DISSERTATION

DISENTANGLING ISLAND FOOD-WEB CONNECTIONS IN GUAM AFTER THE BROWN TREESNAKE (*BOIGA IRREGULARIS*) INTRODUCTION

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2025

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ABSTRACT

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Shifts in predator abundance or identity strongly affects prey populations. If predators decline and predation pressures are relaxed, prey populations can increase, and the plants they feed on may experience more herbivory in a trophic cascade. Additionally, behaviors prey uses to escape from predators may decline. After an apex predator (brown treesnake [*Boiga irregularis*]) was introduced to Guam in the Pacific in the 1940's, forest birds that had previously been the top predators of arthropods and other small vertebrates were functionally extirpated. In this dissertation, I evaluate whether the loss of birds has led to a tropic cascade in which arthropods increase in abundance, leading to increased herbivory on plants. I quantify the effects of the loss of birds on arthropods and plants in Chapter 1, I explore shifts in predation in Chapter 2 and measure shifts in anti-predator behaviors in Chapter 3. My overarching goal is to deepen our understanding of how removal of former top predators influences trophic ecology, behavior and community structure.

In Chapter 1, I investigated how the loss of birds in the island of Guam have affected arthropod communities and herbivore damage to plants. Based on smaller scale experiments, I expected that the loss of birds in Guam would trigger a classic trophic cascade, such that we would observe greater abundance of all arthropod groups and higher rates of herbivory on plants in Guam compared to nearby islands that retain bird communities. I sampled arthropods using beating sheets and baits to sample ants, and quantified damage on leaves in Guam (without birds), as

well as Rota and Saipan (with birds). Contrary to my expectations, I found that the island without birds had the lowest arthropod abundance compared to islands with birds. This pattern held for arachnids and ants, which were two of the more common arthropod groups. Again, contrary to my initial hypothesis, but matching my data on arthropod abundance, I found that plants experienced less herbivory in the island with no birds compared to the islands with birds. I separated leaf samples into plants native to the islands or introduced and found that native plants experienced more herbivory than introduced plants on all islands. I did not observe a classic trophic cascade. Instead, my findings suggest that the effects of the loss of birds can be quite complex, and the effects of predator reduction at large scales may not reflect results found in smaller scale experiments.

In Chapter 2, I investigated the indirect trophic impacts of invasive snakes on arthropods. I hypothesized Guam, without birds, would have reduced predation pressure on arthropods compared to the nearby islands of Rota and Saipan, which have birds. To evaluate my hypothesis, I measured attack rates on model caterpillars, combining data I collected in 2022 with data from collaborators collected in 2013. In both years, attack rates from all possible predators (e.g. birds, arthropods, etc.) on caterpillars were greatest in islands with birds present, and lowest in Guam where no birds were present. However, from identifying the identity of the predators, differences in attack rates were driven by arthropods and lizards rather than birds. On Guam, I observed high attack rates by arthropods. The suppression of birds and small reptiles by snakes have been linked to the release of predacious arthropods. Contrary to smaller-scale experimental studies that reveal the release of herbivorous arthropods when birds are excluded, I found that birds played a minimal role in predating caterpillars on all islands. Thus, my results suggest that reptiles may be underappreciated predators in tropical forest food webs.

Finally, in Chapter 3, I asked whether the dramatic declines of insectivorous birds from Guam following the introduction of the brown treesnake (*Boiga irregularis*) has caused changes in abundance or anti-predator behaviors of butterflies. I addressed this question by comparing butterfly abundance and behaviors in two Mariana Island locations: Guam, which has limited avian insectivores and Saipan, numerous insectivores birds persist. Except for *Eurema* species, butterflies were less abundant in Guam. Behaviors of a common butterfly (*Euploia eunice*) hypothesized to be anti-predator behaviors were also reduced in Guam. Specifically, when butterflies were approached with a model bird, butterflies allowed the model predator to get closer before they took flight when compared to butterflies in Saipan. My study indicates that ecosystem-scale bird declines may have altered both the abundance and behavior of butterflies. These results are important to consider when reintroducing birds to areas where butterflies no longer exhibit defenses against them.

In summary, my dissertation found that the loss of birds did not trigger a trophic cascade as expected from literature and bird exclusion studies (Chapter 1). Instead, I found that arthropods and lizards may be key predators in the tropics (Chapter 2). Finally, I found that shifts in butterfly anti-predator behavior have occurred due to the loss of birds (Chapter 3). Through this work, I hope to shine light on the ecological effects of the brown treesnake on the island of Guam and to inspire the people of Guam to write their own scientific narratives.

ACKNOWLEDGEMENTS

At the start of my scientific journey, I did not think that a brown girl from a small island in the Pacific had a place in this field. It turns out, people like me just needed the right opportunities and support to become a scientist. I would not be where I am today without the village that always believed in my abilities and supported my dreams.

First and foremost, I would like to thank my wonderful advisors Dr. Ruth Hufbauer and Dr. Ian Pearse. They believed in my dreams and ideas from the start and taught me how to pursue my curiosities. Thank you, Ruth and Ian, I would not be the scientist I am today without your encouragement and ferocious support. I also had wonderful committee members, Dr. Liba Pechjar and Dr. Paul Ode, who have truly enriched my training through their expertise. I'd also like to give a special thanks to Dr. Melia Nafus, who has always supported my work and dreams of working in the Pacific.

The long days in the field and successful data collection would not have been possible without my amazing field assistants: Stephenie Santos, William Naden, Corey Santos, and Joseph Castro. I will never forget ending the hot days with ice cold Zesto juice pouches under the coconut trees. I'm very thankful for my science colleagues turned friends who have helped me a lot whenever I had a random plant question or needed suggestions on places to collect: Chris Rosario, James Bamba, and Kawika Davis. Thank you to the various government agencies that has helped with this project (the Guam Department of Agriculture, US Fish & Wildlife Service, CNMI Department of Lands and Natural Resources). Thank you to my alma matter the University of Guam for all the support throughout the years and for starting my love for science. Thank you to Dr. Jonathan Koch and the UH PIPES program, for helping me turn my love for science into a career.

I'd also like to give a shout out to my wonderful Hufbauer labmates Dr. Eliza Clark, Dr. Laure Olazcuaga, Dr. Lily Durkee, Liana McIsaac, Jackie Billotte, Mattew Wallace, and Dr. Enakshi Ghosh. You will all forever be a part of my academic family and I'll never forget the friendships we have forged. Special thanks also to the AgBio front office that have changed throughout the years but helped me with the logistical nightmare fieldwork in the Pacific entails. Shout out to the Graduate Degree Program in Ecology as well for providing me with various financial support and great cohorts that have become lifelong friends.

Lastly, I'd like to thank the village that raised me which consists of my wonderful friends and family. Thank you to my "city girls" and friends who always gave me things to look forward to outside of science. I'd like to thank my husband, who have always supported my dreams. We met at the end of my MS degree and have since built a wonderful life together that has only continued to motivate me to succeed. I wouldn't be here without his and our three doggies' (Gracie, Momo and Rocket) support. I wouldn't be where I am today without my mom and my sister who supported my dreams even when it required me to leave home. Despite the thousands of miles between us, they always made me feel like home wasn't too far away. I'd also like to thank my in-laws and aunts who always supported me and kept me fed. Last but not the least, the final stretch of my PhD has been a two-man effort with my son, Vinh. Thank you, baby, for not making the last 8 months too cumbersome and being the new light and inspiration of my life.

Receiving the opportunity to pursue a PhD is something that this brown girl from the island of Guam will never take for granted. I hope to use my training to serve my community and make a difference in the world.

DEDICATION

To my family who has given me time, love, and support to continually learn.

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INTRODUCTION

Declines among top predators is a matter of considerable concern, given the important effects of predators on the trophic levels below (Williams et al. 2004) and the overall structure of communities (Berger et al. 2001, Terborgh et al. 2001, Dulvy et al. 2004, Frank et al. 2005). Loss or gain of a top predator can produce a trophic cascade, where herbivores increase in abundance and plants decrease (Ripple et al. 2016). In the extreme, predator loss can lead to extinction of taxa at lower trophic levels (Borrvall and Ebenman 2006) and reduced recruitment of plants (Terborgh et al. 2001, Hebblewhite et al. 2005). However, ecological systems can be complex, and loss of predators does not always result in a trophic cascade. For example, a meta-analysis on terrestrial trophic cascades found that effects of predator removals on the biomass of primary producers are weaker on land compared to aquatic systems (Halaj and Wise 2001). As declines of top predators continue worldwide, understanding how these shifts affect all trophic levels will enable us to predict future impacts and establish better prevention efforts (Estes et al. 2011).

The effects of changes in predators on communities have been studied in two main ways: through small-scale experiments and through large-scale shifts in communities driven by anthropogenic disturbance. The small-scale ecological experiments often entail predator exclosure experiments (Marquis and Whelan 1994, Mooney et al. 2010) and are typically conducted at relatively small spatial scales compared to the foraging distance of those predators. However, understanding changes in predators at large-scale is important because it reflects a more accurate depiction of what may happen in the community. Thus, large-scale anthropogenic disturbances, though not aimed to provide ecological information, have been leveraged to serendipitously increase the understanding of community structure and function. An example of this is in Venezuela, where a set of predator free islands were created by a hydroelectric impoundment and revealed that predators normally limit the population of rodents, monkeys, iguanas and leaf-cutter ants, which would not have been observed through small-scale exclosure studies (Terborgh et al. 2001). The case study of Guam may allow us to expand what we know from small scale bird exclosure experiments and further our understanding of how the loss of birds can affect the arthropod community.

In the 1940s, *Boiga irregularis*, henceforth brown treesnake, was introduced to the island of Guam (Savidge 1987). Naïve to predators, native, including several endemic, birds in Guam were decimated and have all nearly gone extinct (Savidge 1984). Many studies currently focus on the eradication of the brown treesnakes, and an increasing amount of work has explored the ecological implications of its introduction (Rodda and Fritts 1992, Rogers et al. 2012). The introduction of the brown treesnake to Guam may be an opportunity to conduct a large-scale study on how the absence of top predators affect lower trophic levels. The brown treesnake has not been introduced to nearby islands, which still have populations of native birds. These islands provide similar communities for comparison with Guam to infer the ecological changes that might have occurred following the introduction of the brown treesnake.

Many observed changes to the community have occurred since the introduction of the brown treesnake and the loss of birds, but we have still yet to know how its introduction have altered the arthropod community and plants. Prior to brown treesnake introduction (Fig. 1a), birds were top predators, which fed on herpetofauna (ex. lizards and geckos), arachnids (ex. spiders) and other arthropods, including both predatory and herbivorous species. After the brown treesnake was introduced, it fed on birds, which functionally extirpated them from the community (Fig 1b) (Rodda and Savidge 2007). A few birds remain and those that do are mostly introduced species such as House Sparrows and chickens that are restricted to towns and cities (Wiles et al. 2003, Vice et al. 2005). Thus, the island of Guam has functionally lost its former top predators (birds). The effects of bird loss on the trophic levels below are just beginning to be understood (Rogers et al. 2012, 2017, Caves et al. 2013, Freedman et al. 2018, 2022). Herpetofauna, while released from bird predation in Guam, are likely suppressed by direct predation from brown treesnakes (Rodda and Fritts 1992a). In contrast, there is strong evidence for release of large, web-building spiders from bird predation, resulting in greater density of spider webs in Guam then in neighboring islands that retain birds (Rogers et al. 2012). The loss of birds has also had a direct effect on plant recruitment in Guam, hindering plant species that rely on bird dispersal (Caves et al. 2013). Predation pressure on arthropods such as caterpillars is lower in Guam than in other islands (Jardeleza et al. in prep a), and some groups of insects, such as ant-tended aphids (Freedman et al. 2018). In contrast, native butterflies (Jardeleza et al. in prep b), are more abundant in Guam than in other islands. Based on DNA barcoding, Guam currently has a distinct arthropod community composition from its neighboring islands, a trend that would be consistent with trophic effects of the brown treesnake (Calaor 2024). How changes in arachnids and herpetofauna populations have affected lower trophic levels including other arthropods and plants have yet to be investigated. However, there is currently no evidence whether the introduction of the brown treesnake has led to an increase in the abundance of arthropods, or to an increase in plant damage due to release of herbivorous arthropods, as would be expected in a classic trophic cascade.

Arthropod abundance varies naturally over space and time (Root and Cappuccino 1992), so it is important to account for factors known to influence arthropod abundance to infer the effects of predator shift by comparing islands with different predators. First, because many herbivorous insects are host specialists, native plants tend to host greater abundance of arthropods and experience greater herbivore damage than non-native plants (Carpenter and Cappuccino 2005, Bezemer et al. 2014). Likewise, the abundance of arthropods tends to be higher along forest edge habitats than in forest interiors (De Smedt et al. 2019, Magura and Lövei 2024). For example, in coniferous forests, arthropod abundance was found to decrease from the forest edge to the forest interior (Jokimäki et al. 1998). Arthropod abundance also varies considerably by habitat type (Jokimäki et al. 1998, Carpenter and Cappuccino 2005, Litt et al. 2014).

To assess the role of brown treesnake introduction and subsequent loss of birds on arthropod abundance and plant damage, we compared arthropod abundance and damage to plant leaves between Guam (where the brown treesnake was introduced) and two neighboring islands (Rota and Saipan) that lack brown treesnake and retain birds. We address the following questions: 1.) How do arthropod abundance and the composition of the arthropod community differ between islands with and without birds? 2.) How does herbivory differ between islands with and without birds? If a trophic cascade had affected arthropods and herbivory rates, we expected that, after accounting for factors, such as plant native status, habitat type, and edge/interior effects, we would observe greater arthropod abundance and greater herbivory to plants in Guam than on nearby islands.

METHODS

Sites This study was conducted in three islands in the Mariana Islands chain: Guam (541 km^2), Saipan (115 km^2) and Rota (85 km^2) (Figure 2a). The islands experience similar temperature and rainfall pattern and are within 200 km of each other. The brown treesnake (*Boiga irregularis*) was introduced to Guam in the 1940s and extirpated the native forest birds (Savidge 1987). Collections were conducted in Guam, Rota and Saipan during the dry season from April-June 2022 to avoid difficult wet sampling conditions. I collected in 18 sites in Guam, 18 sites in Rota and 17 sites in Saipan. To compare similar habitats found on all islands, limestone forest and coastal strand sites were chosen. To look at abundance gradients in a forest, each site was located near a forest edge and a cleared pathway.

Arthropod Survey Two 10 m transects were placed per site perpendicular to the forest edge leading into the forest interior, resulting in measurements made along a gradient of 'distance to edge' (Figure 2). I sampled using beating sheets at every meter. To avoid hot temperatures, I sampled only in the morning before 12:00. Beating sheets were composed of a 90 x 90 cm square white cloth, held flat using two pieces of PVC or wood for crossbars (Montgomery et al. 2021). A 60 cm wooden stick was used to strike the vegetation 10 times moving from the base to the top of the plant (Montgomery et al. 2021). Organisms that fell off the branches were collected in the beating sheet and preserved in ethanol.

Ant Survey In order to thoroughly sample the ant community, ant baits were placed at 0 m, 3 m, 6 m, and 9 m of each transect line and were left for 30 minutes. Two baits: 1) processed canned pork and ham 'Spam ©' (Hormel Foods) and 2) peanut butter. The spam was cut up into 5–9 g squares and placed in an open vial and laid flat on its side. The peanut butter was spread on a popsicle stick and struck to the ground. The peanut butter and spam baits were placed on opposite sides of each other along the transect and alternated. The number of ants and morpho-species were recorded, and samples were collected for identification. Ants are social and aggregate around food sources, thus measuring their abundance based on the number of ants on the bait may not accurately represent their population. Hence, presence/absence of ants at each trap was used for data analysis.

Arthropod Identification Arthropods collected from the beating sheet surveys were morphologically identified to their respective class and then to order (Table 1). The three classes Chilopoda, Diplopoda, and Pauropoda were placed into the super class Myriapoda. Ants were identified to species (Table 2).

Herbivory Plants at alternating sides of the transects were collected at 0m, 3m, 6m and 9m. Plant identification was completed using various books on the flora of Guam (Vogt, Scott R.; Williams 2008, Raulerson, Lynn; Rinehart 2018). Twenty random leaves were chosen per plant. Each leaf was then photographed and edited to have no background. The damage on the leaves was then marked digitally with a red marker. The photo was then analyzed using ImageJ (Abràmoff, M.D., Magalhães, P.J. and Ram 2004) and R (R Core Team 2016) to measure % leaf damage as Red (damage) pixels / Total pixels of any color (Figure 3).

Analysis To evaluate potential differences in arthropod communities between islands with and without brown treesnakes, I examined overall abundance of arthropods collected (number per beat sheet), and the abundance of each class of arthropods (Arachnida, Insecta, Myriapoda). I additionally evaluated the presence of ants collected from the baited traps only and excluded ants collected from the beating sheets from the overall abundance of arthropods. I decided to exclude ants because during collections a multitude of ants would drop from the foliage, which would over inflate the arthropod count. For all four models of abundance, I ran a generalized linear mixed models with a negative binomial error distribution in the glmmTMB package (Brooks et al., 2017). The number of arthropods collected per beat sheet (total and number for each class: Arachnida, Insecta, and Myriapoda subphylum) were the response variables. The predictor variables were island (Guam, Saipan, or Rota), distance from the forest edge, habitat type (coastal strand or limestone forest), and the interaction between island and distance from the edge. To account for unobserved site- and transect-level variation, I included transect nested within site as a random effect in all models.

To assess the binary probability of ants being present, a generalized linear mixed effects model was created and evaluated using the lme4 and the lmerTest packages (Bates et al. 2015, Kuznetsova, A., Brockhoff, P.B., Christensen 2017). As above, the predictor variables were island (Guam, Rota, and Saipan), distance from the edge, and interaction between island and distance from edge. I added the "bobyqa" optimizer to my generalized linear mixed model, which extended the maximum number of iterations of my model and improved the processing of the lmerTest package and model convergence (Powell 2009). To control for unobserved heterogeneity, I included site as a random effect. In addition, the species richness of ants for each site were calculated using the Vegan package (Oksanen J., F. Guillaume Blanchet, Michael Friendly et al. 2019). A linear model was then created to assess how island (predictor) affected species richness (response).

To assess how herbivory varied between islands, I constructed a generalized linear model with quasi-Poisson family (R Core Team 2016). The response variable was the proportion of damage found on each leaf sample and the predictor variables were island, whether the plant was native or non-native and the interaction between these two terms. Unidentified leaves were removed from analysis.

Data analysis and visualization were conducted using the R statistical program language with RStudio (RStudio Team 2016a, R Core Team 2016). The emmeans package was also used to determine the differences in means in response to the experimental temperatures and to visualize the interactions for all the models (Lenth 2019). Figures were created using ggplot2 (Wickham 2016).

RESULTS

The total abundance did vary by island (χ_1^2=8.8, *P<0.05*). Guam (no bird present) had the least total arthropod abundance, Rota (birds present) in the middle and Saipan (birds present) had the highest (Figure 4). However, the total abundance of arthropods did not vary significantly by distance from edge of forest (χ_1^2=,0.39 *P =0.53*), habitat type (χ_1^2=3.1, *P =0.78*), or the interaction between island and distance from edge (χ_2^2=2.65, *P =0.27*). Arachnid abundance did vary by island (χ_2^2=19.7, *P <0.001*), and habitat type (coastal strand/ limestone forest) (χ_1^2=8.25, *P<0.01*). Guam had on average approximately 50% fewer arachnid individuals compared to Rota and Saipan (Figure 5a). I also found that throughout all the islands, coastal strands had significantly fewer arachnids compared to limestone forests (Figure 5b). However, the abundance of the arthropods in the class Arachnida did not vary by distance from edge (χ_1^2=2.38, *P =0.122*), or the interaction between island and distance from edge (χ_2^2=0.3, *P =0.86*). The class Insecta did not vary significantly by island (χ_2^2=3.35, *P =0.19*), distance from edge (χ_1^2=0, *P =1*), habitat type (χ_1^2=0.7, *P =0.4*), and the interaction between island and distance from edge (χ_2^2=2.59, *P =0.27*). The subphylum Myriapoda, also did not vary significantly by island (χ_1^2=0.63, *P =0.73*), distance from edge (χ_1^2=0.35, *P =0.55*), habitat type(χ_1^2=1.29, *P =0.26*), and the interaction between island and distance from edge (χ_2^2=1.19, *P =0.55*). Lastly, ants were more likely present at baits in Rota than in Guam or Saipan ($\chi_2^2 = 26.9, P < 0.001$, Figure 6). All ants were present on all islands except for *W. auropunctata*, which is yet to establish in Rota and Saipan. All the ants were invasive or introduced to the islands. Distance from edge ($\chi_1^2 = 2.26, P = 0.13$), habitat type ($\chi_6^2 = 11.7, P = 0.07$) and the interaction between island and distance from edge ($\chi_2^2 = 0.12, P = 0.94$) were not significant predictors of ant presence. Guam and Rota had higher ant species richness compared to Saipan ($F(2,64) = 8.2$, $P < 0.001$). Ants collected and identified were: *Anoplolepis gracilipes*, *Monomorium pharaonis*, *Odontomachus simillimus*, *Pheidole megacephala* and *Wasmannia auropunctata* (Table 2).

Overall rates of herbivory for both native and invasive/introduced plants in all islands were less than 6% (Figure 7). Plant leaves in Guam (1.8%) and Rota (1.7%) experienced lower overall herbivory compared to Saipan (3.8%) (χ^2_2=29.3, $p < 0.001$). Native plants generally experienced 3% more herbivory compared to invasive/introduced plants (χ^2_1= 106.6, $p < 0.001$). The effect of island on percent leaf damage depended on the native status of the plant (χ^2_2= 11.9, $p<0.01$). Native plants received proportionally more leaf damage in Saipan than on other islands compared to introduced plants.

DISCUSSION

I did not observe a classic trophic cascade as expected. I expected overall higher arthropod abundance in Guam compared to other islands due to the release of arthropods from bird predation. Instead, I found Guam to have less arthropod abundance compared to the nearby islands that have maintained their native bird population. I also expected herbivory to be higher in Guam due to the release of herbivores from predation, but I found Saipan to have higher herbivory rates compared to Guam and Rota. My study suggests that the loss of birds through the introduction of the brown treesnake did not result in a classic (+) apex predator – (-) predator – (+) herbivore – (-) plant trophic cascade as expected.

There are at least three possible explanations for why I did not observe patterns of arthropod abundance and plant damage consistent with a classic trophic cascade. First, the introduction of the brown tree snake in Guam may not have resulted in a trophic cascade extending to herbivorous arthropods. Second, a trophic cascade may extend to arthropods and plant damage in Guam, but in a species-specific way that is not detectable with my broad-scale study. Lastly, even if a trophic cascade has occurred in Guam, it is possible that I could not detect it because the reference islands were different from Guam in other ways that were not accounted for. I weigh the evidence for these three explanations of my results below.

Trophic cascades do not always occur. For example, the removal of wolf spiders in Northeast Greenland did not find a detectable effect on plant damage or seed production due to their generalist feeding behavior, which diluted their predation pressure (Visakorpi et al. 2015). This has also been observed in other systems. For example, a trophic cascade was not observed in an experimental microbial-based soil food web that consisted of bacteria and fungi as lower trophic levels, and predatory nematodes as higher trophic levels. Changes in the higher trophic levels had no effect on microbial biomass or productivity (Mlkola and Sktälä 1998). Another example can be found in marine preserves. The reserve provides refuge for the predators of sea urchins, which should theoretically maintain sea urchin numbers and prevent overgrazing of kelp forests. Instead, sea urchin biomass increased and there is no evidence that giant kelp is positively affected by the reserves (Malakhoff and Miller 2021). In Guam, there is substantial evidence that the addition of an apex predator has resulted in major shifts in predator communities, which could suggest trophic cascades occurring in other aspects. For example, birds have been functionally extirpated, the herpetofauna has been substantially suppressed, and there has been a release of large web-building spiders (Rodda and Fritts 1992a, Rogers et al. 2012). Moving to lower trophic levels, there is some evidence of reduced predation rates of arthropods in Guam compared to nearby islands (Jardeleza et al. in prep a), there is an apparent loss of anti-predator responses of butterflies in Guam (Jardeleza et al. in prep b). However, my results suggest that the change in predation pressure has not led to overall differences in arthropod abundance or rates of herbivory to plants.

The mechanisms that stabilize food webs, such that they are buffered against structural changes after the introduction of a top predator are of key interest (Hastings 1988, Downing et al. 2014). Processes, such as prey switching, and food web properties, such as redundancy, are thought to stabilize food webs (Post et al. 2000, Biggs et al. 2020) and are both common properties in the food webs in Guam. For example, Jardeleza et al. (in prep a) found a negative relationship between reptile and arthropod predation on arthropods among islands. This suggests that if one form of top-down pressure to arthropods decreases, it may be compensated by another. Likewise, the rise of large native spiders in Guam may compensate for loss of predation by vertebrates (Rogers et al. 2012, Calaor 2024). What may be happening is that in the islands with birds, spiders are getting smaller as predators are targeting the more visible large web building spiders. On the contrary, there are no birds in Guam to predate on large web building spiders, which have allowed their numbers to increase. My results may seem contradictory to previous work that suggests a release in arthropods due to the loss of birds in Guam (Rogers et al. 2012, Calaor 2024), but instead it adds to the complexity of the system. First, my sampling method predominantly catches small arthropods found in foliage. Thus, even if there were more large web building spiders in Guam compared to the neighboring islands, we would not be able to measure that in my sampling design. Second, I may also not be seeing a trophic cascade in Guam despite the documented meso-predator release because large spiders in Guam may be opportunistically feeding on a wide variety of arthropods. The general feeding strategy may also be diluting their predation pressure like what was found in the wolf spider removal study in Northeast Greenland (Visakorpi et al. 2015).

A trophic cascade may be happening in Guam due to the introduction of the brown treesnake, but it may only affect certain members of each trophic level, such that the abundance of some, but not all arthropods might be altered. Likewise, the amount of damage to some plants may be increased, but not to all plants. Arthropod diversity studies in Guam and neighboring islands have provided some evidence for this. For example, Calaor (2024) found that arthropod communities in Guam differed from other islands, and those differences were largely due to altered frequencies of springtails, which are omnivorous soil-dwelling arthropods. Likewise, there are marked differences in butterfly abundance (Jardeleza et al. in prep. b) and ant-tended aphid abundance between Guam and neighboring islands (Freedman et al. 2018), suggesting that altered top-down control may affect some arthropods but not others.

Finally, trophic cascade may extend to arthropods and plant damage, but I have not observed it due to the complexity of the islands. Despite being close to each other and having very similar characteristics, each of the Northern Mariana Islands have unique environmental and historical factors. The island of Guam has always had more inhabitants and anthropogenic developments (ex. land development), which may have resulted in significant differences in arthropod composition. Furthermore, Calaor (2024) found that ungulates in Guam and Rota may have influenced the arthropod community. Specifically, litter dwellers such as springtails (Poduromorpha) were less abundant in Guam due to the lack of leaf litter from ungulate disturbance (Calaor 2024). The effects of ungulates (mostly wild boar) may explain the similarities in arthropod abundance I found between Guam and Rota despite Rota maintaining its populations of native birds. It is possible that Saipan may have a more intact community due to differences in ungulate effects and bird composition compared to Rota, which may also explain the differences in results observed despite both islands having native bird populations. Unlike birds, lizards and predacious arthropods can be spread more evenly throughout the forest regardless of canopy cover or foliage density. If lizards were one of the main drivers of arthropod predation in Guam, then I would expect Guam to have significantly fewer arthropods compared to the nearby islands. On the contrary, instead of releasing the reptile community from predation, they have been suppressed by the brown treesnake. (Savidge 1988, Rodda et al. 1992).

In conclusion, while there was meaningful variation in arthropod abundance and damage to plants among Northern Mariana Islands, I did not observe evidence of a classic trophic cascade, as I had expected. It seems like the system is quite complex and does not follow what have been observed in much simpler exclusion studies. Due to time constraints my study did not separate the arthropods by feeding guilds, which may have obscured an important link in the trophic cascade and something future studies should take account. The effects of bird loss in the island of Guam have been ongoing for more than 35 years. There are not too many ecological opportunities that allow scientists to observe the long-term effects of bird loss in such a large scale as a whole island. As bird populations continue to decline worldwide, we should capitalize on this tragic opportunity to not only further test the results of small-scale manipulative experiments, but to also test the efficacy of reintroduction programs.

TABLES

Table 1 – Arthropods collected broken down into class, order and common names.

Class	Order	Common Names	Total # of Individuals	
Arachnida	Aranea	• spider	Guam	113
			Rota	270
			Saipan	382
	Ixodida	• tick	Guam	25
			Rota	47
			Saipan	46
	Pseudoscorpiones	• pseudoscorpion	Guam	1
			Rota	0
			Saipan	43
Insecta	Blattodea	• cockroach • termite	Guam	108
			Rota	10
			Saipan	6
	Coleoptera	• beetle	Guam	58
			Rota	117
			Saipan	205
	Dermaptera	• Earwig	Guam	0
			Rota	4
			Saipan	0
	Diptera	• mosquito	Guam	2
			Rota	0
			Saipan	0
	Hemiptera	• aphid • stinkbug	Guam	149
			Rota	170
			Saipan	366
	Lepidoptera	• caterpillar • moth	Guam	5
			Rota	0
			Saipan	15
	Mantodea	• praying mantis	Guam	0
			Rota	0
			Saipan	3
	Neuroptera	• wasp	Guam	0
			Rota	2
			Saipan	0
	Orthoptera	• cricket • grasshopper • katydid	Guam	3
			Rota	2
			Saipan	12
	Polyphaga	• ladybug	Guam	1
			Rota	3
			Saipan	0
	Trichoptera	• caddisfly	Guam	2
			Rota	55
			Saipan	99
Myriapoda (Chilopoda, Diplopoda, and Pauropoda)	Multiple orders	• centipede • millipede • paurapod	Guam	30
			Rota	4
			Saipan	10

Table 2 – Ant species collected at each island and the number of times they were observed at each meter interval surveyed.

Ant Species	Island	# of times observed
Anoplolepis gracilipes	Guam	28
	Rota	19
	Saipan	30
Monomorium pharaonis	Guam	25
	Rota	62
	Saipan	28
Odontomachus simillimus	Guam	8
	Rota	23
	Saipan	1
Pheidole megacephala	Guam	1
	Rota	62
	Saipan	47
Wasmannia auropunctata	Guam	37
	Rota	0
	Saipan	0
Unidentified	Guam	256
	Rota	215
	Saipan	113

FIGURES

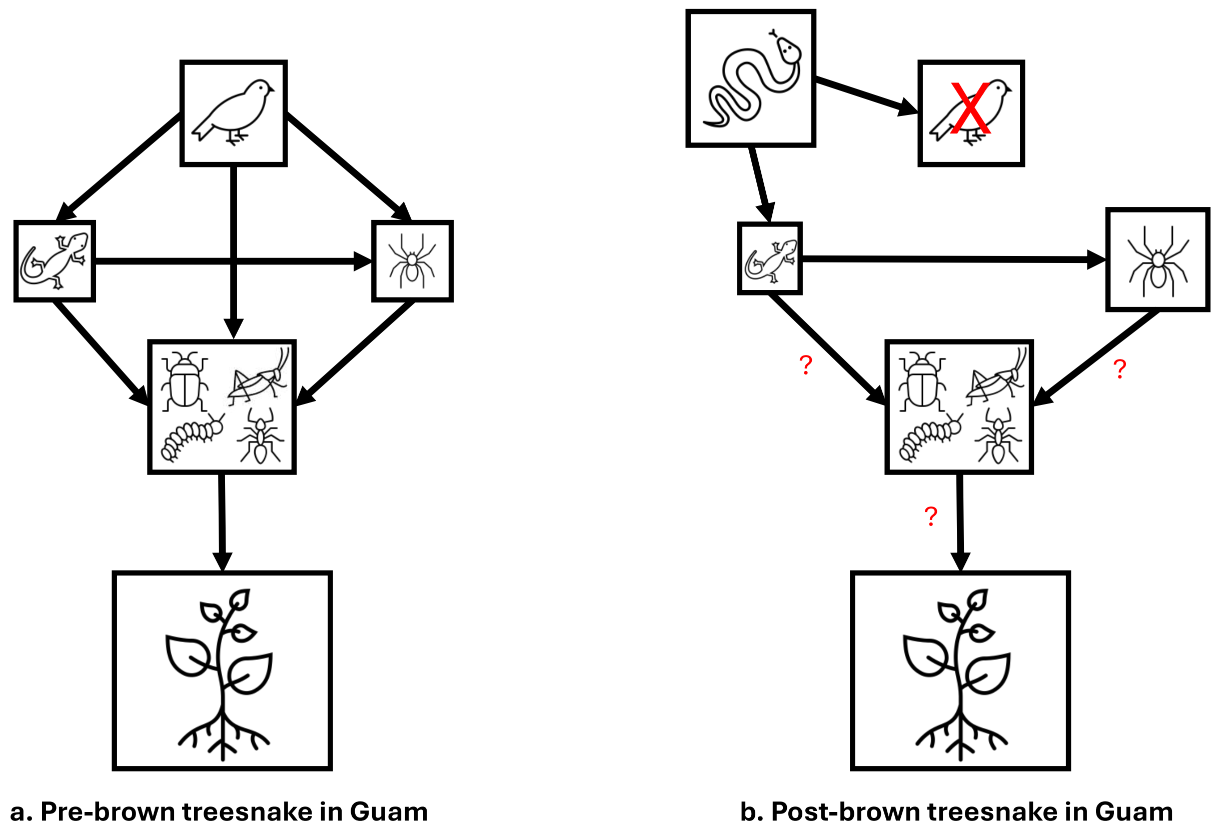

Figure 1 – Simplified, hypothesized community structure in Guam's forests prior and post the brown treesnake invasion.

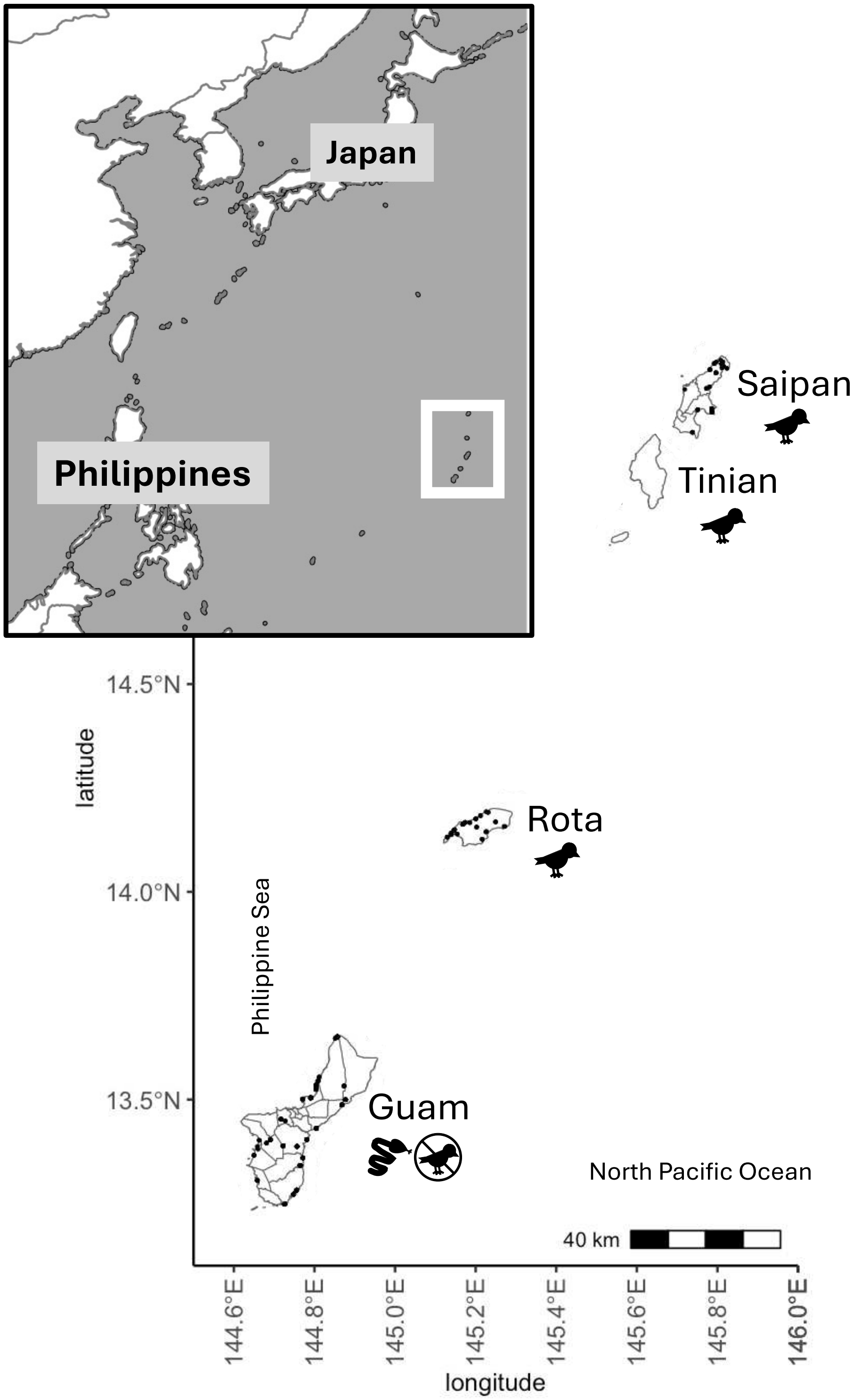

Figure 2 – Map of collection sites. Dots represent collection sites.

Figure 3 – Image processing steps. First a photo of the leaf was taken and marked for damage. The photo was then inputted into ImageJ to analyze the number of leaf damage pixels and total leaf pixels. Lastly, the % leaf damage was calculated and analyzed.

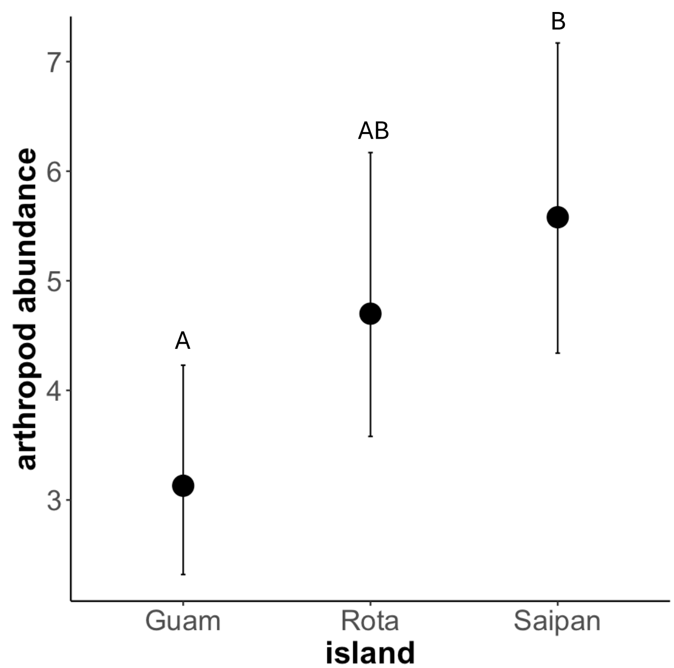

Figure 4 – Arthropod abundance at each island. The confidence limits indicate the 95% confidence intervals. The letters indicate a post-hoc Tukey test.

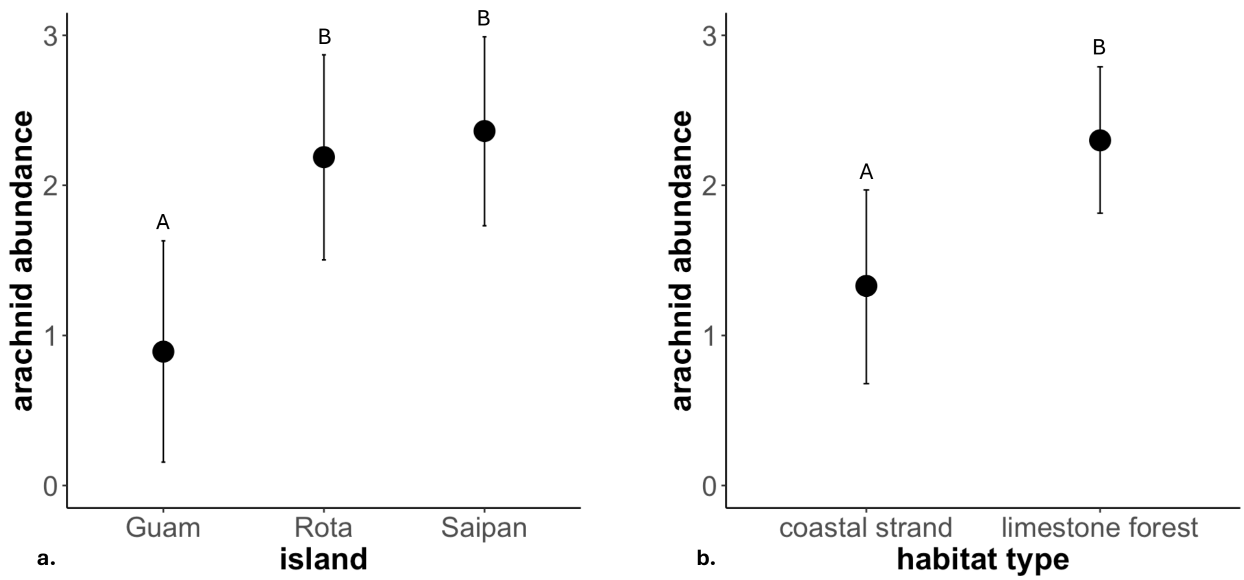

Figure 5 – **a.** Arachnid abundance at each island. **b.** Arachnid abundance at each habitat type. Error bars are 95% confidence intervals. The letters indicate the significance of difference between pairs of group means using a post hoc Tukey test.

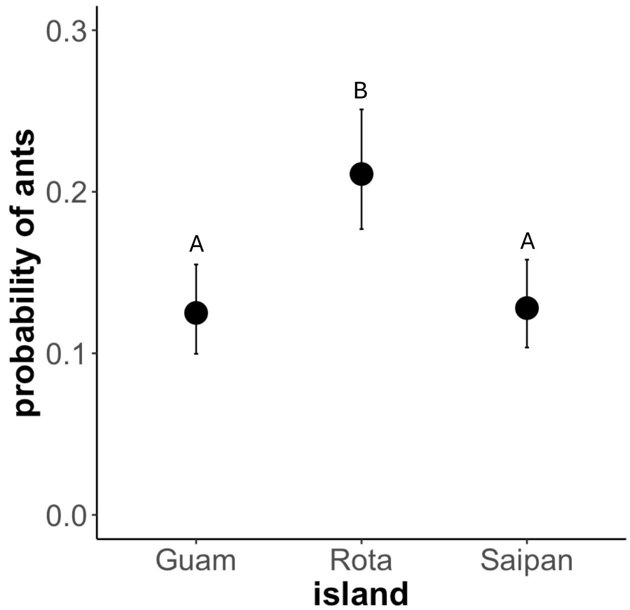

Figure 6 – Ant abundance at each island. Error bars are 95% confidence intervals. The letters indicate the significance of difference between pairs of group means using a post hoc Tukey test.

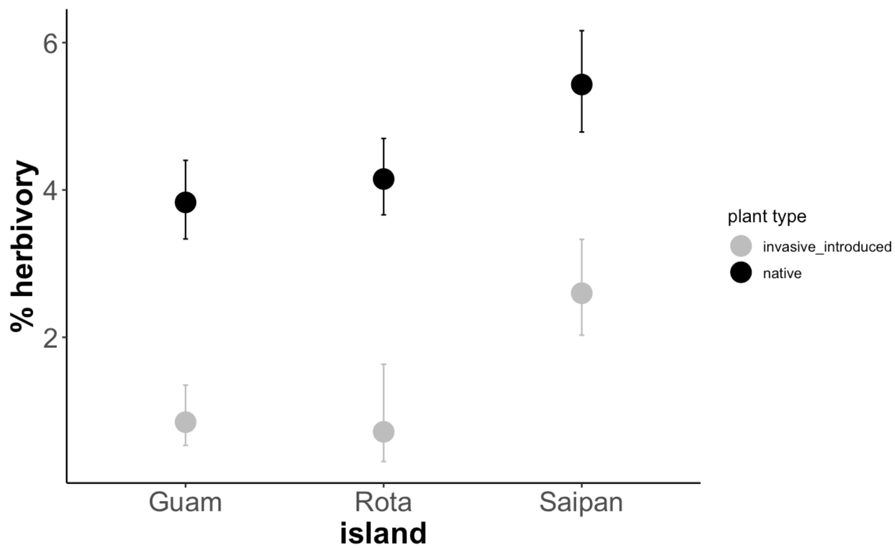

Figure 7 – Herbivory rate on native and invasive/introduced plants on each island. Error bars are 95% confidence intervals.

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CHAPTER 2 – ARTHROPODS AND LIZARDS DRIVE ATTACK RATES OF MODEL CATERPILLARS IN A TROPICAL ISLAND WITH NO FOREST BIRDS

INTRODUCTION

Predators often have oversized effects on the structure of a community due to top-down control (Paine 1966). Understanding how changes in predator populations affect prey species can provide insights into community function and management decisions (Hobbs et al. 2024). There is a strong body of experimental research addressing community responses to predator removal, and particularly to the removal of birds. Excluding birds from terrestrial arthropod communities commonly leads to increases in the abundance of both predatory and herbivorous arthropods (Mooney et al. 2010). Likewise, experimental exclusion of lizards has also been shown to increase arthropod abundance (Pacala and Roughgarden 1984, Spiller and Schoener 1988).

For practical reasons, most experimental research addressing community responses to predators is conducted at relatively small spatial scales compared to the foraging distance of those predators. Understanding predation and top-down control at larger scales, however, is important. Larger spatial scales contain multiple habitat types, which are likely to support distinct communities that may not respond in the same way to changes in trophic relationships (Tu et al. 2020). Likewise, compensatory processes such as intraguild predation (predation on members of the same guild or trophic level) and meso-predator release (an increase in intermediate predators due to the removal of a top predator) may dampen the effects of predator loss at larger spatial scales (Rogers et al. 2012, Donadi et al. 2017). Scaling up ecological experiments is often difficult, but case studies where the absence of a species or guild create an "accidental experiment", or natural exclusion study allow us to address if these patterns are consistent at larger spatial scales (HilleRisLambers et al. 2013).

Islands are excellent systems to study the effects of species introductions and extirpations due to their isolated geographical layout, which can enable a larger-scale examination of community responses. In an example of a trophic cascade, small islands were created in Venezuela after a hydroelectric dam was built (Terborgh and Kenneth 2010). The smallest islands (<20 ha) were unable to support large vertebrate predators (e.g. jaguar and pumas), which allowed densities of vertebrate herbivores and omnivores to increase leading to reduced plant biomass (Terborgh and Kenneth 2010). Community responses to changes in predation are not always direct trophic cascades. For example, in the formerly predator-free Aleutian Islands, introduced foxes preyed on the seabird population, drastically reducing their numbers, which reduced inputs of guano that fertilized the islands. This led to the more nutrient limited plants to become less abundant (Croll et al. 2005). Thus, such island-scale additions or removals of predators provide the opportunity to investigate the inner workings of complex communities.

In the mid–1900s, the brown treesnake (*Boiga irregularis*), was accidentally introduced into the US Territory of Guam, an island in the Western Pacific, via military cargo (Rodda et al. 1992). As an apex predator, it extirpated many bird species, which were previously top predators in Guam, including 7 of 9 invertebrate-feeding native bird species (Savidge 1987, Rodda and Fritts 1992). With few birds remaining, the brown treesnakes became shifted to a diet of lizards and introduced small mammals (Savidge 1988, Rodda and Fritts 1992). Thus, in Guam, the snakes have suppressed most arthropod-feeding vertebrates (birds, lizards, and small mammals), which could release herbivorous arthropods from predation pressure in a trophic cascade. Guam has greater numbers of web-building spiders, ants, and aphids compared to nearby islands in the

Marianas chain, Rota and Saipan, that have historically similar flora and fauna but lack the brown treesnake (Rogers et al. 2012; Freeman et al. 2018). However, the extent of the trophic cascade, and the identity of the predators driving the response in invertebrate prey is still unknown.

Non-native plants may provide fewer invertebrates for vertebrate predators to feed on than native plants (Tallamy et al. 2020), thus the effect of predators on invertebrate prey may also be weaker when those preys are on non-native plants or in forest dominated by non-native plats. After disturbance left by WWII in Guam and surrounding islands, much of the regenerating forest was dominated by non-native species, including a legume (*Leucaena leucocephala*). Today in the Marianas, intact forest dominated by native species has higher densities of many forest bird species and lizard species than forest dominated by *Leucaena*. I thus hypothesize that the strength of predation is lower on non-native plants/forests compared to native plants/forest in the Marianas.

I assessed predation risk to arthropods using clay caterpillar models in Guam and neighboring islands to assess the large-scale effects of an apex predator on predation rates to arthropods. I address three questions:1) How do attack rates differ between islands with and without brown treesnakes? 2) Which predator taxa contribute to these differences? 3) Is attack rate influenced by habitat type or by plant origin (native/introduced)? I hypothesized that the snake, an apex predator, could reduce attack rates on arthropods because of the suppression of invertebrate-feeding birds and reptiles. Alternatively, the loss of birds as predators could lead to mesopredator release of spiders (e.g., Rogers et al. 2012) or lizards, such that the overall amount of predation to arthropods might remain constant, while the identity of predators would shift. In addition, I predict that this effect would be weaker in forest dominated by non-natives and for caterpillars placed on non-native plants.

METHODS

Study area This study was conducted on three islands in the Mariana Islands chain in the Pacific Ocean: Guam, United States of America (541 km^2), Rota, Commonwealth of the Northern Mariana Islands (CNMI) (85 km^2), and Saipan, CNMI (115 km^2) (Figure 1a, Appendix S1: Table S1). The islands experience similar temperature and rainfall patterns and are within 200 km of each other. The brown treesnake is only present in Guam and not currently present in the other Mariana Islands. There are 12 native, including endemic, terrestrial birds in the Mariana Islands, 10 of which are present on Saipan and Rota and two of which are still present in Guam but not found at my study sites (Jenkins 1983). Other introduced insectivorous birds include the Black Drongo (*Dicrurus macrocercus*) and Eurasian Tree Sparrows (*Passer montanus*) (Appendix S1: Table S2). Herpetofauna include insects in their diets and are present in all the islands, though in different densities and species combinations; the brown treesnake has had a negative effect on many skink, anole, and gecko species in Guam as well (Wiles et al. 1990, Rodda and Fritts 1992). Other possible predators of caterpillars include introduced black rats (*Rattus diardii*) and shrews (*Suncus murinus*; both reduced in abundance on Guam due to the snake), and predatory arthropods (e.g., spiders, higher abundance in Guam compared to Saipan and Rota). This study occurred in two different time periods and were not originally connected, which explains the difference in methods between the time periods. Nevertheless, I believed that the methods and results were similar enough to combine into one manuscript

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Sites In 2013, the study was conducted in disturbed and intact limestone forests. The limestone forest sites had mixed karst and soil substrate and were dominated by native plant species such as

Meiogyne cylindrocarpa, Aglaia mariannensis, Cynometra ramiflora, and *Premna serratifolia.* I defined intact limestone forest sites as being dominated by native species with a karst substrate, indicating little prior disturbance or clearing. Disturbed limestone forest sites were dominated by *Leucaena leucocephala* and other non-native species and had evidence of disturbed substrate.

In 2022, the study was conducted in limestone and in coastal forests. The coastal sites had native coastal species such as *Casuarina equisetifolia, Cocos nucifera*, *Ochrosia oppositifolia, and Thespfesia populnea.* In 2022, both site types contained some non-native species. In the limestone forest sites, 61% of the model caterpillars were placed on native plant species, while 86% of model caterpillars in coastal forests were placed on native plant species (Appendix S1: Table S3).

Model caterpillars experiment I constructed model caterpillars of clay and deployed them in Guam, Rota, and Saipan from July-August 2013 (1,650 total) and from May-June 2022 (660 total). Additionally, 336 model caterpillars were deployed only in Guam in 2021 (due to COVID-19 travel restrictions), which allowed for a comparison of attack rates with an additional year in Guam. I present the analysis and results of this comparison in Appendix S2.

Model caterpillars were made with polymer, malleable, non-toxic and non-air-drying clay. They were made to loosely resemble one of several common, green caterpillars in Mariana Island forests that are larvae of *Eurema blanda* (host = Fabaceae), *Papilio polytes* (host = Rutaceae), *Melanitis leda* (host = *Poaceae*), or *Catopsilia pomona* (host = *Fabaceae*) following Howe et al (2009). In 2013, caterpillars were made using one shade of Sargent Art ® green modeling clay and rolled by hand into smooth tubes 3 cm long and 3 mm in diameter. In 2022, they were made using several shades of Sculpey III ® Polymer green clay and a metal clay extruder was used to create uniform figures 5 cm long by 8 mm in diameter (Appendix S1: Figure S1). Initial analysis suggested that color did not affect attack rates by any group of predators, so all colors were combined for the 2022 study.

2013 Survey Caterpillars were deployed along four 300 m transects in Guam and Rota, two in intact and two in disturbed limestone forest (Figure 1b). Three 300 m transects were used in Saipan, one in an intact and two in disturbed limestone forest. Caterpillars were attached to tree branch stems or leaves located between 1 – 2 m above the ground using rubber cement (Figure 1b). All models were placed on the top of the stem or leaf to be clearly visible from predators overhead (Appendix S1: Figure S1). A caterpillar was placed every two meters for 150 per transect. After 48 hours, caterpillars were retrieved and examined for attack markings. They were recorded as attacked (markings or pinches), not attacked (smooth), missing, or on ground. Attack marks on each caterpillar were categorized as attacks from a bird, arthropod, lizard, small mammal (i.e., a rat), or of unknown origin based on Howe et al (2009) and Tvardikova and Novotny (2012).

2022 Survey Caterpillar models were deployed on 9 m transects at 28 limestone forest sites and 17 coastal habitat sites on each of the three islands (Figure 1a). Transects were placed perpendicular to the forest edge, which provided a gradient of tree densities (denser canopy deeper in the forest) (Figure 1c). To account for attacks at various heights, model caterpillars were placed at three heights: a few centimeters off the ground (low), about 1 m off the ground (medium) and about 2 m off the ground (high) (Figure 1c). Model caterpillars were superglued to the center of leaves, placed at 0 m, 3 m, 6 m, and 9 m marks. I recorded the identity of the plant on which each caterpillar was placed. After 72 hours, caterpillars were retrieved and evaluated for attacks due to a bird, arthropod (including hermit crabs), lizard, small mammal, or being of unknown origin following Low et al. (2014) (Appendix S1: Figure S1).

Game Camera Footage Game cameras, *Reconyx HyperFire Covert IR Camera* (Holmen, WI, USA), were placed near model caterpillars in the Rota sites in 2022 to record predator activity and identity. The game camera took a photo every minute for up to 3 days.

Statistical analysis I analyze the 2013 and 2022 results separately due to differences in the experimental design. For both, I categorize attack on model caterpillars as a binary value (attacked or not by a particular predator type). In a few cases, a caterpillar was attacked by multiple predator types (e.g. attacks by a reptile and an arthropod). In these cases, I scored an attack by each of those predator types. For both years I constructed four models, one for each of four binary responses of predator type, to test the role of island and habitat type on attack rates. The four responses were (1) total attack by any predator, (2) attacks by reptiles, (3) attacks by mammals (2022 only), and (4) attacks by predatory arthropods. Attacks from birds were not analyzed separately, as there were not enough attacks analyze.

For *2013*, predictors included island and habitat type as fixed effects. No random effects were added due to the limited replication of sites within habitat types in 2013. For *2022,* total attack was analyzed using a model that included island, habitat type, and the interaction of those terms as fixed effects, with site and transect as nested random effects. Models for individual predator types were similar, but they failed to converge with habitat type as a predictor, so the interaction term was removed from these models. Additionally, to test whether the identity (native or non-native) of the plant affected probability of attack, I analyzed total attacks (by any predator) using a generalized linear model including identity (native or non-native) of the plant as a fixed effect.

Data analysis and visualization were conducted in the R statistical program language (R Core Team 2018),), using packages *lme4* (Bates et al., 2015) *lmerTest* (Kuznetsova, A., Brockhoff, P.B., Christensen 2017) *emmeans* (Lenth 2019b) and *ggplot2* (Wickham 2016b). I added the “BOBYQA” optimizer to my generalized linear mixed model, which extended the maximum number of iterations of my model and improved the processing of the lmerTest package and model convergence (Powell 2009).

RESULTS

Game cameras captured multiple rats in the vicinity of model caterpillars and rat bite marks were later confirmed on those caterpillars (Appendix S1: Figure S1). Three reptile taxa (geckos, anoles, and skinks) were captured on camera and likely attacked based on marks found. Arthropods were also captured on camera near the model caterpillars but were typically too small to identify.

Overall rates of attack on model caterpillars by all predators were similar across years and showed similar trends among islands, with Guam experiencing lower overall attack than the other islands (2013: X_2^2=58.9, *P<0.001;* 2022: X_2^2=11.6, *P<0.001*; Figure 3). Surprisingly, attack on model caterpillar by birds was too low to analyze. In 2013 there were some bird attacks ($n_{Guam} = 0, n_{Rota} = 4, n_{Saipan} = 10$) but there were none in 2022. There were too few rat attacks to analyze statistically in 2013 (n_{Guam} =11, n_{Rota} =3, $n_{Saipan} = 0$), while in 2022, there was no significant difference in rat attacks by island ($X_2^2 = 1.7,\ P = 0.4$) or placement level ($X_2^2 = 2.5,\ P = 0.3$).

Attack by reptiles differed significantly among islands in both years (2013: $X_2^2 = 86.3$, $P < 0.001;\ 2022: X_2^2 = 24.57,\ P < 0.001$, Figure 3), being consistently the lowest in Guam, the island with the introduced brown treesnake. In 2022, on all islands, reptile attack was most likely on model caterpillars placed higher in the vegetation (high: 9% attacked, medium: 7%, low: 3%; high-low comparison; $X_2^2 = 11.0,\ P < 0.01$).

In 2013, predatory arthropod attacks did not differ significantly by island ($X_2^2 = 1.3,\ P = 0.52$) (Figure 2a). In contrast, in 2022 attack by predatory arthropods varied significantly among islands ($X_2^2 = 9.4,\ P < 0.01$), with Saipan having the lowest attack rate (Figure 2b). Placement level did not affect the probability of attack by arthropods ($X_2^2 = 1.2, P = 0.54$).

Habitat type significantly influenced the probability of total attacks in both 2013 and 2022 surveys. In 2013, disturbed forests had 7% higher probability of total attacks compared to intact limestone forests ($X_1^2 = 12.2,\ P < 0.001$) and a post hoc Tukey test indicate significant differences between the habitat types. In 2022, model caterpillars in coastal habitats had a 9% higher probability of total attacks compared to mixed limestone forests ($X_1^2 = 3.9, P < 0.01$) and a post hoc Tukey test indicate significant differences between the habitat types. The provenance (native/non-native) of the plant upon which the model caterpillar was placed did not influence attack rates in the 2022 surveys ($X_4^2 = 7.4,\ P = 0.1$).

DISCUSSION

I assessed differences in attack rates on model caterpillars between Guam, which has near complete extirpation of native forest birds, reductions in lizards and small mammals, and the nearby islands of Rota and Saipan, which lack the invasive top predator, and still have native birds and more diverse lizard communities (Wiles and Guerrero 1996). The surveys conducted 9 years apart found similar patterns: overall, attack rates on model caterpillars were consistently lower in Guam than in the other two nearby islands. Thus, my results suggest that the introduction of the brown treesnake may have altered attack rates on arthropods in Guam. However, the effect of the brown treesnakes on attack on model caterpillars was driven primarily by reptiles and predatory arthropods rather than by avian predators. Surprisingly, birds were infrequent attackers of model caterpillars on any of the islands.

Predation of arthropods by reptiles was the dominant driver of overall differences in predation rates among islands and may be a primary effect of brown treesnake introduction on caterpillars. These trends contrast other systems, in which lizards act as meso-predators and are suppressed by birds. For example, in tropical Bahamian anoles, islands with fewer bird species had greater lizard survival rates (Schoener and Schoener 1982). However, brown treesnakes in Guam have fed extensively on lizards and suppressed their populations (Savidge 1988, Rodda et al. 1992). The reduced attack rate in Guam compared to Saipan and Rota is consistent with the suppression of the reptile community due to the brown treesnake.

Herpetofauna like lizards may play significant roles in arthropod control in the tropics. Studies have found a positive effect of excluding lizards on arthropod abundance (Pacala and Roughgarden 1984, Spiller and Schoener 1990, Dial and Roughgarden 1995). Reduced attack rates by predatory arthropods in Saipan could be, in part, due to the considerable abundance of native and introduced lizards on that island (e.g. Rodda & Fritts, 1992; Wiles & Guerrero, 1996), which may suppress populations of active-feeding predatory arthropods. Saipan might also experience greater bird predation on arthropods by understory birds such as the golden white-eye (*Cleptornis marchei*) and bridled white-eye (*Zosterops conspicillatus*), which are absent and rare (referring to the congeneric Rota Bridled White-eye), respectively, in Rota (Linck et al. 2020). These understory birds also feed on predatory arthropods such as spiders, which may explain why Saipan has fewer web-building spiders compared to Rota and Guam (Rogers et al. 2012). The limited predation by lizards found in Guam and Rota may also explain the significantly higher arthropod predation from those islands compared to Saipan.

My study shows that the type of habitat the model caterpillar is placed in can significantly affect the probability of attack. In 2013, I found that disturbed limestone forest dominated by non-native species had significantly higher attack rates compared to intact limestone forests. This may be due to differences in vegetation, as lizards have been anecdotally observed to be abundant in *Leucaena leucocephala* that is common in disturbed forests (Wiles and Guerrero 1996). However, I did not find plant provenance (native/non-native) to influence attack rates of model caterpillars placed on that plant.

In 2022, I found that model caterpillars placed in coastal habitats had a higher probability of attack compared to limestone forests. Interestingly, Wiles and Guerrero (1996) found lizard abundance to be lower in coastal strands compared to limestone forests, contrasting my observation of attack rates. Many predaceous arthropods such as ants and hermit crabs are common in coastal areas and may account for this trend.

Overall attack rates were quite consistent despite being 9 years apart (2013 and 2022). Likewise, the relative rates of attack among islands and among predator types were similar between 2013 and 2022, when all islands were sampled. The Mariana Islands are dynamic terrestrial ecosystems, characterized by year-to-year variation in climate and major weather events such as typhoons, however the annual rainfall for the years the surveys were conducted was similar (Weatherspark.com n.d.). All surveys were conducted at the end of the dry season, so it is unlikely that seasonal differences would bias inter-island comparisons. However, it would be interesting to explore seasonal patterns in attack rates in these systems given that web-building spiders in Saipan and Rota have a strong seasonal abundance pattern compared to Guam, where they are in high abundance year-round (Rogers et al 2012).

Sentinel prey provides a powerful tool to assess risk of attack rates, but they can have disadvantages when predators do not attack prey models in the same way as actual prey. For example, some predators disproportionately attack prey that are moving or have scent characteristics that are not mimicked by clay models (Lövei and Ferrante 2017). Nonetheless, model caterpillars have been used successfully to mirror attack rates of caterpillars that feed in a variety of ways (Tvardikova and Novotny 2012) and to demonstrate differences in attack risk globally (Roslin 2017, Rodriguez-Campbell 2024). This is because many predators interact with clay models in a similar way to real prey (Remmel and Tammaru 2009). Another concern with clay models in that predators learn to avoid them over time because they are not useful prey items. In my study, I allowed predators to interact with clay models for only a maximum of three days, and model caterpillars were at a relatively low density, minimizing this effect. Similarly, my reported average attack rate of clay models in the Mariana Islands (26.5% in 3-day trials) was within the range of attack rates found in tropical systems globally (Roslin 2017), suggesting that my methods resemble those used broadly to assess attack risk.

The results of my study are consistent with top-down effects of an apex predator reducing attack risk for herbivorous insects. If this effect on attack risk is pervasive, it could translate into differences in arthropod communities among islands with and without the apex predator and ultimately into differences in rates of herbivory experienced by plants. Assessing overall differences in arthropod communities can be difficult on tropical islands where even the basic taxonomy of potentially very diverse arthropod groups is poorly known, and efforts to better understand arthropod biodiversity on these islands and their response to predation will be valuable. Overall, my study provides evidence of a trophic cascade on Guam due to the introduction of the brown treesnake, resulting in lowered attack rates to caterpillars. However, I found that this trend was probably driven by declines in lizards rather than birds, indicating an underappreciated role of this group of predators. These findings suggest that predators other than birds may play larger roles on island food webs than expected.

FIGURES

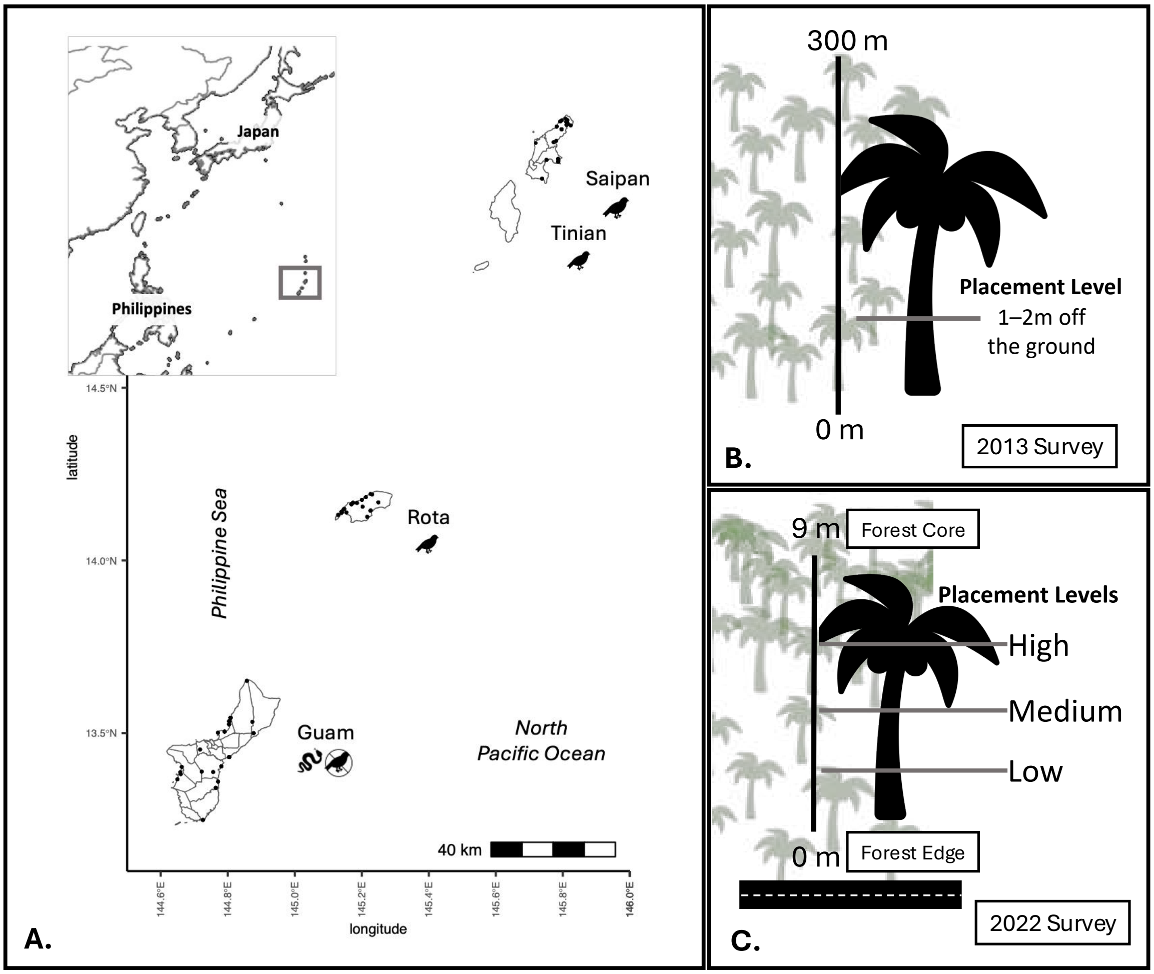

Figure 1- a. Map of transect locations from 2022. Transect layout and placement level in **b.** 2013 and **c.** 2022.

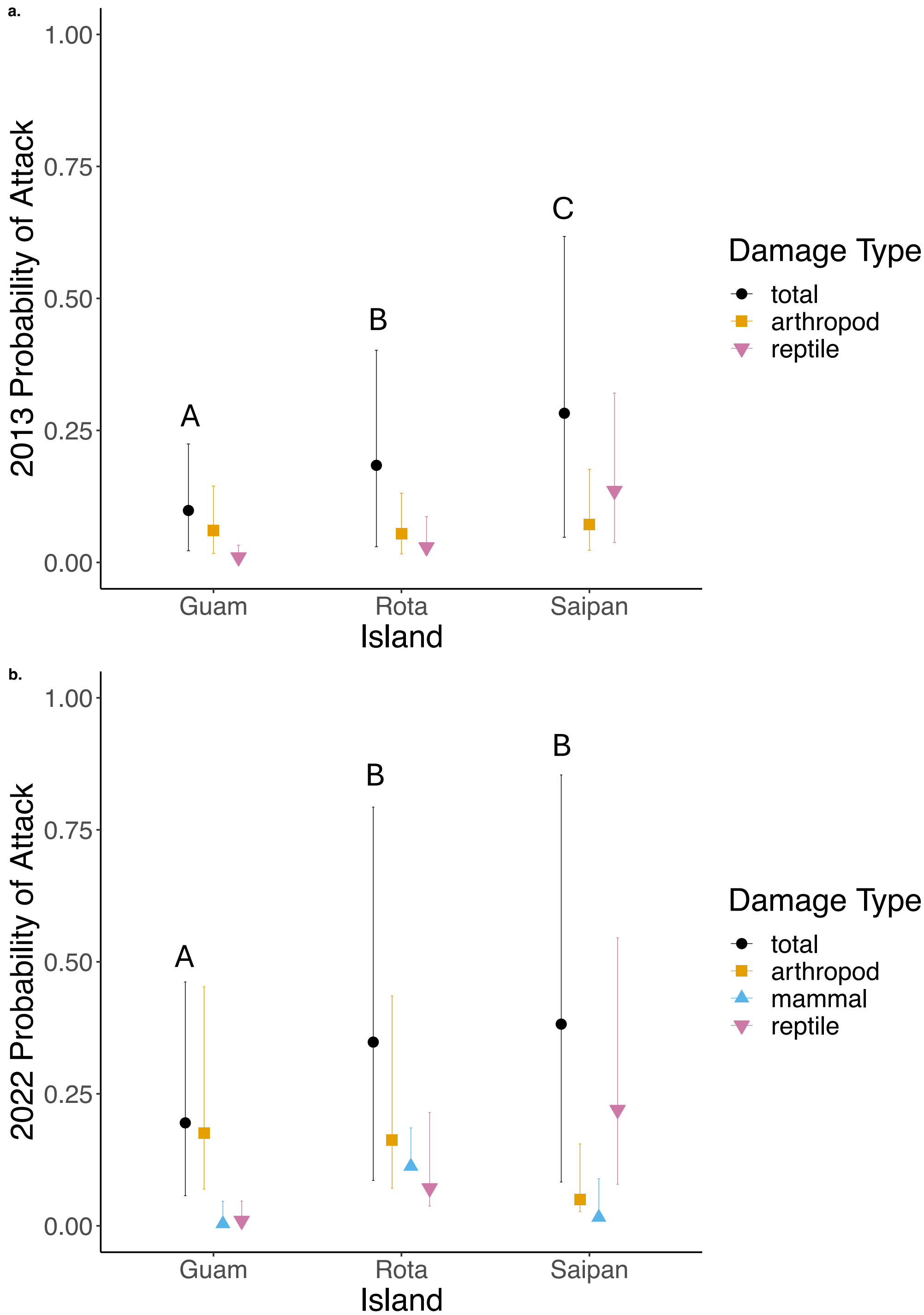

Figure 2– The probability of attack and 95% CIs on model caterpillars in Guam, Rota and Saipan in **a.** 2013 and **b.** 2022. The symbols indicate predator types: arthropod (square), mammal (triangle), and reptile (upside-down triangle). The black circle indicates the summed total damage. The letters indicate the significance of differences between the total damage only, using a post hoc Tukey test within individual year. The values for individual predators do not necessarily add up to the total attacks because other categories like "unknown" were included in the total attacks model.

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SUPPLERMENTARY MATERIAL

Appendix S1

Table S1: GPS of sites for 2022 study.

island	latitude	longitude	year	location
guam	13.24813	144.726274	2022	talofofo falls
guam	13.248235	144.725915	2022	besbes
guam	13.282849	144.755944	2022	Inarajan UOG Farm
guam	13.365951	144.650006	2022	Nimits Agat
guam	13.387	144.658622	2022	Agat old firestation
guam	13.388523	144.722337	2022	tarzan falls
guam	13.402041	144.662973	2022	Inn on the bay
guam	13.403735	144.781166	2022	tagachang
guam	13.430376	144.804507	2022	uog 1
guam	13.43089	144.804642	2022	uog 2
guam	13.452481	144.71794	2022	san carlos
guam	13.499737	144.877252	2022	pagat
guam	13.504317	144.790986	2022	ypao 2
guam	13.525006	144.803991	2022	gun beach 1
guam	13.525626	144.804096	2022	gun beach 2
guam	13.533843	144.804869	2022	Two lovers point 1
guam	13.533942	144.804903	2022	ypao 1
guam	13.534345	144.804212	2022	Two lovers point 2
guam	13.544392	144.808381	2022	tanguisson 1
guam	13.544421	144.808362	2022	tanguisson 2
guam	13.65112	144.857147	2022	ritidian
rota	14.126516	145.216269	2022	15_9
rota	14.131781	145.12953	2022	7_1
rota	14.139187	145.154157	2022	tweksberry beach
rota	14.14107	145.13943	2022	uncle janry's ranch
rota	14.144018	145.225612	2022	11_16
rota	14.149425	145.147494	2022	10_5
rota	14.155775	145.2024	2022	19_15
rota	14.166603	145.185677	2022	10_18
rota	14.166944	145.173969	2022	us memorial beach park
rota	14.167014	145.174143	2022	teteto beach
rota	14.168364	145.249506	2022	2_9
rota	14.175515	145.200328	2022	guata

rota	14.175673	145.200299	2022	11_15
rota	14.183226	145.211975	2022	4_17
rota	14.18323	145.212025	2022	swimming hole
rota	14.191417	145.23089	2022	19_1
rota	14.191459	145.230898	2022	3_17
saipan	15.106088	145.738041	2022	Obyan Beach
saipan	15.15547	145.786109	2022	Forbidden Island
saipan	15.160546	145.751182	2022	Lau Lau Beach
saipan	15.163423	145.785858	2022	Kagman 3, Pine Dr, Chopak Dr
saipan	15.211783	145.772484	2022	Old Man by the sea
saipan	15.215667	145.780268	2022	Jeffries?
saipan	15.245599	145.800345	2022	Intersection between Pale Arnold Road and Kalebera
saipan	15.24925	145.796003	2022	Old Pacific Radar
saipan	15.249255	145.79644	2022	PauPau Beach
saipan	15.260397	145.823704	2022	Grotto
saipan	15.261726	145.811193	2022	El Torro Hike
saipan	15.262033	145.811321	2022	Bird Island Hike
saipan	15.264666	145.814915	2022	Saipan Sign
saipan	15.269752	145.806201	2022	Road to Suicide Cliff by Parcourse 11
saipan	15.270792	145.810286	2022	Middle Rd by Curve
saipan	15.271954	145.792325	2022	Wing Beach

Table S2. Native, endemic and introduced insectivorous and omnivorous birds that were potential predators of model caterpillar present at the time of study in Guam, Saipan and Rota.

Island	Food Type	Provenance	Bird Species
Guam	omnivorous	endemic	Guam Rail – "ko'ko'", *Gallirallus owstoni*)
	insectivorous	native	Mariana Gray Swiftlet – "yåyaguak", (*Aerodramus bartschi)*
	omnivorous	native	Micronesian Starling – "såli", (*Aplonis opaca*)
	carnivorous	native	Yellow Bittern – "kakkak", (*Isobrychus sinensis*)
	omnivorous	native	Bridled White-eye – "nosa'", (*Zosterops conspicillatus*)
Saipan & Rota	carnivorous	native	Collared Kingfisher – "sihek", (*Todiramphus chloris*)
	omnivorous	native	Common Moorhen – "pulattat", (*Gallinula chloropus*)
	omnivorous	native	Mariana Crow – "åga", (*Corvus kubaryi*)
	insectivorous	native	Mariana Swiftlet – "yåyaguak", (*Aerodramus bartschi)*
	omnivorous	native	Micronesian Megapode – "sasangat", (*Megapodius laperouse*)
	omnivorous	native	Micronesian Starling – "såli", (*Aplonis opaca*)
	omnivorous	endemic	Rota White-eye – "nosa Luta", (*Zosterops rotensis*)
	insectivorous	native	Rufous Fantail – "chichirika or naabak", (*Rhipidura rufifrons*)
	insectivorous	native	Saipan reed warbler – "ga'ga' karisu", (*Acrocephalus hiwae*)
	insectivorous	native	Tinian Monarch – "chuchurikan Tinian", (*Monarcha takatsukasae*)
	insectivorous	introduced	Black drongo – (*Dicrurus macrocercus*)
Introduced birds (all islands)	omnivorous	introduced	Chicken – (*Gallus gallus domesticus*)

Table S3. Provenance of plants on which clay caterpillars were placed on during the 2022 study.

plant type	coastal habitat	limestone forest
crop	2%	5%
invasive	7%	20%
native	86%	61%
naturalized	0%	7%
unknown	5%	7%

Figure S1 Example of model caterpillars made of clay and attacks observed (1. Marks left by rats; 2. Marks left by hermit crabs; 3. Freshly placed model caterpillar).

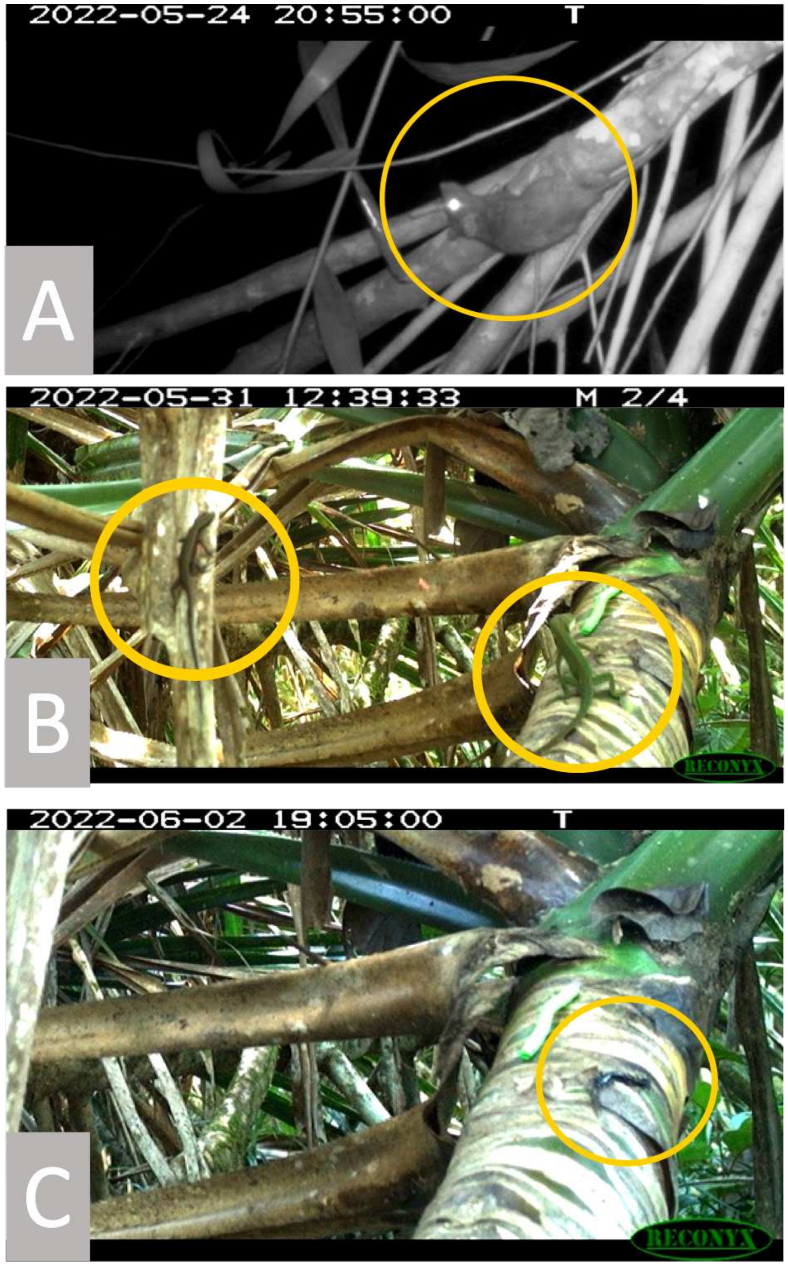

Figure S2. Images from game camera placed at sites in Rota n 2022 **(A)** Multiple rats were captured on camera in the vicinity of model caterpillars and bite marks indicated they attacked the model caterpillars. (B) Three reptile taxa were captured on camera in the vicinity of the caterpillars and may have attacked based on marks found on the model caterpillar (geckos, anoles, and skinks) Some of the lizard species observed were *Gehyra oceanica, Hemidactylus frenatus, Gehyra mutilata* and *Lepidodactylus lugubris*. Fig. B shows *Anolis carolinensis* (anole) and *Emoia caeruleocauda* (skink). Arthropods were also captured in the vicinity the model caterpillars but were often too small to identify. (C) Larger arthropods, here a centipede, and a katydid (Phaneropterinae) were photographed near the caterpillar and may have attacked based on arthropod marks found on the model.

CHAPTER 3 – LOSS OF BIRDS ALTER BUTTERFLY ANTI-PREDATOR BEHAVIOR

INTRODUCTION

Almost all animal species face predation and need to avoid or defend themselves from it (Ferrari et al. 2009, Vail and McCormick 2011). To avoid predation, many species use simple strategies such as evading or hiding from predators, while others create toxic chemical compounds that make them unpalatable (Santos et al. 2003, Francke et al. 2008, Abarca and Boege 2011). When isolated from predators, anti-predator behavior that may no longer be functional can be lost (Kavaliers 1990). Many studies that detect changes in anti-predator behaviors are from evolutionary shifts over millions of years. For example, a study looking at flocking tendencies between island birds and mainland counterparts found island species less likely to flock, due to a reduction in aerial predators of birds on islands (Beauchamp 2004). Likewise, macropodid marsupials that colonized islands lost anti-predator behaviors in favor of greater foraging ability, due to the reduced predation risk on islands (Blumstein and Daniel 2000). However, changes in anti-predator behavior can also occur in a shorter time scale in response to the arrival of novel predators. For example, endemic species in New Zealand such as the South Island Robins (*Petroica australis*) historically were not exposed to mammalian predators. Upon the introduction of predatory mammals, they developed anti-predator responses (e.g. alarm calls or flight), which have also subsequently been lost when mammals were removed from ecosanctuaries (Muralidhar et al. 2019).

In the island of Guam, birds have historically been the top predators of invertebrates. However, after WWII, the brown treesnake (*Boiga irregularis*) was introduced to the island

(Savidge 1984b) and the native birds in Guam were nearly extirpated. I hypothesized that, because of reduced predation pressure from birds, butterflies in Guam would be both more abundant and exhibit fewer anti-predator behaviors than butterflies in other Northern Mariana Islands that do not have the brown treesnake and thus do have native birds. Anecdotal observations of large butterfly emergences (e.g. *Weather conditions ripe for Butterfly Boom* (2019) give weight to this hypothesis, though my study is the first to quantify butterfly abundance and behavior among the Northern Mariana Islands. I measured the abundance of any species of butterfly observed in Guam, Saipan, and Rota at multiple study sites to test the hypothesis that butterflies were more abundant in Guam than on the other islands that retain birds. I then focused on the behavior of a single common butterfly, *Euploia eunice*, to test whether antipredator behaviors were lower in Guam than in other islands. To test these two hypotheses, I addressed two questions: 1) How does butterfly abundance differ between islands with birds and without birds? 2) How do butterfly behaviors differ between islands with birds and without birds? I estimated butterfly abundance in the islands using Pollard walks and analyzed butterfly behavior by measuring how closely I could approach butterflies with a model bird (Supplementary Figure 1) before they took flight (flight initiation distance) and compared putative predator-evasive and non-predator-evasive behaviors.

METHODS

Study System This study was conducted in three islands in the Mariana Islands chain: Guam (541 km^2), Saipan (115 km^2) and Rota (85 km^2) in January 2023. The islands experience similar temperature and rainfall pattern and are within 200 km of each other. The brown treesnake (*Boiga irregularis*) is only currently present in Guam. I visited 5 sites in Guam, 7 sites in Rota, and 6 sites in Saipan in coastal regions where *Euploia eunice* were known to frequent but only found *E. eunice* in Guam and Saipan. In Saipan, 5 out of 6 sites had butterflies present. In contrast, Rota, had no butterflies in the 7 sites I visited, even though all the butterfly species have been recorded from Rota (Schreiner and Nafus 1997). Given this, I was unable study behavior in Rota, and thus my behavioral findings focus in Guam (island with no birds) and Saipan (island with birds).

Butterfly Species The blue-banded king crow butterfly (*Euploia eunice*) is a common butterfly in Guam and in neighboring islands with native bird populations. *Euploia eunice* is in the Danainae, a subfamily with many species that sequester toxins. However, closely related butterflies such as *Euploia core*, do not sequester toxins even when reared on toxic hosts (Petschenka and Agrawal 2015), thus *E. eunice* is also thought to be palatable, and like other palatable invertebrates, to use a variety of behaviors to escape potential predators.

Butterfly Abundance To estimate relative abundance of butterflies I conducted Pollard walks (Pollard 1977) in which I recorded all butterfly species within a 5 m band on both sides of a 300 m transect at each site, while walking at a slow and steady pace. Taxa were identified visually to genus or species. Transects were walked in the middle of the day and sampling was limited to calm conditions. I did not record butterflies observed outside of the survey area.

Butterfly Behaviors

Flight Initiation Distance Flight initiation distance (also known as FID) describes an individual's tendency to flee when danger is perceived (Harbour et al. 2019). The potential danger I used was an unidentified taxidermy bird mounted on a retractable stick (Figure 1a). Working in pairs, I targeted *Euploia eunice* that were perching on vegetation or resting on the ground. My approach was started at least 1 m away, with one person holding the retractable stick and moving the bird slowly toward the butterfly. When the butterfly took flight, the observer measured the distance between the beak of the model bird and the location where the butterfly had been perching (Figure 1a). I then analyzed the difference in flight initiation distance between islands.

Flight characteristics Behaviors, such as fast and erratic flight paths or maintenance of proximity to hiding spots, are often described as anti-predator behaviors because they increase predator reaction time to prey and make capture less likely (Humphries and Driver 1967). While there is empirical evidence in various taxa to support the role of erratic movements and proximity to hiding spots as reducing predation risk (Hedenström and Rosén n.d., Lehtiniemi 2005), these behaviors may also serve other functions, and there is no clear consensus as to which behaviors reduce predation under different circumstances (Tan et al. 2024). Thus, the following characterization of butterfly behaviors as anti-predator behaviors are hypothesized. After conducting preliminary observations, I found butterflies to either be *flying* or *perching*. Within flight, I found *bobbing*, *hovering*, *gliding* and flying *straight* to be common butterfly flight behaviors (Figure 1b). I also observed butterflies to *perch while flapping their wings* (Figure 1b). I hypothesized observed behaviors to fit into two categories *evasive behaviors* and *non-evasive behaviors* (Figure 1b). The flight pattern *bobbing* represents an erratic movement, and *hovering* occurred near forest and shrub thickets, representing a means of escape to a hiding place. Perching while flapping their wings also took place within areas that would be difficult for predators to approach (Finkbeiner et al. 2012). In some butterfly species communal roosting or group perching on branches have been found to be an effective form of anti-predator behavior (Finkbeiner et al. 2012). Likewise, perching takes place on branches where butterflies can quickly hide. Thus, I considered perching to be a potentially evasive behavior. Additionally, flapping while perching allows the butterfly to regulate body temperature and allow it to take off as soon as a predator is near (Kingsolver 1985). Thus, I hypothesize that these behaviors are evasive of predators. On the contrary, flight patterns such as *gliding* and flying *straight* are more relaxed movements, thus they were hypothesized to be *non-evasive behaviors*.

Butterfly observations were conducted with two people working together. One person took notes and the other called out observations. Observations occurred at least 5–10 m away using binoculars. A butterfly was then followed for 10 maximum “moves.” A “move” referred to a specific behavior that includes perching and flying (e.g. *bobbing*) (Figure 1b). Observations lasted for a maximum of 3 minutes. If a butterfly spent 1 minute conducting one behavior (e.g. perch for 1 minute continuously), then the observation was concluded. A total of 20 butterflies per site were observed. Since *Euploia eunice* were numerous in Guam, I was able to randomly observe 5 butterflies in each cardinal direction from the center point of a site. Butterflies were not as abundant in Saipan; thus, behaviors were observed as butterflies were found. Observations (ethograms) were recorded on the cell phone application Behayve (Fulton 2024). Ethograms consisted of series of behaviors and the amount of time spent at each behavior.

Analysis Data analysis and visualization were conducted using the R statistical program language (R Core Team 2016) on RStudio (RStudio Team 2016). The *car* package was used to create linear regression models and run an Analysis of Variance (ANOVA) (Fox and Weisberg

2014). The *emmeans* package was also used to determine the differences in means in response to the experimental factors and to visualize interactions for all the models and to run a post-hoc Tukey analysis (Lenth 2023). All figures were created using *ggplot2* (Wickham 2016b). The average number of butterflies observed per island and the average number of butterflies per species observed during the 300 m Pollard Walk were calculate and graphed along with its standard deviation.

Behaviors were all analyzed with linear models to examine how they varied between the two islands (with island as a fixed effect). Approach distance (m) was analyzed without transformation, while flight and perching response variables (proportion of time spent performing each behavior) were transformed with log(x+1) to improve normality of the residuals. I first examined the proportion of time spent flying and perching and then looked closer at the different types of flight behaviors observed including *bobbing*, *gliding*, *hovering*, and flying *straight*. I also examined the proportion of time butterflies spent perching and flapping their wings (*perch-flap*).

RESULTS

Butterfly Abundance Saipan had the highest abundance of butterflies when grouping individuals of all butterfly species, but this was due to the particularly high abundance of individuals from the genus *Eurema* in one site (Figure 2). *Eurema* may be abundant in Saipan because one of the larval hosts, flame trees (*Delonix regia*), is a popular ornamental plant and is widely planted. Furthermore, the butterflies in the genus *Eurema* are agile fliers, which allow them to avoid predators (Pinheiro and Campos 2019). The focal species, *Euploia eunice,* was most abundant in Guam as hypothesized given the absence of birds there (Figure 2).

Flight Initiation Distance In Guam, *Euploia eunice* butterflies had a shorter flight initiation distance (FID) compared to those in Saipan (Average FID_{Guam} = 9 cm; Average FID_{Saipan} = 16 cm; F (1, 223) = 3.9, $P < 0.05$; Figure 3), indicating that butterflies in Guam allowed predators to approach more closely.

Behavior Butterflies in Guam spent more time flying compared to butterflies in Saipan (F (1, 258) = 26.8, $P < 0.001$; Figure 4). Because the behaviors flying and perching are inverses of each other (as the butterfly will either be perching or flying) butterflies in Guam spent less time perching compared to butterflies in Saipan (F (1, 258) = 24.9, $P < 0.001$; Figure 4). The butterflies, and especially those in Saipan, tended to perch in very thick densely branched plants (Appendix 1 Figure 1). I then analyzed the observations by individual behaviors.

In terms of evasive behaviors, butterflies in Saipan (island with birds) spent more time *hovering* (F (1, 258) = 7.5, $P < 0.01$) (Figure 5). *Bobbing* was not significantly different between the island with birds and without birds (F (1, 258) = 0.13, $P = 0.72$; Figure 5). During the proportion of time butterflies were observed perching, butterflies in the island with birds spent more time and *perching and flapping* (F (1, 258) = 21.1, $P < 0.001$). Finally, in terms non-evasive behaviors butterflies in Guam (island with no birds) spent more time *gliding* (F (1, 258) = 7.5, $P < 0.01$), and *flying straight* (F (1, 258) = 11.2, $P < 0.001$) (Figure 5).

DISCUSSION

I assessed butterfly abundance and potential changes in anti-predator behaviors in butterflies due to the loss of birds in Guam relative to Saipan, which retains birds. *Euploia eunice* were more abundant in the island without birds than in the island with birds. Butterflies from the island without birds had shorter flight initiation distances and spent more time conducting behaviors I hypothesized to be non-evasive, such as gliding slowly in the air and flying straight. In contrast, butterflies in the island with birds had longer flight initiation distances, spent more time perching on branches, and conducting hypothesized evasive behavior such as hovering along branches. My results suggest that changes in anti-predator behavior have occurred due to the loss of birds.

I know relatively little about the efficacy of butterfly behaviors that I assume to be defensive against predators, though some evidence supports the role of these behaviors in avoiding predation (Tan et al. 2024). For example, due to higher abundance of predators in rural environments, rural birds have been found to have longer flight initiation distances compared to urban populations (Møller 2008). This suggests that rural birds react more quickly and fly away as soon as they notice a predator approaching. Butterflies from the island without birds had fewer erratic flight behaviors that were hypothesized to be evasive against predators. Butterflies from the island without birds spent more time flying while butterflies from the island with birds spent more time perching. I hypothesize that prolonged flying time increases their exposure to predators while likely increasing their ability to forage and find mates. Evaluating whether flight is more dangerous than perching for butterflies on Saipan would be an important next step in testing this hypothesis. Perching, on the other hand, allows butterflies to hide from predation and shelter from environmental hazards (Lederhouse et al. 1987). However, weather conditions can limit long-term perching's effectiveness because butterflies in a perching position may be at risk of predation if their body temperature is too low to take flight quickly (Kingsolver 1985, Mattila 2015). Additionally, prolonged roosting during inclement weather has been observed to have 35% higher mortality due to increased predation during daylight periods (Lederhouse et al. 1987). The constant danger of being consumed by vigilant predators in the island with birds may explain butterflies hovering and perching in dense thickets. These thickets were so dense that if birds tried to enter, they would likely have needed to stop flying and hop twig to twig (Appendix 1, Figure 1). I propose that hovering over branches allows butterflies to stay close to thickets and quickly gain refuge if a predator approaches.

The reduction or loss of anti-predator behavior observed in butterflies in the island with no birds is similar to what have been observed in other studies assessing loss of anti-predator behavior after isolation from predation (Blumstein and Daniel 2005). Similarly, when raised in the absence of predators, Bahamian mosquitofish were unable to recognize and had a muted response to their predator (Fowler et al. 2018). Concordant with my results, recent work on monarch butterflies (*Danaus plexippus*) shows that this species sequesters less cardenolide toxins used for defense in Guam compared to neighboring islands and other regions of the world (Freedman et al. 2022).

An important future direction will be to understand whether the changes in anti-predator behavior represent an evolutionary shift or a plastic change. The evolutionary loss of anti-predator behavior may have drastic consequences if the predator is re-introduced, while plastic changes in behavior might be quickly reverse with the reintroduction of predators. Thus, information on whether the loss of anti-predator behaviors may help us understand the consequences of future bird re-introduction efforts for butterfly populations in Guam. In other ecosystems, gradual exposure to novel predators increased wariness of animals to those predators (Weiss 2019), though it is unclear how behavioral change would happen in these butterflies. These dynamics may be important because Guam has multiple rare butterfly species, such as the endangered Mariana 8-spot butterfly (*Hypolimnas octocula marianensis*) and the Mariana wandering butterfly (*Vagrans egistina),* which are both of conservation concern *(*Rubinoff and Holland 2018*).* The effects of bird loss in the island of Guam have been ongoing for more than 35 years and this is the first study to measure possible changes in behavior in the absence of predation. The results of this work can help predict the effects of future bird reintroductions and conservation management decisions.

FIGURES

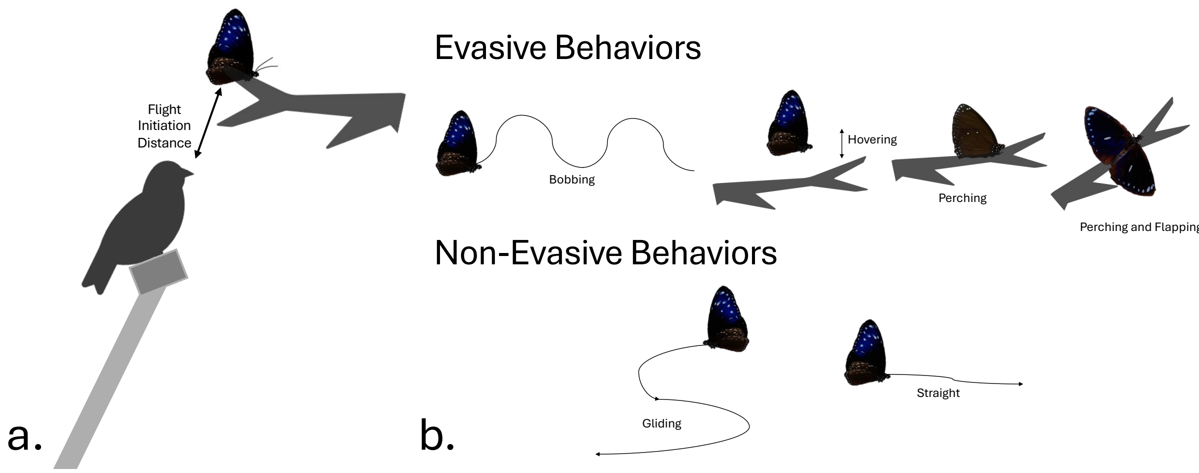

Figure 1 – **a.** Model bird on a retractable stick used to measure flight initiation distance of butterflies. **b.** Butterfly behavior patterns measured.

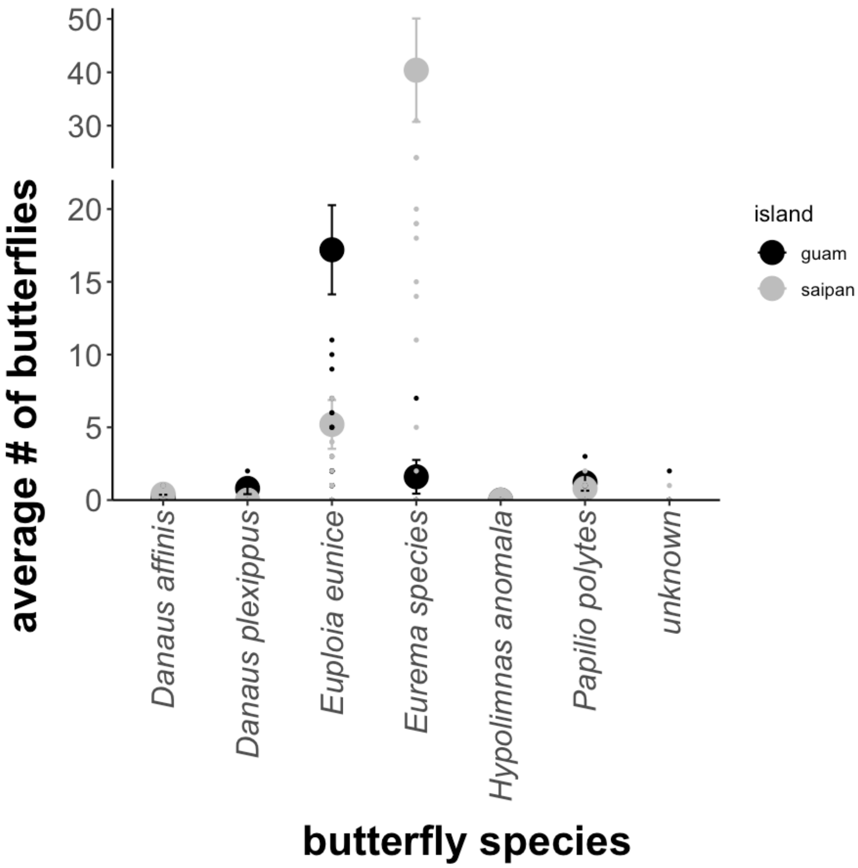

Figure 2 – Average number of butterflies per site observed for each butterfly species and data on individual butterflies observed at each site. The x-axis is the average number of butterflies, and the y-axis are the butterfly species. The error bars represent the 95% confident intervals.

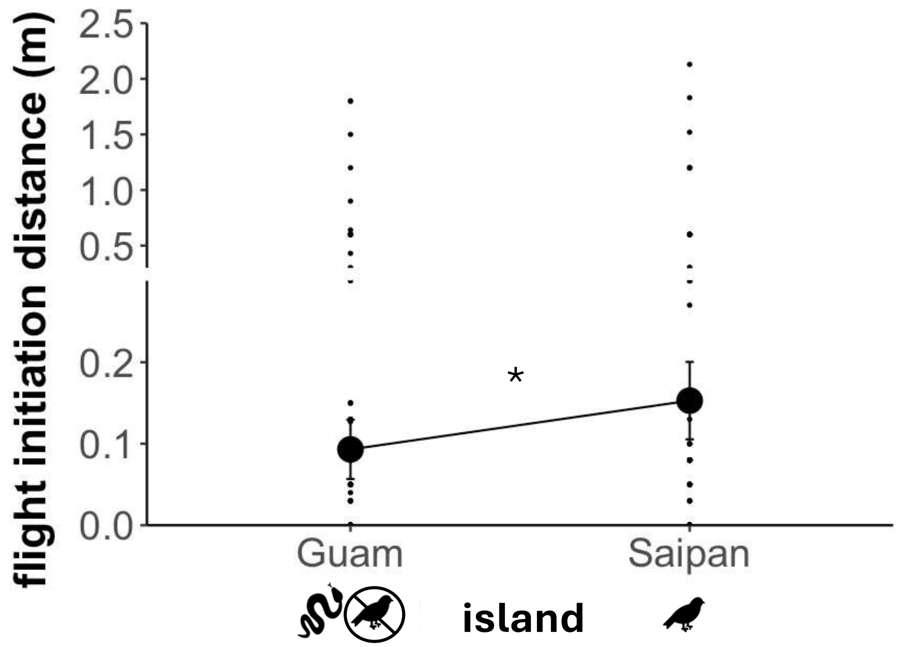

Figure 3 – Flight initiation distance of butterflies found in Guam and Saipan showing means and data on individual butterflies. Error bars are 95% confidence intervals. The * indicate the significance of difference between pairs of group means using a post hoc Tukey test (**P-value*<0.05).

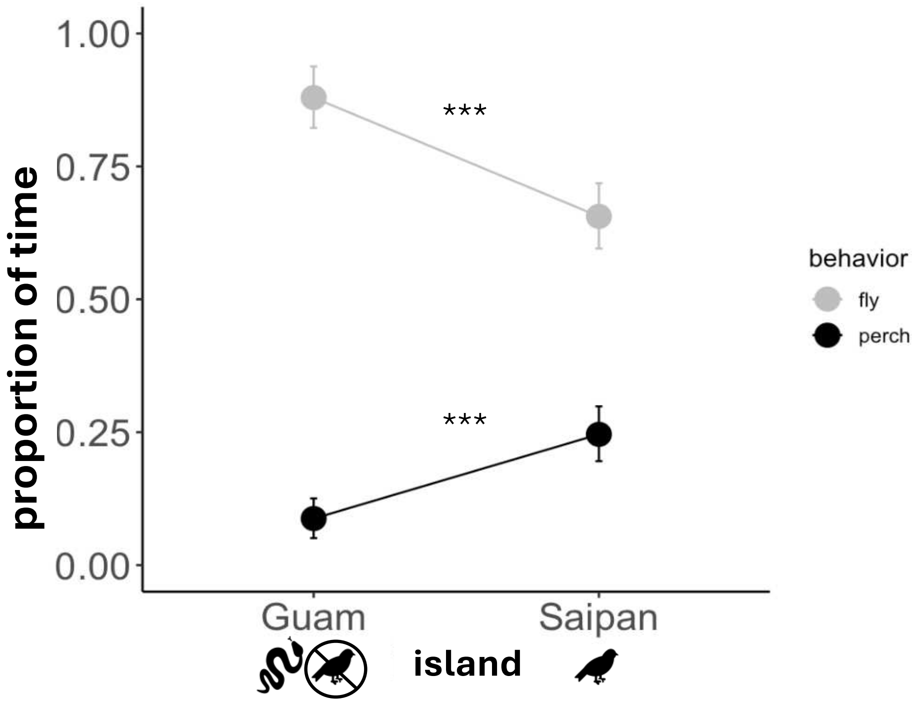

Figure 4 – Proportion of time butterflies spent either flying or perching. Error bars are 95% confidence intervals. The * indicate the significance of difference between pairs of group means using a post hoc Tukey test (****P-value*= 0.001).

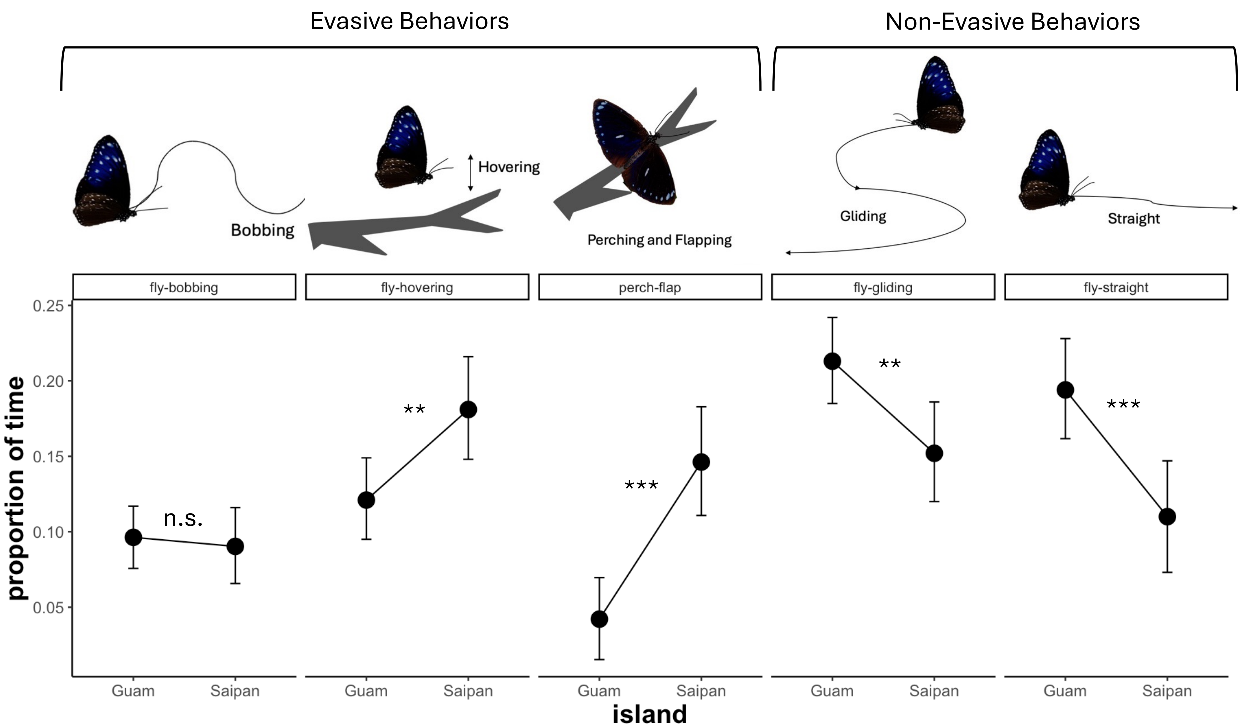

Figure 5 – Proportion of time spent conducting evasive and non-evasive behaviors observed in Guam and Saipan. Error bars are 95% confidence intervals. The * indicate the significance of difference between pairs of group means using a post hoc Tukey test (****P-value*= 0.001; ***P-value*=0.01; [n.s.]*P-value>0.05*).

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SUPPLERMENTARY MATERIAL

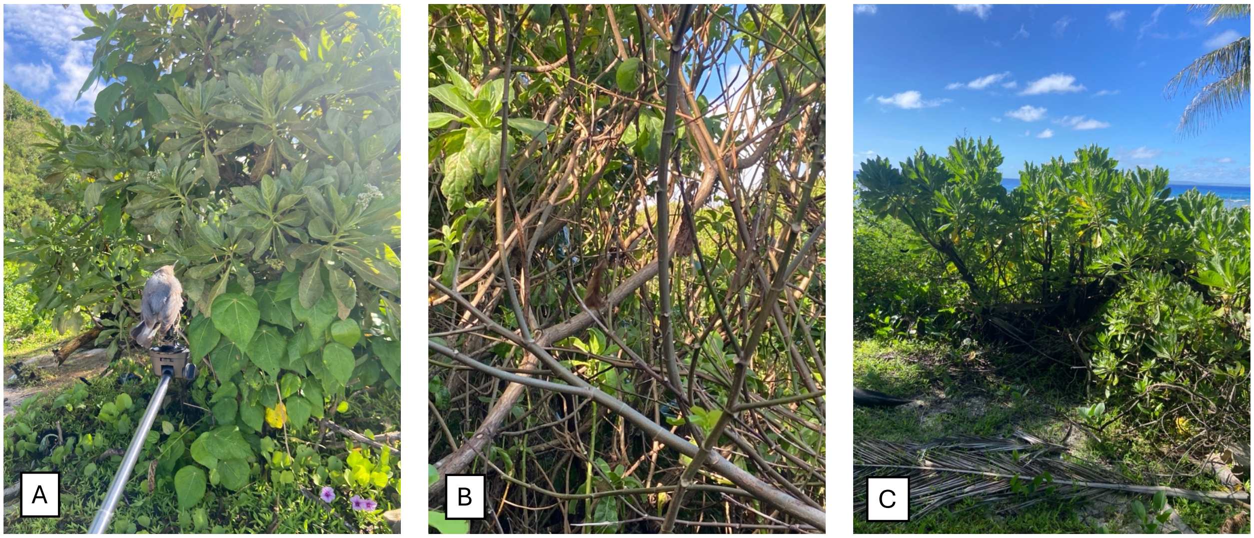

Figure 1 – A. Photo of model bird used to measure approach distance for butterflies. B. Common thicket of branches *Euploia eunice* to perch at in Saipan. C. *Tournefortia argentea* in Saipan where *E. eunice* were abundant.