E. O. Wilson. *Conservation Biology* 2:402–403.
- Terborgh, J., and J. A. Estes, editors. 2010. *Trophic cascades: predators, prey, and the changing dynamics of nature*. Island Press, Washington, D. C., USA.
- Thomson, L. A. J., L. Englberger, L. Guarino, R. R. Thaman, and C. R. Elevitch. 2006. *Pandanus tectorius* (pandanus). Pages 563–590 in C. R. Elevitch, editor. *Traditional Trees of Pacific Islands: Their Culture, Environment, and Use*. Permanent Agriculture Resources, Hōlualoa, Hawai'i, USA.
- Tristiani, H., and O. Murakami. 2003. Rates of population increase in the ricefield rat (*Rattus argentiventer*) as a function of food supply: an enclosure study in Jatisari, West Java. *Journal of Zoology* 259:239–244.
- Vanderwerf, E. A. 2009. Importance of nest predation by alien rodents and avian poxvirus in conservation of Oahu Elepaio. *Journal of Wildlife Management* 73:737–746.
- Weather Atlas. 2019. Monthly weather forecast and Climate, Rota, Northern Mariana Islands, USA. <<https://www.weather-us.com/en/northern-mariana-islands-usa/rota-climate>>. Accessed 7 Aug 2019.
- Whisson, D. A., J. H. Quinn, and K. C. Collins. 2007. Home Range and Movements of Roof Rats (*Rattus rattus*) in an Old-growth Riparian Forest, California. *Journal of Mammalogy* 88:589–594.
- White, T. C. R. 2008. The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews* 83:227–248.
- Wiewel, A. S., A. A. Yackel Adams, and G. H. Rodda. 2009a. Distribution, density, and biomass of introduced small mammals in the southern Mariana Islands. *Pacific Science* 63:205–222.

- Wiewel, A. S., A. A. Yackel Adams, and G. H. Rodda. 2009b. Evaluating abundance estimate precision and the assumptions of a count-based index for small mammals. *The Journal of Wildlife Management* 73:761–771.
- Wiles, G. J., J. Bart, R. E. Beck Jr., and C. F. Aguon. 2003. Impacts of the brown tree snake: Patterns of decline and species persistence in Guam's avifauna. *Conservation Biology* 17:1350–1360.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of Two Density Estimators of Small Mammal Population Size. *Journal of Mammalogy* 66:13–21.
- Yackel Adams, A. A., J. W. Stanford, A. S. Wiewel, and G. H. Rodda. 2011. Modelling detectability of kiore (*Rattus exulans*) on Aguiguan, Mariana Islands, to inform possible eradication and monitoring efforts. *New Zealand Journal of Ecology* 35:145–152.
- Zarones, L., A. Sussman, J. M. Morton, S. Plentovich, S. Faegre, C. Aguon, A. Amar, and R. R. Ha. 2015. Population status and nest success of the critically endangered Mariana Crow *Corvus kubaryi* on Rota, Northern Mariana Islands. *Bird Conservation International* 25:220–233.
- Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution* 16:454–459.

APPENDIX

Appendix A: Models used to evaluate the importance of the effects of sex on rat apparent survival and capture probabilities on Rota, Commonwealth of the Northern Mariana Islands, USA. The dataset used was a subset of the full dataset including only those individuals with known sex. Model parameters included apparent survival (S), initial capture probability within a trapping session (p), and recapture probability within a trapping session (c). Covariates included sex and time since the first trapping day in a session, and the operator “+” represents an additive term between covariates. Model parameters held constant are denoted with a (1).

Model description	Parameter count	AIC _c	Delta AIC	Model weight	Deviance
S(1)p(time)c(time)	5	4851.54	0.00	0.81	4727.71
S(1)p(time+sex)c(time+sex)	7	4854.50	2.96	0.19	4726.63
S(1)p(1)c(1)	3	4977.36	125.82	0.00	4857.55
S(sex)p(1)c(1)	4	4978.89	127.35	0.00	4857.07
S(1)p(sex)c(sex)	5	4980.93	129.39	0.00	4857.10
S(sex)p(sex)c(sex)	6	4982.55	131.01	0.00	4856.70