THESIS

THE EFFECT OF MULTIPLE STRESSORS ON KAUA‘I’S FOREST BIRDS: DEMOGRAPHY, HEALTH, AND TROPHIC CASCADES

Submitted by

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ABSTRACT

THE EFFECT OF MULTIPLE STRESSORS ON KAUA‘I’S FOREST BIRDS: DEMOGRAPHY, HEALTH, AND TROPHIC CASCADES

Island ecosystems harbor unparalleled biodiversity, providing habitat for a disproportionate share of the world’s species relative to their area. Nevertheless, the vulnerability of islands to disturbances that result in negative consequences renders them among the most endangered environments. Bird populations on islands are particularly susceptible and often strongly affected by invasive species, habitat loss, climate change, and disease, all of which has resulted in widespread decline and extinction. In the Hawaiian Islands, native forest bird populations confront numerous threats, with the majority of remaining native bird populations classified as threatened, endangered, or teetering on the brink of extinction.

To sustain and recover island bird populations, it is essential to understand the direct and indirect impacts of anthropogenic changes on forest bird populations, and to what degree each driver of change influences bird health, demographics, and habitat quality. The goals of this project were to quantify how various stressors influence the body condition and sex ratios of Kaua‘i’s forest birds, and to assess if primary and secondary forest regeneration processes that affect forest bird resource and habitat availability are influenced by invasive rodent control.

To address these questions, I collected and analyzed three years of forest bird banding data in the Alaka‘i Wilderness Preserve on Kaua‘i’s Island (Hawai‘i, U.S.A.) from 2021 to 2023. Birds were banded in and outside of areas that have been subject to intensive rodent control for the past 5-9 years. I focused on four focal species of birds, three native and one non-native, and collected data to assess the body condition and sex of these captured birds. Mixed effects models were used to determine whether body condition was significantly associated with rodent control intensity on a local and landscape scale, malarial infection status, mean temperature during the peak mosquito breeding season, frequency of extreme rain events, canopy density, and topographic wetness index (TWI). Similarly, I used general linear models to test if rodent control intensity, malarial infection status, or date of capture was associated with a higher or lower likelihood of encountering a female. I found that body condition was negatively associated with positive malarial status for all but one of the focal species, and higher average temperatures and TWI were negatively associated with body condition for all species. None of the predictor variables evaluated were strong predictors of the sex of captured birds.

To evaluate the effects of rodent control on forest regeneration processes that sustain bird habitat in the Alaka‘i Wilderness Preserve, I examined whether rodent control was associated with changes in seed rain, fruiting density, and seedling emergence. Seed traps were established in February of 2023 and were checked periodically over a six-month period to obtain seed rain data from within and outside of areas of rodent control. Seeds collected from traps were identified to the lowest possible taxonomic level. During each visit to collect seed trap contents, the number of fruits on all fruiting plants within five meters of each seed rain trap was estimated. These estimates were used to calculate relative fruiting densities in treatment and reference plots. To examine seedling emergence, emergence plots in treatment and reference plots were cleared of all vegetation in July of 2022. I used Mixed Effects Models to compare seed rain, fruiting density, and seedling emergence between sites with and without rodent control and found no differences in seed rain, seedling emergence, or fruiting density within and outside of rodent control.

My findings suggest that variables that are related to disease transmission may be more influential in predicting the health of forest birds than variables related to predation risk or food and resource availability. These findings also suggest that rodent control, at least at current levels of intensity, may not play a significant role in forest regeneration in Kaua‘i’s ‘Alaka‘i Plateau. Further research is needed to understand the effectiveness of rodent control in this system, but reducing the prevalence of avian malaria and mitigating climate change will be critical to alleviating sub-lethal effects on Kaua‘i’s forest birds. This study contributes to our understanding of the sometimes complex and synergistic effects of invasive predators, disease, forest structure, and climate on forest birds and the dynamics of insular ecosystems. My findings and approach could have implications for conservation and restoration in the many areas globally where rat invasion, climate change, and disease may interact to pose similar threats.

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SUMMARY

Island bird species are at high risk of extinction globally. Anthropogenic drivers of loss and decline include invasive species, disease, habitat loss, and climate change. Although population declines are frequently well-documented, it is less clear which stressors are operating alone or interacting to drive these declines. Identifying the relative importance of these stressors is critical to effective conservation interventions given limited funds and time. In this study, I examined six potential stressors that could have sub-lethal effects on the body condition and demography of four forest bird species on Kaua‘i Island, Hawai‘i. I captured birds in mistnets in areas with and without invasive rodent control and collected data on body condition and sex. I then evaluated stressors such as rodent control intensity, avian malaria, climate variables (temperature and precipitation), and habitat quality (canopy density and topographic wetness). I found that topographic wetness and the average temperature during the mosquito breeding season prior to when the bird was caught were negatively associated with body condition for all but one bird species. Both topographic wetness and temperature during the mosquito breeding season can influence the transmission and infection rates of avian malaria. Rodent control, malarial infection, and date of capture were hypothesized to potentially influence sex ratios in forest bird populations. I tested if sex ratios of the focal species were influenced by these variables, however no stressors were good predictors of bird sex. These results suggest that climate change and disease may exacerbate non-lethal negative effects on forest birds. Mitigating the effects of climate change and reducing the transmission of avian malaria are likely to improve health and prevent further population loss of forest bird populations in Hawaiian forests.

INTRODUCTION

Biodiversity on islands often exhibit unique and remarkable evolutionary patterns that contribute to high levels of endemism when compared to continental ecosystems (Fernández-Palacios et al. 2021). Yet, island flora and fauna has also declined rapidly over the last several centuries due to human activities (Russell and Kueffer 2019, Matthews et al. 2022). Bird populations on islands have been particularly vulnerable to these impacts and have suffered disproportionately high extinction rates (Karels et al. 2008). Birds provide essential ecosystem services to the ecology and health of island ecosystems such as seed dispersal, pollination, and pest management (Whelan et al. 2008, Şekercioğlu et al. 2012). Many Indigenous island cultures have unique and deep cultural ties to avian species (Westergaard 2022). Declines in bird population can lead to cascading and sometimes catastrophic effects for ecosystem function, biodiversity, biotic relationships, and biocultural history (Banko et al. 2001, Culliney et al. 2012, Kaushik et al. 2018).

One of the most iconic examples of the effects of human disturbances on island birds is the case of Hawaiian avifauna (Paxton et al. 2022). Often referred to as “the extinction capital of the world”, Hawaiian forest birds have suffered numerous extinctions since human colonization. At least 95 of 142 known species have gone extinct since humans arrived on these islands, and at least 69% of the species that are still extant are federally listed as threatened or endangered (Banko et al. 2001, Gon and Winter 2019). Primary threats driving these extinctions and ongoing population declines include the introduction of invasive predators, disease, habitat loss and degradation, and climate change (Atkinson et al. 2013, Banko et al. 2019). These threats often interact to exacerbate threats to avian populations (Reed et al. 2012). Understanding which of these stressors are the primary driver of population declines, using early warning signs such as poor body condition and skewed sex ratios, could be critical to informing time and cost-effective conservation interventions.

Bird body condition provides insight into the energetic state of an individual, has implications for the ability of an individual to persist in various environments (Schulte-Hostedde et al. 2005), and influences reproductive potential (Labocha and Hayes 2012). Body condition can reflect an individual's response to environmental conditions including habitat quality, presence of introduced predators, and climatic conditions (Benson and Bednarz 2010, Weterings et al. 2022, McCloy and Grace 2023), and individuals with better body condition are more likely to have higher survival rates and reproductive success (Peig and Green 2010), and reduced susceptibility to disease (Catfolis et al. 2023). As such, measuring changes in body condition can provide a valuable indication of the benefits of conservation interventions (Lavers et al. 2010).

In addition to body condition sex ratios can also be used to measure the response of forest bird populations to management interventions such as predator control or disease mitigation (Nadal et al. 2016). Sex ratios of small and declining species tend to be male-biased (Morrison et al. 2016). In most bird species females preferentially incubate nests with males providing nutritional assistance by feeding the incubating females (Bambini et al. 2019). Incubating individuals are at a greater risk of predation (Heinsohn et al. 2019), and the cost of reproduction is often more energetically demanding for females (Sibly et al. 2012). This may lead to an altered sex ratio in the overall population. Skewed sex ratios are important potential barriers to productivity in birds, and at already low population densities can further increase risk of extinction (Reidy et al. 2009, Morrison et al. 2016, Ancona et al. 2020).

Of all stressors to island birds, the effects of invasive rodents have been particularly well documented. Rats and mice are directly or indirectly associated with species extinction and population decline (Courchamp et al. 2003, Witmer et al. 2014, Russel and Holmes 2015, Bellard et al. 2016). Invasive rodents can spread disease, compete with birds for resources, and degrade habitat through frugivory and herbivory (Doherty et al. 2016). Rats are one of the most effective predators of birds (Lavers et al. 2010) and because many rat species are arboreal, nesting females, young chicks, and eggs are especially vulnerable to depredation (Fontaine and Martin 2006, Reidy et al. 2009). This is particularly true on islands where birds have often evolved in the absence of rats, and any former adaptations to coexist with predators like rats have been lost (Moors et al. 1992). Black Rats are the most common rat species in Hawai‘i (Shiels and Drake 2015) and have been implicated in population declines of native seabirds (Raine et al. 2020)) and forest birds (Harper and Bunbury 2015). This species was one of the primary drivers for the rapid decline of Oahu ‘Elepaio (*Chasiempis ibidis*) (Mosher et al. 2010) and is the cause of approximately 16% all passerine nest failures in Hawai‘i’s wet montane forests (Pratt et al. 2009).

Introduced pathogens are another major stressor for island birds, because these species lack a coevolved immunological response (Vanderwerf 2012). The introduction of the mosquitotransmitted parasite, avian malaria (*Plasmodium relictum*) to the Hawaiian Islands has had devastating consequences to avian populations and has fundamentally altered the distribution of native forest birds (Lapointe et al. 2012). Many native species have been extirpated from lower elevations where mosquito populations are high, and constrained to a smaller area of disease-free refuge in higher elevations where the climate is inhospitable for mosquitoes and most of the remaining intact and malaria-free native forest still exists (Samuel et al. 2015, Liao et al. 2017). Avian malaria, spread by the southern house mosquito (*Culex quinquefasciatus*), is associated with a 62-90% mortality rate in Hawaiian birds such as Hawaiʻi ʻAmakihi (*Chlorodrepanis virens*), ʻapapane (*Himatione sanguinea*), and iʻiwi (*Drepanis coccinea*) after a single mosquito bite. In the case of experimentally infected birds, the mortality rate can exceed 90% (Atkinson et al. 1995, 2000; Yorinks and Atkinson 2000). While there is growing evidence for increased tolerance in certain species (Atkinson et al. 2013, Samuel et al. 2015) most native birds face acute infection after exposure, often suffering from damage to internal organs, anemia, lethargy, anorexia, and lowered immune response (Atkinson et al. 1995, Lapointe et al. 2012).

Environmental attributes such as climate and topography can also affect bird fitness and health (Remeš and Harmáčková 2018, Molina-Marin et al. 2022). Extreme temperatures can influence stress response, body size, nesting success, reproduction, and growth (Sauve et al. 2021, McCloy et al. 2023). Additionally, climate change is expected to exacerbate both the frequency and severity of extreme weather events. Even short-term extreme weather patterns can reduce food availability, add to energetic demands, and lead to death in birds with weakened immune systems (Lapointe et al. 2012, Soriano-Redondo et al. 2016, McCloy and Grace 2023). Climate may influence the distribution and prevalence of disease (Kalluri et al. 2007). Mosquitoes that spread disease, including avian malaria, have higher rates of reproduction, faster development, increased adult survival, and increased rates of disease transmission in warmer temperatures. Warming temperatures also mean the transmission of avian malaria at higher elevations, including in the last refuges for Hawaiian forest birds (Benning et al. 2002, Lapointe et al. 2012, Ciota et al. 2014).

Habitat quality and forest structure can affect access to resources, refuge from predators and extreme weather, and the availability of suitable nesting areas. Topographic Wetness Index (TWI) and canopy density could be important predictors of habitat quality for birds in tropical forests. TWI is a measurement that describes how water pools in areas and has been shown to capture patterns of soil moisture and water availability or utilization in an area (Dyer 2009). This water retention can play a major role in determining plant species distributions and community structure (Moeslund et al. 2013) which may have implications for food and habitat availability for forest birds (Økland et al. 2008, Ediriweera et al. 2016).

Vegetation structure can also play a key role in predicting habitat quality for birds by influencing the availability of food resources and nest sites (Hinsley et al. 2006). Increased forest complexity has been associated with better body condition in birds because of greater food availability and better refuge against extreme climatic events (Scheffers et al. 2014, Catfolis et al. 2023). Fretz (Fretz 2002) found that a higher canopy density was related to greater food availability for Hawaiʻi akepa (*Loxops coccineus*), with both individual and population level consequences.

The objective of this study was to evaluate the effect of multiple stressors on the body condition and demography of Kauaʻi's forest birds. Focusing on four focal bird species on Kauaʻi's Alakaʻi Plateau, I used banded birds to assess the relationship between rodent control intensity, malarial status, canopy density, topographic wetness index, temperature during the prior mosquito breeding season, and number of extreme precipitation events in the beginning of the forest bird breeding season, with forest bird body condition. I further tested for associations between the likelihood of a captured bird being a male or female with rodent control intensity, malarial status, and the date of capture. I hypothesized that the negative health effects associated with malarial infection would cause a positive malarial infection status to be negatively correlated with body condition. Additionally, I predicted that increased temperatures during the mosquito breeding season would increase mosquito abundance and malarial infection and would correlate negatively with body condition. A higher number of extreme precipitation events at the beginning of the breeding season was expected to increase energetic demands and stress response for birds, also leading to a negative correlation with body condition. Higher trap density was expected to reduce both predation and competition pressure on focal species leading to increased body condition. Increases in TWI, and canopy density were predicted to lead to higher food and habitat availability and therefore be positively correlated with body condition.

I further hypothesized that a higher rat trap density would result in a higher probability of capturing a female due to decreased predation pressure on incubating females. Finally, I predicted that malarial infection and date of capture may be associated with the sex ratios of captured birds. These predictions were based on findings from previous research that indicate malarial infection may affect sexes differentially, and that birds may have capture probabilities that differ according to behavior and life history characteristics that vary between sexes. The direction of these effects could be either positive or negative due to mixed findings from previous research and differences in behaviors in different species (Lachish et al. 2011, Ágh et al. 2019, García et al. 2023). The results of this study will help us better understand sub-lethal effects of multiple stressors on Kauaʻi's forest birds and could be used to guide management actions in Hawaiʻi and other areas globally.

METHODS

Study Area

This study was located on the island of Kauaʻi, Hawaiʻi (U.S.A.) in the eastern portion of Kauaʻi's Alakaʻi plateau (22° 7' 18'' N and 159° 33' 48'' W) within the Alakaʻi Wilderness Preserve (**Figure 1.1**). This is the region where most of Kauaʻi's native forest birds still persist because it includes the highest elevation terrain on the island, and the native plant community is relatively intact. This preserve, with an area of approximately 70 km^2, is a wet montane forest and receives some of the heaviest rainfall in the world (>6,000 mm of rain per year). Bogs are present throughout the Alakaʻi but most of the region is well drained (Foster et al. 2004). The forest birds in this region have been managed and monitored by the Kauaʻi Forest Bird Recovery Project (KFBRP) since 2003. KFBRP is a collaborative project between the Hawaiʻi Division of Forestry and Wildlife (DOFAW) and the Pacific Studies Cooperative Unit of the University of Hawaiʻi.

Two study sites, Halepaʻakai (22° 4' 46" N and 159° 32' 51" W) and Mohihi (22° 7' 18" N and 159° 33' 48" W) were selected within the plateau to conduct this study (**Figure 1.1**). Halepaʻakai (HPK) is at 1350 m in elevation and Mohihi (MOH) is at 1250 m, and both have been the focus of forest bird research and management by KFBRP over the past decade. A portion of each study site (HPK = 93ha; MOH = 56ha) has been subject to intensive rat control over the past 6-9 years to reduce rodent populations in critical habitat for Kauaʻi's threatened and endangered species. Hereafter, areas with and without rodent control will be referred to as treatment and reference areas respectively. HPK was fenced with all ungulates removed in 2017. MOH is not fenced and contains feral ungulates including deer (*Axis axis*) and pigs (*Sus scrofa*).

The HPK trap grid has about 164 rat traps that have been operating continuously since March 2015 and MOH has been operating about 124 traps since fall 2018. Both HPK and MOH rat control grids contain Goodnature A24 rat traps (**Figure 1.2, Appendix**) in which traps are spaced approximately 100 x 50m apart depending on landscape and habitat. KFBRP staff checked the traps in both grids two to three times per year. Each time traps were visited the lure and CO^2 cartridge was changed as needed to ensure traps remained operational.

Relative rodent abundance in treatment and reference areas was monitored during the breeding season using tracking tunnels (**Figure 1.3, Appendix**). Presence or absence of rat footprints were used to quantify the proportion of tunnels where rat tracks were present relative to the total number of tunnels set. Using these track tunnel data as an index of relative rat abundance, previous studies in this study system have demonstrated lower rodent abundance in the treatment areas (Crampton et al. 2022).

Study Species

This study examined four focal forest bird species: Kauaʻi ʻAmakihi (*Hemignathus stejnegeri*), ʻAnianiau (*Magumma parva*), Kauaʻi ʻElepaio (*Chasiempis sclateri*), and Warbling white-eye (*Zosterops japonicus*). These species were chosen because they have relatively small home ranges and site fidelity (0.015 - 0.45ha; (Guest 1973, van Riper 1995, Tweed et al. 2003, Vanderwerf et al. 2013) relative to other species (e.g., ʻApapane (*Himatione sanguinea*)) that range widely to follow pulses in food availability (Smetzer et al., 202; **Table 1.1, Appendix**). Smaller home ranges decrease the probability that birds in rat-controlled areas are traveling to areas without rat control, and vice versa.

Two of the focal species are Hawaiian Honeycreepers (Fringillidae: Carduelinae). Kauaʻi ʻAmakihi is a generalist that feeds on insects, nectar, and fruit. The ʻAnianiau (*Magumma parva*) is also a generalist that feeds on nectar from flowering plants and gleans adult and larval arthropods from trees, shrubs, vines, and fern fronds. The Kauaʻi ʻElepaio (*Chasiempis sclateri*), is a native monarch flycatcher. This small brown bird feeds primarily on a wide range of arthropods from snags, the ground, logs, rock crevices, and virtually all parts of trees (Pratt et al. 2009). The only non-native species included in this study is the Warbling white-eye (*Zosterops japonicus*). This species is included because it is one of the most successful introduced species in Hawaiʻi and are abundant in the study region. The Warbling White-eye consumes arthropods, nectar, and fruit, and may compete with native birds for both habitat and food resources (Freed and Cann 2014).

Mist Netting and Banding

I used mist nets to capture, band, and collect data on body condition, sex, disease status, and other morphological characteristics of the focal species. Mist netting occurred intermittently from mid-March through August, which covers the primary breeding season for Hawaiian forest birds (Pratt et al. 2009). Mist netting occurred throughout the trapping and reference areas. A variety of banding locations were chosen throughout the Alakaʻi wilderness preserve. These locations were chosen to strategically target areas where bird capture would be the highest and that were also accessible given the challenging terrain, and to make use of data that were collected by other concurrent projects mistnetting birds in the study region (**Figure 1.4, Appendix**). Nets varied in size from 6-12m long and had mesh size of 30 mm. Mist nets were opened only under satisfactory weather conditions and closed in weather conditions that were not suitable according to best banding practice (IACUC protocol 08-585-13). Birds that were caught were fitted with a federal bird band with a unique identifying number and often color bands for identification and resighting. Mass, fat content, body/flight feather molt, and the length of the tarsus, culmen, and wing cord, were recorded when possible. Mass and morphometric measurements were used to assess body condition. A blood sample was taken to be used for malarial screening and sexing before the birds were released.

Body Condition

Body condition is often measured using indices calculated from measurements such as body fat, mass, and other morphometric measurements (Labocha and Hayes 2012, Barnett et al. 2015). Body mass is a morphometric measurement shown to be affected by predator removal programs and can be a reliable predictor of the benefit of removal (Lavers & Wilcox

2010). Body mass is commonly used in combination with a linear body measurement such as tarsus length (Peig and Green 2010). Using methods from Peig & Green (Peig and Green 2009) body condition was assessed using the Scaled mass index ($\widehat{M}_i$). The scaled mass index uses a fixed value of a linear body measurement to standardize body mass. This is based on a scaling relationship between mass and length. The scaled mass index equation is as follows:

$$\text{Scaled mass index } (\widehat{M}_i) = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

In this equation M_i and L_i are the body mass and linear body measurement of the individual i respectively. b_{SMA} Is a scaling exponent estimated by the standardized major axis (SMA) regression of lnM on lnL. L_0 is the arithmetic mean value for the study population, and L_i is the predicted body mass for individual i when the linear body measurement is standardized to L_0. A higher $\widehat{M}_i$ is indicative of better body condition (English et al. 2018).

Covariates

Sexing and Malarial Status

After morphometric measurements were taken from captured birds, approximately 50 µL of blood was collected via brachial venipuncture in heparinized capillary tubes. Blood was then transferred to a lysis buffer to preserve the DNA. Once blood samples were taken out of the field, they were put on ice and shipped to Northern Arizona University (NAU) for molecular sexing and screening for malaria presence. Samples were returned with either a negative or positive malarial status and the sex of the birds.

Rodent Control Intensity

Because previous work in this system demonstrated that trapping decreases rodent abundance (Crampton et al. 2022), and directly measuring rat abundance across the entire study area was beyond the scope of this project, I used rat trap density as an index of rodent control intensity. This will be referred to as the “trap count” from here on forward. Rat control density was calculated as the number of rat traps located within 150 and 300 m from the location where a bird was caught. To evaluate the effects of rodent control, ArcGIS Pro (ESRI version 3.3.1, Redmond WA) was used to summarize the number of rat traps within an 150m and 300m radius from where the bird was caught. These distances were selected because they capture the average home range sizes of the focal study species, which range from approximately 0.015 ha - 0.45ha (Guest 1973, van Riper 1995, Tweed et al. 2003, Vanderwerf et al. 2013).

Topographic Variables

To assess whether topographic variables influence body condition, I acquired high resolution (1m^2) LiDAR imagery for the Alakaʻi Plateau which was taken in 2017 (Fricker et al. 2021). From this imagery, I derived two habitat metrics, which were canopy density and topographic wetness index (TWI). Using ArcGIS Pro (ESRI version 3.3.0, Redmond WA), I summarized TWI and canopy density as the average TWI and canopy density within 150m and 300m from the bird's capture point.

Climatic Variables

To evaluate effects of climate on bird body condition, I obtained daily precipitation and temperature values from a National Oceanic and Atmospheric Administration weather station, made publicly available on https://www.noaa.gov/. I used the Lihue Weather Service Office Station (Network ID: GHCND:USW00022536). To obtain the average temperature during the mosquito breeding season, I summarized the average temperature throughout the peak months of the mosquito breeding season for Hawaiʻi which lasts from July through November (Lapointe et al. 2012, Samuel et al. 2015, Maldinich, personal communication). For precipitation events, I used the daily precipitation values for 10 years prior to the end of this study (2013–2023). Using this information, I calculated the 90th percentile threshold of the daily precipitation values for that 10-year period (Post et al. 2021). Then I found the number of days exceeding this threshold, and summarized the number of extreme weather events that occurred within the first three months of the year when the bird was caught. These months were chosen because these are the months just prior to, and at the beginning of the breeding season where birds are generally gathering energy stores and preparing to reproduce.

Data Analysis

I employed generalized linear mixed models (GLMM) to determine if body condition was associated with any of the stressor variables of interest. Specifically, I used body condition score as the response variable with trap count, sex (male or female), malarial status (positive or negative), average Topographic Wetness Index (TWI), average canopy density, number of extreme precipitation events, and the mean temperature throughout the previous year's mosquito breeding season as explanatory fixed effects. The bird's federal band identification number was added as a random effect to account for individual variability and for recaptured birds.

To evaluate the relationship between stressors and sex ratios, I used a binomial logit-linked general linear model (GLM) sex (male or female) as the response variable. For this analysis I only included fixed effects that were thought to possibly influence sex composition in forest birds. The fixed effects included in the analysis were trap count, malarial status, and julian date when the bird was captured. For the sex analysis, only data from the latest date of capture was used for any recaptured birds throughout the season so all data points were from unique individual birds.

A list of possible models was constructed using a knowledge driven approach. Prior knowledge of the system and literature were used to construct combinations of stressors that were thought to possibly influence the body condition or sex ratio of our focal species. Models were fit using the lme4 package in RStudio version 4.3.2 (R Core Team 2023). A correlation matrix was run to assess collinearity between explanatory variables and variables with high collinearity were not included in the same model. Variables summarized at 150m and 300m (trap count, TWI, canopy density) were tested at both scales in different models. No models included the same variable tested at both scales due to spatial autocorrelation, and top models were examined at each of the two intervals. Akaike's information criteria adjusted for small sample size (Burnham and Anderson 2013) was used to assess the fit of the model and all models were ranked using ΔAICc. The regression coefficients were examined to determine the strength and direction of the relationship between body condition and covariates. Any models with ΔAICc ≤ 2 were considered as alternative models that were equivalent to the top model.

RESULTS

I caught 681 birds of the four focal species across the duration of the study. These represent 604 individual birds because 61 birds were recaptured at least once. Of these 681 bird captures, 399 of them resulted in sufficient data to conduct the body condition analysis. The models thus incorporate data from 74 Kauaʻi ʻAmakihi captures, 49 ʻAnianiau, 115 Kauaʻi ʻElepaio, and 161 Warbling white-eye. We were able to reliably sex 59 Kauaʻi ʻAmakihi, 46 ʻAnianiau, 105 Kauaʻi ʻElepaio, and 147 Warbling white-eye.

Body Condition

Multiple models appeared as equally competitive (ΔAICc ≤ 2) for all of the focal species (**Table 1.2**). At both 150m and 300m, the same top models emerged for Kauaʻi ʻAmakihi. These models were temperature alone, temperature + malaria (positive), temperature + malaria + TWI, and sex (M) + temperature + malaria. For Kauaʻi ʻAmakihi, a higher temperature during the previous mosquito breeding season was correlated with lower body condition, positive malarial status was correlated with higher body condition, higher TWI was associated with lower body condition, and male birds were associated with lower body condition. At both 150m and 300m the null model for ʻAnianiau was within ≤ 2 AICc for all top models, indicating that none of the tested stressors added information regarding body condition for this species. For Kauaʻi ʻElepaio, temperature and temperature + TWI were in top models at both 150m and 300m. At 300m, temperature + malaria + TWI appeared as an equally competitive model. Higher temperatures during the previous mosquito breeding season was associated with lower body condition for Kauaʻi ʻElepaio. For this species a higher TWI was correlated with lower body condition, and a positive malarial status was also associated with lower body condition. For the Warbling white-eye, at both 150 and 300m, temperature and temperature + TWI appeared in the top models. At 150m, temperature + TWI + canopy density appeared as an additional top model, while at 300m sex (M) + temperature appeared as an additional top model. For Warbling white-eye, higher temperatures during the previous mosquito breeding season and higher TWI were both correlated with lower body condition. Higher canopy densities were positively correlated with body condition, and male birds were negatively correlated with body condition (**Table 1.2**).

Sex

None of the models evaluating the relationship between stressors and the probability of capturing female birds were < 2 AICc from the intercept only model (**Table 1.3, Appendix**).

DISCUSSION

Understanding how multiple stressors act individually or synergistically to influence the health and demographics of forest birds is important for sustaining and recovering island bird populations (Benning et al. 2002, Milenkaya et al. 2013, Fernández-Palacios et al. 2021). The purpose of this study was to determine if major stressors to island forest birds are influencing the health and demographics of the forest birds of Kauaʻi. This study suggests that out of six tested stressors, only the temperature during the previous mosquito breeding season and average topographic wetness were consistently negatively correlated with reduced body condition across multiple species (**Figure 1.5; Table 1.4, Appendix**). Malarial infection was negatively associated with body condition for two species, and positively associated with body condition for one species. Kauaʻi ʻAmakihi and ʻAnianiau were the only two species for which sex was associated with differences in body condition, and the direction of this relationship was inconsistent among these species. Contrary to predictions, there was no association between rodent control or extreme precipitation events and body condition for any of the tested species, nor was the probability of a captured bird being female associated with rodent control. These findings suggest that variables associated with disease prevalence may be the most influential in shaping the health of these forest bird populations, and that rodent control, at least at current levels of intensity, is not effective in improving forest bird health and demography in the Alakaʻi Wilderness Preserve. The outcomes of this study could help guide and prioritize management actions for Kauaʻi's rapidly declining forest birds.

Across all species, decreases in body condition were correlated with increases in the average temperatures during the mosquito season prior to when the bird was caught (**Figure 1.6 & 1.7**). This represents the first evidence that climate and disease could together have sub-lethal effects on forest birds on Kauaʻi. Mosquitoes that transmit disease such as avian malaria often have highly temperature dependent life history processes. Elevated temperatures can act as a catalyst and accelerate the development and life cycle of these insects, translating to increased fecundity and higher overall mosquito abundance (Chuang et al. 2011, Ganser and Wisely 2013, Ciota et al. 2014). In contrast, colder temperatures have a suppressive effect on mosquito metabolic processes and lead to decreased mosquito activity. Consequently, behaviors that are crucial for reproduction such as flight, host-seeking, and blood feeding become hampered under colder conditions (Ganser and Wisely 2013, Reinhold et al. 2018, 2022). The cooler temperatures of high elevation forests in Hawaiʻi act as a natural barrier to mosquito expansion, effectively restricting the distribution of these malaria vectors to lower elevations. Consequently, most native Hawaiian forest bird species are restricted to higher elevations where they are protected from this potentially fatal disease. As temperatures increase with climate change, mosquito populations are more frequently being found at higher and higher elevations, and the refuge that these bird populations once had are shrinking (Lapointe et al. 2012, Liao et al. 2017). These results indicate that in addition to the direct mortality caused by avian malaria, there are also sub-lethal effects of rising temperatures and the accelerating risk of mosquito transmission at higher elevations.

Topographic Wetness Index (TWI) is often positively associated with habitat quality for forest birds (Moeslund et al. 2013, Del-Toro-Guerrero et al. 2019, Xie et al. 2021), but had a slight association with poor body condition in this study (**Figure 1.8**). A possible explanation for this could be due to the potential effect of TWI on mosquito larval habitat availability. TWI is built on digital elevation models that predict the likelihood of moisture to pool in an area. Areas where the slope of the terrain leads to increased soil moisture are more likely to produce stagnant water, which provides ideal habitat for mosquito larvae (Ganser and Wisely 2013, Riihimäki et al. 2021). Ganser & Wisley (2013) tested a variety of environmental variables to see which were associated with mosquito abundance and diversity in a mixed grass prairie in Kansas. Of the variables tested, only TWI was significantly positively correlated with mosquito abundance in a mixed grass prairie in Kansas (Ganser & Wisley 2013). Similarly, Cohen et al. (2008) found that proximity to regions with higher wetness indices increased the risk of malaria transmission.

For two out of the three native species in this study, positive malarial status was negatively associated with body condition (**Figure 1.9**). Hawaii's native flycatchers are often less vulnerable to avian malaria compared to honeycreepers and can live with the disease without experiencing fatal effects (Vanderwerf et al. 2006). Nonetheless, my findings demonstrate that Kauaʻi ʻElepaio are still being affected on a sub-lethal level. Many introduced birds such as the

Warbling White-eye live with moderate levels of disease infection and are considered as reservoirs of avian malaria (McClure 2017). This is a likely reason why malarial infection did not appear in any of our top models for this species. Because honeycreepers are particularly susceptible to avian malaria (Paxton et al. 2022), it is unsurprising that although the correlation was not strong, avian malaria status was negatively correlated with body condition in all top models for ʻAnianiau, one of the two honeycreepers in this study. However, in contrast to predictions, the other honeycreeper species, Kauaʻi ʻAmakihi, was positively associated with malaria status. Some subpopulations of Hawaiʻi ʻAmakihi (*Chlorodrepanis virens*) have developed resistance to avian malaria and are able to coexist with mosquitoes that transmit avian malaria (Atkinson et al. 2013). It is possible that the Kauaʻi ʻAmakihi is developing resistance to this disease as well. Yet, given the absence of this species at lower elevations on Kauaʻi, a more likely explanation could be that malarial infection is reducing host activity and viability to a point where individuals with lower fitness that are testing positive for malaria are less likely to be captured. Malarial parasites may cause hosts to exhibit lethargic behaviors and reduce overall activity (Lapointe et al. 2012, Garamszegi et al. 2015), potentially leading to a reduction in capture rates (McPherson et al. 2012, Holmes et al. 2024). Higher body condition has been correlated with higher resistance to disease, and the ability to survive infection (Gleeson et al. 2005), therefore these individuals with higher fitness also would be more likely to be captured in nets. There is however opposing evidence that parasitic infections can also lead to increased foraging due to increased energetic demands and increased risk-taking behaviors that increase capture rates (Garamszegi et al. 2015, Remacha et al. 2023), therefore more research is warranted to determine why body condition in Kauaʻi ʻAmakihi is positively associated with avian malaria status.

We found no correlations between avian malaria infection and sex in our focal species. These results align with literature, which is mixed on sex-related differences in malarial infection. For example, Garcial et al. (2023) found that the prevalence of malarial parasites was higher in males than in females for Red-legged partridges (*Alectoris rufa*) while Lachish et al. (2011) found malarial infection rates were greater for males than for females in Blue tits (*Cyanistes caeruleus*). Agh et al. (2019) found no sex related differences in malaria prevalence for European robins (*Erithacus rubecula*).

The relationship between body condition and sex was inconsistent among the two focal honeycreeper species. Several factors may contribute to these observed differences in body condition of males and females. Studies have revealed potential biases related to energy expenditure and breeding behaviors or avian life history (Bryant 1997, Hambly et al. 2007). The cost of reproduction for female birds may have significant impacts to their overall body condition. Additionally, birds that are sitting on nests or sleeping are often more vulnerable to depredation by arboreal rats. This can be sex dependent as many female birds preferentially incubate nests as in the case of Hawaiian honeycreeper species. Conversely, male birds may engage in more territorial defense behavior and may spend more time foraging leading to a higher energy expenditure and consequences to fitness and body condition. Energy expended on nest building can also vary between sexes and be dependent on species (Sibly et al. 2012, Jacobs et al. 2013, Mainwaring et al. 2021). It is possible that male Kauaʻi ʻAmakihi spend considerably more time foraging for resources and defending territory leading to a higher cost of fitness than females while female ʻAmakihi exhibit a higher cost of reproduction to fitness. Research on sex-specific time allocation for energy demanding behaviors in Honeycreepers is limited and warrants further investigation.

Extreme precipitation was not in any of the top models across all species for body condition. Extreme weather has been known to have negative effects on tropical forest birds (Van Riper and Scott 2001, Şekercioğlu et al. 2012), but Kauaʻi's forest birds evolved in forests which regularly experience high rainfall (Calhoun and Fletcher 1999, Paxton et al. 2016) and they may be adapted to these conditions. Additionally, the period in which we sampled for extreme precipitation could be insufficient to capture effects in body condition. Further, body condition may be better explained by extreme precipitation in other parts of the year, or perhaps by the number of sustained extreme precipitation events over a certain period prior to the birds' capture.

This study failed to show any relationship between rat trap density and body condition or the probability of a captured bird being female. This is in contrast with other studies that have found differences in both sex ratios and stress levels before and after the introduction of mammals, particularly in the case of island avian species (Clinchy et al. 2004, Slos and Stoks 2008, Donald 2011, Heinsohn et al. 2019, Weterings et al. 2022). It is possible that rodents are not influencing body condition and demography in this system, but trapping may also not be at sufficient densities to see significant changes in our response variables (Nelson et al. 2002). Further, rat trap density is likely an imperfect measure of true rat abundance (Vanderwerf et al. 2011). Measuring abundance of small mammals at large scales is costly and logistically difficult and most methods of doing so have limitations (Sollmann et al. 2013, Palmer et al. 2018). Nonetheless, measuring rat densities more directly, or trapping at higher intensities may provide more insight into how invasive rodents influence body condition and demographics of Hawaiian forest birds.

This study provides new insights into the stressors associated with sub-lethal effects on Kaua‘i’s forest birds. However, there are several factors that limit my inference, and highlight opportunities for future research. The strength of these relationships between stressors and body condition were marginal as demonstrated by R^2 values (**Table 1.2.**). Other factors not tested in this study such as age, breeding status, or food availability in the environment may also be associated with body condition (Milenkaya et al. 2013, Deikumah et al. 2015). The age of captured birds was assessed upon banding, but the number of hatch year birds that were caught in this study were too low (0.06-33%) to test whether age could be a potential driver of body condition. Other factors potentially driving body condition in island forest birds, such as food availability, were beyond the scope of this study but should be explored in future research. Although I did not detect strong relationships between stressors and body condition, I suggest that the patterns and directions that emerged are of conservation relevance given that these species are relatively poorly understood and in crisis (Şekercioğlu et al. 2012).

In addition to the constraints associated with our index of rat control, as discussed above, we were also limited by sample sizes. Although the sampling effort across the study areas within and outside of rodent controlled areas was consistent, the sampling effort throughout the years was variable, resulting in smaller sample sizes in year three (2023). Additionally, capture rates are particularly low for Kaua‘i’s forest birds (e.g., typically 0-7 birds/day with 4-10 nets in operation), perhaps because of rapidly declining populations (Crampton et al. 2022). ‘Anianiau had the lowest sample size (n=49), which could explain why this was the only species to not show strong correlations between the tested stressors and body condition. It is likely that a long-term study with sustained sampling effort could provide greater insight to the non-lethal effects of these stressors. Long-term monitoring of forest bird body condition could also improve overall understanding of how body condition varies with annual temperature and precipitation.

Conservation Recommendations

Island birds play important ecological roles, contribute to global biodiversity, are central to the culture and history of islands (Paxton et al. 2022), and provide a source of enjoyment for residents and visitors (Steiner 2001). Yet, Hawaiian forest birds are facing a conservation crisis, and urgent action is needed to prevent further species extinction (Reed et al. 2012, Paxton et al. 2022). Conservation managers often face difficult decisions when deciding how to allocate limited conservation dollars (Pejchar et al. 2020). This study suggests that climatic and topographic factors associated with the spread of avian malaria may be the strongest predictors of body condition in Kauaʻi's forest birds. If invasive mosquito populations are not controlled or eliminated rapidly, avian malaria infection will continue to spread with rising temperatures (Benning et al. 2002). A promising tool to reduce mosquito populations is a naturally occurring and symbiotic bacteria called Wolbachia (Pinto et al. 2021, Ogunlade et al. 2023, Velez et al. 2023). When mosquitoes with different strains of Wolbachia mate, eggs can be rendered infertile. The release of non-biting males with a different strain of Wolbachia than the wild population can reduce mosquito populations to near zero in treated areas (Werren 1997, Baldacchino et al. 2015). One of the challenges with this management action is the expense of implementing the treatment at large scales. Our finding that TWI is associated with poor body condition could indicate that targeted application of Wolbachia to these areas has the potential to be cost-effective. Immediate implementation of Wolbachia releases and other tools to mitigate against the effect of climate change and invasive disease will be critical to ensuring that Kauaʻi's forest birds, and other island birds facing similar plights globally, are here for generations more to come.

TABLES AND FIGURES

Table 1.2 The most competitive models within 2 AICc of the top AICc model explaining the association between stressor variables and body condition for Kauaʻi forest birds. Temperature = Mean temperature of mosquito breeding season prior to capture, Malaria = Positive malarial status, TWI = Mean Topographic Wetness Index, Sex = Male sex, Canopy Density = Mean canopy density. AICc = Akaike's Information Criterion with small-sample bias adjustment (Burnham and Anderson 1998).

Species	**Distance (m)**	**Fixed effects**	**AICc**	**Marginal R^2**	**Conditional R^2**
Kauaʻi ʻAmakihi	150	Temperature + Malaria (Positive)	283.4	0.118	0.360
		Temperature + Malaria (Positive) + TWI	283.9	0.119	0.385
		Temperature	285.2	0.064	0.288
		Sex (M) + Temperature + Malaria (Positive)	285.3	0.124	0.383
Kauaʻi ʻAmakihi	300	Temperature + Malaria (Positive)	283.4	0.118	0.360
		Temperature + Malaria (Positive) + TWI	284.1	0.117	0.376
		Temperature	285.2	0.064	0.288
		Sex (M) + Temperature + Malaria (Positive)	285.3	0.124	0.383
ʻAnianiau	150	Malaria (Positive)	143.3	0.082	0.755
		Malaria (Positive) + TWI	143.4	0.111	0.784

		Null Model	144.7		
		Temperature + Malaria (Positive)	144.9	0.093	0.777
		Temperature + Malaria (Positive) + TWI	145.0	0.123	0.804
		Temperature	145.1	0.034	0.778
‘Anianiau	300	Malaria (Positive)	143.3	0.082	0.755
		Malaria (Positive) + TWI	144.4	0.088	0.762
		Null Model	144.7		
		Temperature + Malaria (Positive)	144.9	0.093	0.777
		Temperature	145.1	0.034	0.778
Kaua‘i ‘Elepaio	150	Temperature	411.7	0.075	0.370
		Temperature + TWI	412.6	0.081	0.400
Kaua‘i ‘Elepaio	300	Temperature	411.7	0.075	0.370
		Temperature + TWI	411.8	0.085	0.400
		Temperature + Malaria (Positive) + TWI	413.7	0.093	0.401
Warbling White-eye	150	Temperature + TWI	548.9	0.096	0.612
		Temperature	549.8	0.082	0.575
		Temperature + Canopy Density + TWI	550.2	0.126	0.578
Warbling White-eye	300	Temperature	549.8	0.082	0.575

	Temperature + TWI	550.2	0.089	0.595
	Sex (M) + Temperature	551.8	0.090	0.575

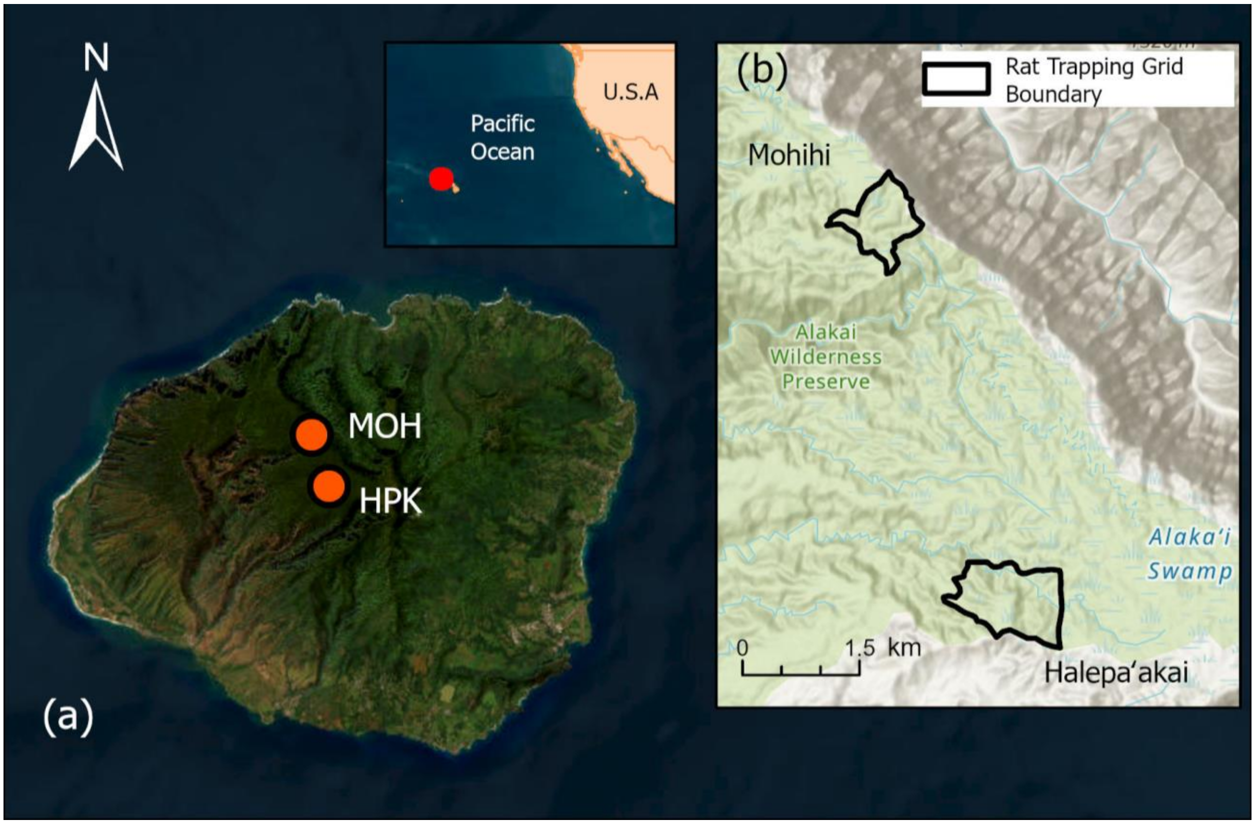
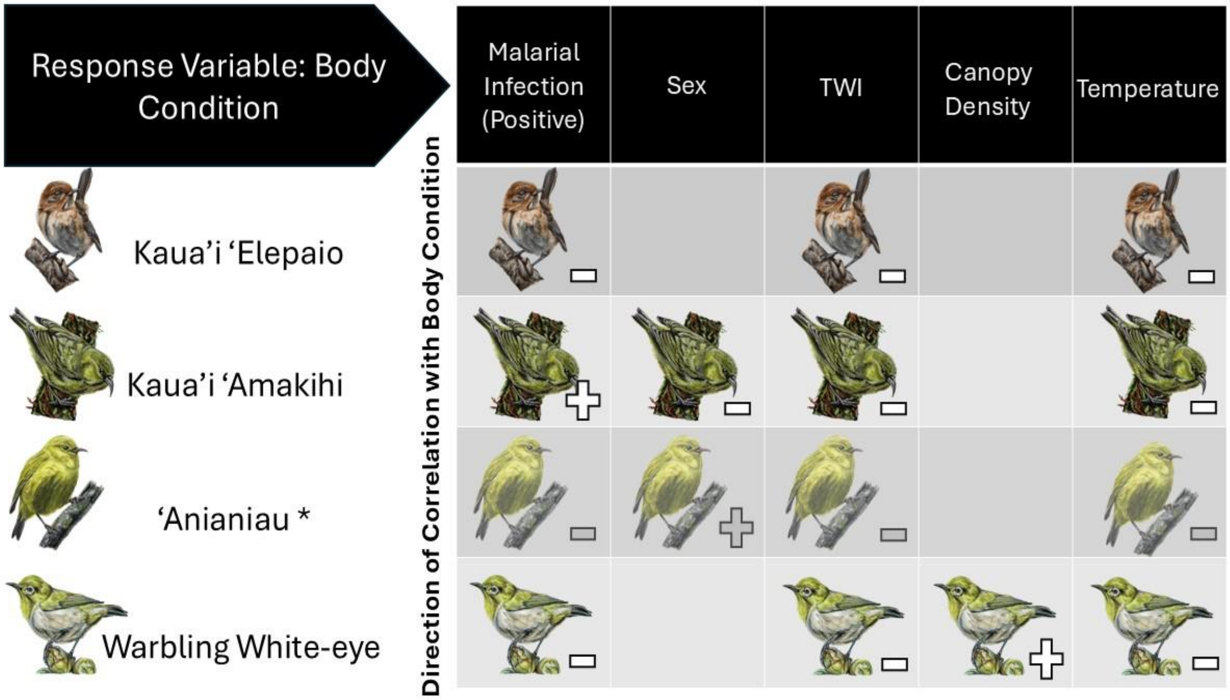


Figure 1.1. (a) Orange circles mark the study site locations (Halepaʻakai (HPK) and Mohihi (MOH)) for assessing the effect of multiple stressors on forest birds on the island of Kauaʻi, Hawaiʻi (U.S.A), and (b) black lines denote the boundaries of areas with rodent control at each location.



Direction of Correlation with Body Condition

Response Variable: Body Condition	Malarial Infection (Positive)	Sex	TWI	Canopy Density	Temperature
Kaua'i 'Elepaio	−		−		−
Kaua'i 'Amakihi	+	−	−		−
'Anianiau *	−	+	−		−
Warbling White-eye	−		−	+	−

Figure 1.5. Infographic of variables that appeared in the top models for relationships between stressors and body condition. Symbols represent respective species, and positive or negative signs represent the direction of the correlation between body condition for that species and the stressor. * Stressors for'Anianiau were not strongly correlated with body condition due to null model appearing amongst the top competitive models.

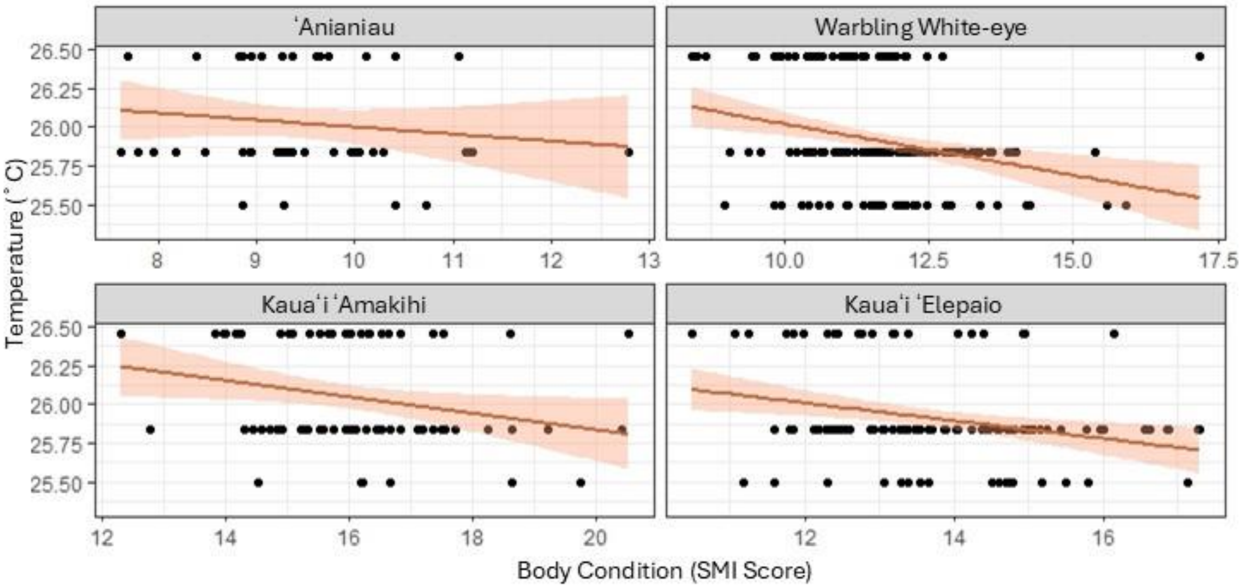


Figure 1.6. Relationship between body condition (SMI Score) and the average temperature during the mosquito breeding season prior to when the bird was caught for four focal bird species in the Alakaʻi Wilderness Preserve, Kauaʻi, Hawaiʻi. The solid lines represent the linear trend between body condition and temperature, with shaded areas indicating the 95% confidence intervals.

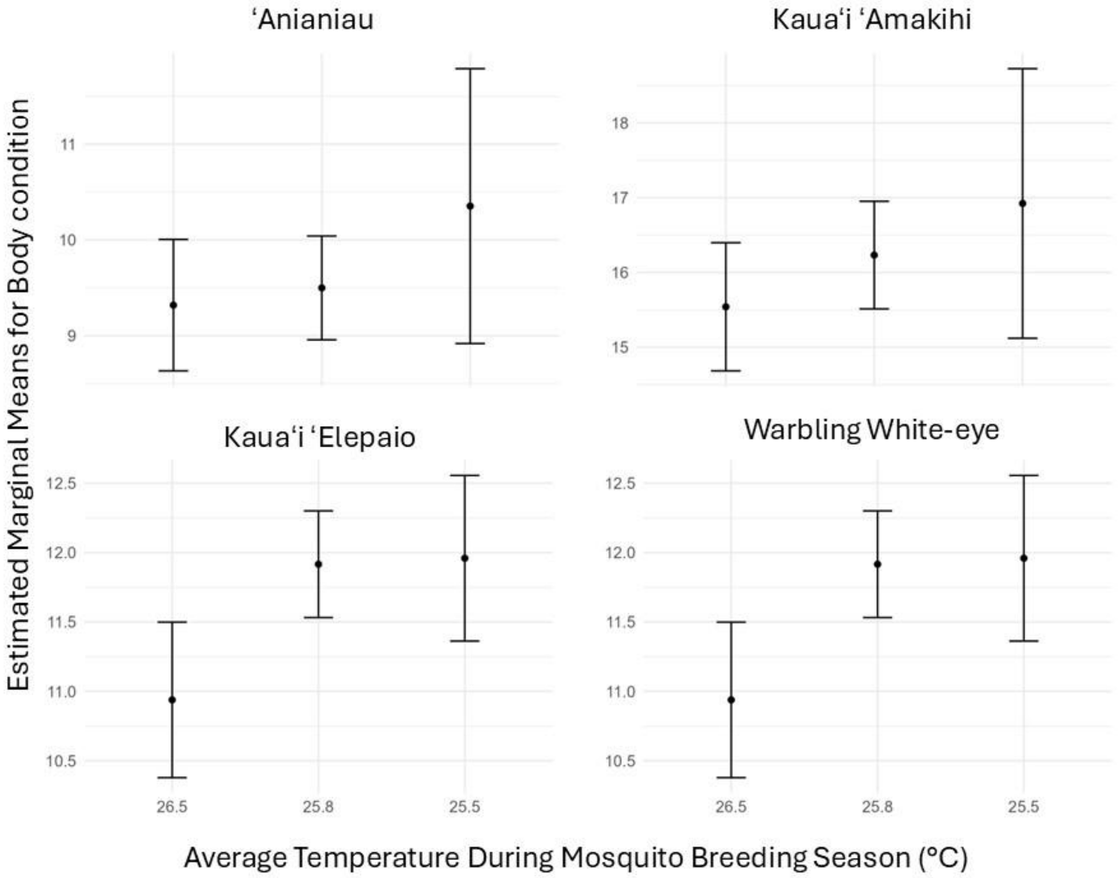


Figure 1.7. Relationship between the average temperature during the mosquito breeding season and body condition of birds. This figure displays the estimated marginal means of body condition for the temperature only mixed model across four focal bird species in the Alaka‘i Wilderness Preserve, Kaua‘i, Hawai‘i. The temperature only model appeared as a top competitive model in all four species.

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CHAPTER TWO - EVALUATING THE EFFECT OF INVASIVE RAT CONTROL ON HABITAT REGENERATION FOR KAUAʻI'S FOREST BIRDS

SUMMARY

Introduced rats can have detrimental impacts on forest regeneration processes, with consequences for other trophic levels. Rats frequently consume or damage fruit, seeds, and seedlings, which can disrupt ecosystem processes that provide food and habitat for bird populations. These impacts are exacerbated on oceanic islands where plants and animals have evolved without mammalian herbivores and seed predators, and many native species are at risk of extinction due to invasive species and other stressors. The goal of this study was to evaluate the relationship between rodent control and three variables, fruiting density, seed rain, and seedling emergence, that influence forest regeneration processes in the Alakaʻi Wilderness Preserve on Kauaʻi Island, Hawaiʻi (U.S.A.). This area is one of the last remaining refuges for Kauaʻi's native forest birds. Seed traps and seedling emergence plots were set in areas with and without rodent control, and seed rain, fruiting density, and seedling emergence were monitored at and adjacent to these plots from February - June 2024. We found no difference in seed rain, seedling emergence, or fruiting density inside and outside of areas of rodent control. These findings suggest that, at least at current levels of rodent control, this management action has not significantly influenced forest regeneration processes in the Alakaʻi Wilderness Preserve. If these findings are consistent at higher, more sustained levels of rodent control, it may be beneficial to focus conservation funds on reducing or eradicating other invasive taxa, such as ungulates and plants, to improve native forest bird habitat on Kauaʻi.

INTRODUCTION

Rats are often considered a major threat to island biodiversity, due to their ability to adapt to and exploit diverse environments (Keitt et al. 2015). They are agile, have a high reproductive rate, can exist in many different types of habitats, and are omnivorous and opportunistic foragers that are able to exploit most food resources (Witmer et al. 2014, Harper and Bunbury 2015, Duron et al. 2017a). Higher rainfall and primary productivity found in insular ecosystems may also lead to higher densities in rat populations due to an abundance of food resources throughout the year (Harper and Bunbury 2015). Their ability to establish and invade new areas is further enabled by the frequent absence of competition, because islands are often too isolated to have native mammal populations (Doherty et al. 2016). Invasive rats can change the trophic structures of communities, and this may lead to negative indirect impacts on the species that rely on these ecological processes (Ringler et al. 2015) and play a role in maintaining them (Mäntylä et al. 2011).

Rats consume all stages of plants from seeds to adults (Wolf et al. 2018), and over half of the diet of rats often consists of plant material (Harper and Bunbury 2015). Seeds and seedlings are preferred over other plant parts, likely due to the higher energy and nutrient concentration of seeds. Predation of seeds is likely the biggest influence that rats inflict on forest composition and structure in ecosystems. Rats can disrupt bird-mediated seed dispersal by destroying the seeds of plants past the point of viability (Grant-Hoffman and Barboza 2010). The high reproductive potential of rats (Witmer et al. 2014) combined with their voracious feeding habits can lead to overconsumption of native seed banks and seedlings (Harper and Bunbury 2015) thus playing a role in seed dispersal limitation (Kaushik et al. 2018) and diminished recruitment of native plants (Grant-Hoffman and Barboza 2010, Shiels and Drake 2011, Harper and Bunbury 2015), contributing to a form of invasional meltdown (Simberloff 2006).

Rat removal can help restore and maintain plant community composition and ecosystem function (Grant-Hoffman et al. 2010). For example, rats were identified as one of the top reasons for lack of recruitment of an extremely endangered Hawaiian plant hau kuahiwi (*Hibiscadelphus giffardianus*). After rat removal the mean retention of fruit for the plant was more than doubled from pre-treatment levels (Gill et al. 2018). On Palmyra Atoll, seedling recruitment increased for five out of six native tree species that were studied after the eradication of rats from the island (Wolf et al. 2018). Similarly, on the island of Oahu in Hawaiʻi, an endangered native palm (*Pritchardia kaale*) went from almost zero juveniles to close to 1,600 individuals in only a few years after goats were removed and rats were suppressed. On Breaksea Island in Fiordland, New Zealand, where rats were responsible for declines in recruitment of Nothofagus and other tree and shrub species, forests saw an increase in the number of seedlings following rat removal (Allen et al. 1994).

Studying changes in forest health following rat control can provide valuable information about the effect of introduced predators on trophic interactions. The objective of this study was to assess how invasive rodent control affects habitat structure and resource availability for Kauaʻiʻs native forest birds in the Alakaʻi Wilderness Preserve. To do this, I evaluated the relationship between rodent control and three forest regeneration processes that contribute to food and habitat availability for forest birds: fruit density, seed rain, and seedling emergence. The results of this study could help guide management actions to improve quality for Kauaʻi's forest bird populations, and other island communities facing similar threats.

METHODS

Study Area

This study was located in the Alakaʻi Wilderness preserve on Kauaʻi Island, Hawaiʻi (U.S.A). The preserve is a wet montane forest that contains some of the most intact native forest on the island and serves as a refuge and sanctuary for many of the islands' remaining native flora and fauna. The Kauaʻi Forest Bird Recovery Project (KFBRP) established two areas within the preserve to control rat populations with self-resetting Goodnature A24 rat traps (http://goodnature.co.nz). My research questions were addressed in one of these areas, Halepaʻakai (HPK; **Figure 2.1**) from February - June 2023. Halepaʻakai was chosen because it is the only site that includes areas with and without rodent control that is also fenced to exclude non-native ungulates (e.g., feral pigs (*Sus scrofa*)). Ungulates disturb the soil surface and consume plants, affecting seed emergence and seedling survival (Hart et al. 2020). The rodent control grid has approximately 164 traps and has been operating continuously since March 2015. Previous research in this study area have used tracking tunnels as a proxy for relative abundance and have shown that relative rat abundance is substantially lower on the rat grid compared to areas without rodent control (Crampton et al. 2022).

Halepaʻakai is at an elevation of ~1300m with an average rainfall of 13m per year. The dominant vegetation at this study site is ʻōhiʻa lehua (*Metrosideros polymorpha*) in the canopy and lapalapa (*Cheirodendron platyphyllum*), ʻōlapa (*Cheirodendron trigynum*), ʻōhiʻa hā (*Syzygium sandwicensis*), kāwaʻu (*Ilex anomala*), alani (*Melicope spp.*), and manono (*Kadua terminalis*) in the canopy and sub-canopy. The understory has various other native woody plants such as pilo (*Coprosoma spp.*), pūkiawe (*Styphelia tameiameiae*) ʻukiʻuki (*Dianella sandwicensis*) hāhāʻaiakamanau (*Clermontia fauriei*) ʻōhelo (*Vaccinium calycinum*), and ʻohe naupaka (*Scaevola glabra*). Prominent invasive plants are himalayan ginger (*Hedychium gardnerianum*), blackberry (*Rubus argutus*), thimbleberry (*Rubus parviflorus*) and strawberry guava (*Psidium cattleianum*) (Foster et al. 2004, Kaushik et al. 2018, Fricker et al. 2021).

Study Design

Six sites were selected within the study area to collect data on fruiting density, seed rain, and seedling emergence. These sites were chosen to be somewhat evenly distributed and to be complimentary with a concurrent study on forest bird health and demographics (Chapter 1). Three of these sites were located within the rodent control grid, and three were located outside of the grid (**Figure 2.1**); hereafter referred to as the trapping and reference areas respectively. The center of each of the six sites were at least 200m away from the next nearest site to ensure independence (Lieberman et al. 1996, Aplet et al. 1998, Inman-Narahari et al. 2013)

Tree and Fruit Density

To assess the density of fruiting plants, the number of fruiting trees of each species and estimated fruit density within a 5m radius of each seed trap was recorded. To reduce observer bias, the number of ripe fruits on a single branch or bunch was counted as a unit index and then a tally counter was used to estimate the number of each of the estimated units of fruits on each tree. The total number of fruits on each fruiting plant was then extrapolated using those numbers. To assess the fruiting density for comparison in trapping and reference plots these extrapolated numbers were used for analysis. The height, maximum width, and length of the fruiting tree was recorded to obtain the estimated total size of the tree in m^3. This was used to account for the size of the plant in relation to local fruiting density in analyses. All observations were performed by a single observer to reduce bias.

Seed Rain

At each of the six sites, four seed traps were installed for a total of 12 seed traps within the trapping area and 12 within the reference area (n=24 traps). Every seed trap was placed at least 20m away from the next (**Figure 2.2, Appendix**). Following established methods (Marques

& Oliveira 2008, Rose et al. 2017, Matsuoka 2020), each seed trap was composed of a mesh basket with a diameter of 1m. Baskets were lined with a silkscreen to catch all seeds >1mm and the basket was tied to trees in the canopy to capture the seed rain in the forest (**Figure 2.3, Appendix**). All traps were hung at a height of 3m, and the bottom of the trap was secured with a string to the ground to prevent the trap from flipping over during strong wind events. All plants with fruiting bodies within a 5m radius from each seed trap were noted and the fruiting density of these plants were calculated. Traps were checked every 4-6 weeks depending on weather and logistics. Upon checking these traps the contents were collected, labeled, and stored in a bag while in the field. Once the bags were removed from the field, the samples were stored in a freezer on Kaua'i, and then taken back to Colorado State University to be dried, examined under a light microscope, and sorted. Where possible, seeds were identified to the lowest taxonomic level using a seed library for Hawaiian plant species (Kingsley et al. 2022).

Seed Emergence and Survival

Three 1x1m seedling emergence plots were placed randomly within a 100 m radius from the center of each of the six sites in July 2022 (**Figure 2.4, Appendix**). Plots were placed in areas under closed canopy, avoiding gaps to ensure consistent light conditions. Each 1x1m plot was cleared of all vegetation upon establishment. Plots were visited again in June of 2023, approximately one year after the initial clearing. The 1x1m plot was then split into nine smaller even sections and pictures of each subsection were taken. Pictures were screened and all seedlings in each subsection were counted. It was not possible to identify seedlings to species given their size (5-20mm) and lack of defining characteristics.

Data Analysis

Fruiting density

To assess whether rat control influences fruiting density in this study system, the total estimated count of fruit per each fruiting plant was logged. Overdispersion was detected in this data therefore a negative binomial GLMM was used with the estimated fruit count as the response variable, and a dichotomous explanatory variable indicating whether the plot was on or off the rodent control grid as a fixed effect. The site ID, the size of the plant canopy in m^3, and the plant species were included as fixed effects to account for individual differences in each plot and the overall plant biomass in the area and to avoid pseudoreplication. The plant species was included as a random effect to account for individual size and species-specific differences in counts. All data analysis for forest regeneration studies was performed using the RStudio version 4.3.2 (R Core Team 2023). All models were fit using the lme4 package (Bates et al. 2015).

Seed rain

To evaluate whether rat control influences seed rain, the total number of seeds, whole fruits, and partial fruits collected per seed rain trail were totaled and then divided by the total number of trap days. This resulted in a daily dispersal rate which was then multiplied by 100 to calculate the rate of dispersal per 100 days. This rate of dispersal was compared between treatment and control plots. The data were not sufficient to fit a mixed model that included site specific differences. The residuals of the seed rain dispersal rates within individual sites were then observed to determine if there were significant differences in seed rain within each site. This was determined to not be the case therefore the site was not included as a random effect. For these analyses, I employed a negative binomial GLM with either the seed, whole fruit, or partial fruit dispersal rate as the dependent variable, and whether the seed trap was located on the trapping or reference plot as the independent variable. Underlying assumptions for a negative binomial GLM assumes that the response variable is an integer, so the dispersal rates were rounded to the nearest integer before model fitting.

Seedling emergence

To evaluate the response of seedling emergence to rat control in the Alaka‘i Wilderness Preserve, the amount of seedling recruitment approximately 11 months after the initial plot clearing was calculated. The total number of seedlings that appeared over the 11 months were counted and these values were compared within and outside of the rodent control area. Total emerged seedlings for each subsection of each plot were counted and logged. Due to overdispersion in the data, I chose to use a negative binomial GLMM with the emerged seedling count as the response variable, and a binomial explanatory variable indicating whether the plot was on or off the rodent control grid as a fixed effect. The plot ID was included as a random effect to account for individual differences in each plot and to avoid pseudoreplication.

RESULTS

Fruiting Density

The mean fruiting density for trapping areas was 435.0 fruits ± 555.1 (SD) and the mean fruiting density for reference areas was 404.5 fruits ± 527.1 (SD) (**Figure 2.5**). The analysis showed no evidence that fruiting density was influenced by rodent control (Incidence Rate Ratio = 1.01, CI = 0.77-1.31, p = 0.966, $\sigma^2 = 0.81$, Marginal $R^2 = 0.000$).

Seed Rain

Most (94%) of the seeds, and all the fruits, and partial fruits in seed traps were of the *Cheirodendron* genus, but we were unable to confidently identify these seeds or fruits to species. Because all fruits and partial fruits were of this genus, the analysis of fruits and partial fruits only reflect *Cheirdendron* dispersal rates. Two separate analyses were employed for seed dispersal. One for total seed dispersal rate and the other for *Cheirodendron* seed dispersal rates. The mean seed dispersal rate for all species in the trapping area was 2.16 ± 2.85 (SD) seeds per 100 days in the trapping areas and 2.47 ± 3.66 (SD) seeds per 100 days in reference areas. The mean seed dispersal rate for *Cheirodendron* in the trapping area was 1.40 ± 2.49 (SD) seeds per 100 days and 2.02 ± 3.39 (SD) in the reference area. The mean *Cheirodendron* whole fruit dispersal rate was 4.67 ± 7.76 (SD) fruit per 100 days in the trapping area and 2.86 ± 7.53 (SD) fruit per 100 days in the reference area. The mean *Cheirodendron* partial fruit dispersal rate was 3.31 ± 5.38 (SD) partial fruit per 100 days in the trapping area and 4.20 ± 13.39 (SD) partial fruit in the reference area (**Figure 2.6**). Our model results provide no evidence of an effect of rodent control on total seed dispersal rate (Incidence Rate Ratio = 0.83, CI = 0.28-2.44, p = 0.74, R^2 Nagelkerke = 0.007), *Cheirodendron* specific seed dispersal rate (Incidence Rate Ratio = 0.65, CI = 0.16-2.63, p = 0.54, R^2 Nagelkerke = 0.025), *Cheirodendron* whole fruit dispersal (Incidence Rate Ratio = 1.63, CI = 0.28-9.46, p = 0.57, R^2 Nagelkerke = 0.022), or *Cheirodedron* partial fruit dispersal (Incidence Rate Ratio = 0.80, CI = 0.07-8.76, p = 0.84, R^2 Nagelkerke = 0.007).

Seedling Emergence

I found no strong evidence for an effect of rodent trapping on seedling emergence. The mean number of seedlings that emerged was 3.80 ± 5.27 (SD) in trapping areas and 2.29 ± 2.67

(SD) in reference areas (**Figure 2.7**) (Incidence Rate Ratio = 1.61, CI = 0.79-3.30, p = 0.19, σ^2 = 0.76, Marginal R^2 = 0.047).

DISCUSSION

Invasive rodents contribute to a large proportion of population declines and extinctions globally, with particularly acute effects on island biodiversity (Wolf et al. 2018). Invasive rats predate on fruits, seeds and seedlings (Shiels and Drake 2011, Harper and Bunbury 2015), which can limit forest regeneration and reduce habitat quality for other native taxa (Allen et al. 1994, Courchamp et al. 2003, Wolf et al. 2018). Controlling invasive rodents through self-resetting traps is a promising approach for reducing rat abundance in remote island systems. Such efforts are often focused on reducing predation on native fauna, with secondary consequences for forest regeneration less well understood. In this study, we found no evidence of differences in seed rain, fruiting density, or seedling emergence in areas with or without rodent control in the Alaka'i Wilderness Preserve, the last remaining refuge for Kaua'i's native forest birds. These findings suggest that either rats are not a major limiting factor for forest regeneration in this system, or that current levels of rodent control are not sufficient for restoring ecological processes.

Rats have been implicated as a significant pre-dispersal predator of many plant species. Other studies have shown effects of invasive rodents on fruiting density of plants before and after experimental control of rodent populations or after the introduction of rats to an island (Hutton et al. 2007, Athens 2008, Shiels and Drake 2011, Pender et al. 2013, Gill et al. 2018). For example, the invasion of the Canary Islands by black rats (*Rattus rattus*) diminished the fruit availability of *Viburnum tinus* fruits for birds, destroying most of the seeds in the process (García 2002). On Oahu, Hawai'i, rats consumed about half of all ripe fruits of a population of an endangered Hawaiian lobeliad (*Cyanea superba*), but in areas where rodent control was implemented only 4% of fruits were consumed (Pender et al. 2013). Yet, our results suggest that fruiting density in the Alaka'i Wilderness Preserve may not be limited by rodents. There are several possible explanations for this finding. First, some fruiting species of plants are adapted to produce an abundance of fruit to compensate for predation (Crawley 2014). About 90% of the fruiting trees that were recorded in our fruiting density surveys were *Cheirodendron* spp, and this genus also accounted for the largest portion of fruiting plants in the overstory in all study areas. If *Cheirodendron* spp. uses high fruit production to overcome predation, then we may not expect to see a significant difference of fruit in trapping and reference areas. Second, some plants also escape predation by rats due to traits such as palatability to rats or nutrient content (Grant-Hoffman and Barboza 2010), but it is not known if rats select for or against *Cheirodendron* spp. Lastly, birds also play a major role in fruit consumption and dispersal in Hawaiian forests (Foster and Robinson 2007, Kaushik et al. 2018, Matsuoka 2020) and rats have been found to influence bird populations by preying on eggs, chicks, and even adult birds (Fontaine and Martin 2006, Reidy et al. 2009). If rats are significantly influencing bird mortality in areas without rodent control, we may expect that fruit consumption in areas with rodent control would be replaced by frugivorous bird species (García 2002, Kaushik et al. 2018, Bombaci et al. 2021).

Rats consume fruit and seeds directly from trees and shrubs as well as the forest floor, which can affect plant regeneration rates and forest composition (Grant-Hoffman and Barboza 2010) and through reduced fruit availability, also hamper seed dispersal services provided by birds (García 2002). Conversely, rats can also act as seed dispersers, particularly for small-seeded species (La Mantia et al. 2019; Shiels & Drake 2011). However, all the seeds collected in this study system were >5mm, which suggests that the seeds collected were bird rather than rat dispersed. In contrast, the partial fruits collected in traps were likely to have been predated by rats. It is possible that the lack of difference in rat-predated seeds between trapping and reference areas indicates that trapping is not occurring at sufficiently high densities to reduce seed predation by rats or influence bird-mediated seed dispersal.

As with fruit density and seed rain, we found no effect of rodent control on seedling emergence. Seedling recruitment for these plant species in the Alakaʻi Wilderness Preserve may not be limited by rodents, and removal of invasive ungulates may be sufficient to sustain forest regeneration. Although rodents have been shown to reduce seedling abundance in other systems (Wolf et al. 2018), it is possible that rats are not major herbivores of young seedlings on Kauaʻi. Instead, rats, which are generalists (Courchamp et al. 2003), may prefer other food sources such as invertebrates, herbaceous plants, or bird eggs and chicks. Further, other studies have shown that large mammals can be more detrimental to seedling recruitment than small rodents in some systems (Courchamp et al. 2003, Shiels and Drake 2015, Hart et al. 2020). For example, DeMattia et al. (2006) found that large and small-bodied mammals had negative but differential effects on seedling recruitment in a tropical forest in Costa Rica. Of 22 plant species in the seedling recruitment plots, only one species was significantly affected by small rodents, and all others were negatively affected by large mammals. If large ungulates are the major limiting factors in seedling recruitment in montane Kauaʻi, we may not see any variation in seedling recruitment in trapping and reference areas at Halepaʻakai, because ungulates have already been removed from this area.

Conservation Implications and Priorities for Further Research

Many previous studies have shown that rats impact regeneration processes of multiple species of Hawaiian plants, but these species are often rare, threatened, or declining (Pender et al. 2013, Shiels and Drake 2015, Wolf et al. 2018, Gill et al. 2018). When choosing locations for seed traps and germination plots, an effort was made to avoid areas with potentially sensitive species of plants. Therefore, our inference was limited to species that are widespread and abundant in the Alakai Wilderness Preserve. If rats prefer plant species that are already less abundant, potentially due to higher palatability (Grant-Hoffman and Barboza 2010), it is less surprising that we would not detect differences in seed rain, fruiting density or seedling emergence for common species. Future studies that focus on evaluating the effects of rat control on threatened plants in this system could provide new insight. Additionally, rats consume a variety of resources other than plant material and other food resources may comprise a considerable proportion of the diet of rats in Hawaiʻi (Sugihara 1997). In a study on Maui which classified the stomach contents of black rats (*Rattus rattus*) and Polynesian rats (*Rattus exulans*), invertebrates were the most common food item in rat stomach contents. However, the relative abundance of invertebrates to other food types for Polynesian rats was 83.1% while black rat stomach contents averaged only 39.5% invertebrates (Sugihara 1997). Plant material, including fruits and seeds, were the next most common food group in rat stomach contents. However, two studies of Polynesian rats on Kure Atoll and Eniwetok Atoll found that that rats diet consisted of 62% and 92% plant material respectively (Wirtz 1972, Harper and Bunbury 2015). Most of the rats trapped in our study system are black rats, but the diet of this population has not yet been assessed. It is possible that black rats in montane Kauaʻi consume primarily invertebrates and vertebrates; if so, the direct effect of rodent control on plant populations would be expected to be marginal.

Alternatively, the levels of rodent control in this area may be insufficient to see change in any of the tested forest regeneration processes. Crampton et al. (2022) found that rats were detected on 0-9% of tracking tunnels in the rodent control grid and on 35-50% of tracking tunnels in the control grid. Although these findings indicate that rat populations in rodent controlled areas were reduced, the complete eradication of rodents has been shown to be more effective in mitigating the negative impacts from rats compared with population suppression alone (Keitt et al. 2015, Spatz et al. 2022). Wolf et al. (2018) found an increase in recruitment of several native tree species on Palmyra Atoll following eradication of rats from the island. It is possible that even at lower population levels, the rats in trapped areas may be affecting seed rain, recruitment, and fruiting density enough to have an indistinguishable effect on these processes when compared to reference areas. Eradication of rodents would be extremely difficult, if not impossible, on Kauaʻi due to the size of the island, expense, potential impacts on non-target species, potential for recolonization from other islands, and public perception of rodenticide use (Glen et al. 2013, Pejchar et al. 2020). An increase in rodent control intensity and diversification in the types of rodent controls used in the forest may prove successful in reducing rodent populations, but the maintenance and costs of supplies and equipment for these management measures are often non-trivial (Duron et al. 2017b). Given the costs of rodent control, more research on the role of invasive rodents and the effectiveness of rodent control (rather than eradication) in restoring ecological processes is warranted before spending limited conservation funds on trapping in this system. Removal of invasive ungulates has been shown to have positive effects on forest regeneration in Hawaiian forests and this alone may be sufficient to restore ecosystem functioning (Camp et al. 2010, Shiels and Drake 2015, Hart et al. 2020).

In this study system, there may be no significant effect of rodent control on forest regeneration processes, but it is important to note that this study only reflects data obtained from a single year, a single site, and only a portion of the fruiting season for fruiting density and seed rain. The length of this study may be insufficient to detect differences in these forest regeneration processes as a result of rodent control, and replication of this study in multiple similar sites is warranted. A limitation to the seedling emergence portion of this study is that the seeds of many native Hawaiian plants have low germination rates (Cordell 2009, Matsuoka 2020). Year-round and multi-year studies could provide better information on forest regeneration processes and would provide more confidence in our results.

Rodent control is often effective, and sometimes critical, for conserving and restoring populations of rare and endangered plant species on islands (Pender et al. 2013, Shiels and Drake 2015, Wolf et al. 2018, Gill et al. 2018). Yet, we found little evidence that rodent control affects forest regeneration processes for common plant species in Kaua‘i’s montane forests. If future research supports these findings, focusing management on removing invasive plants and ungulates might be more effective at sustaining forest ecosystems for Kaua‘i’s rarest birds.

TABLES AND FIGURES

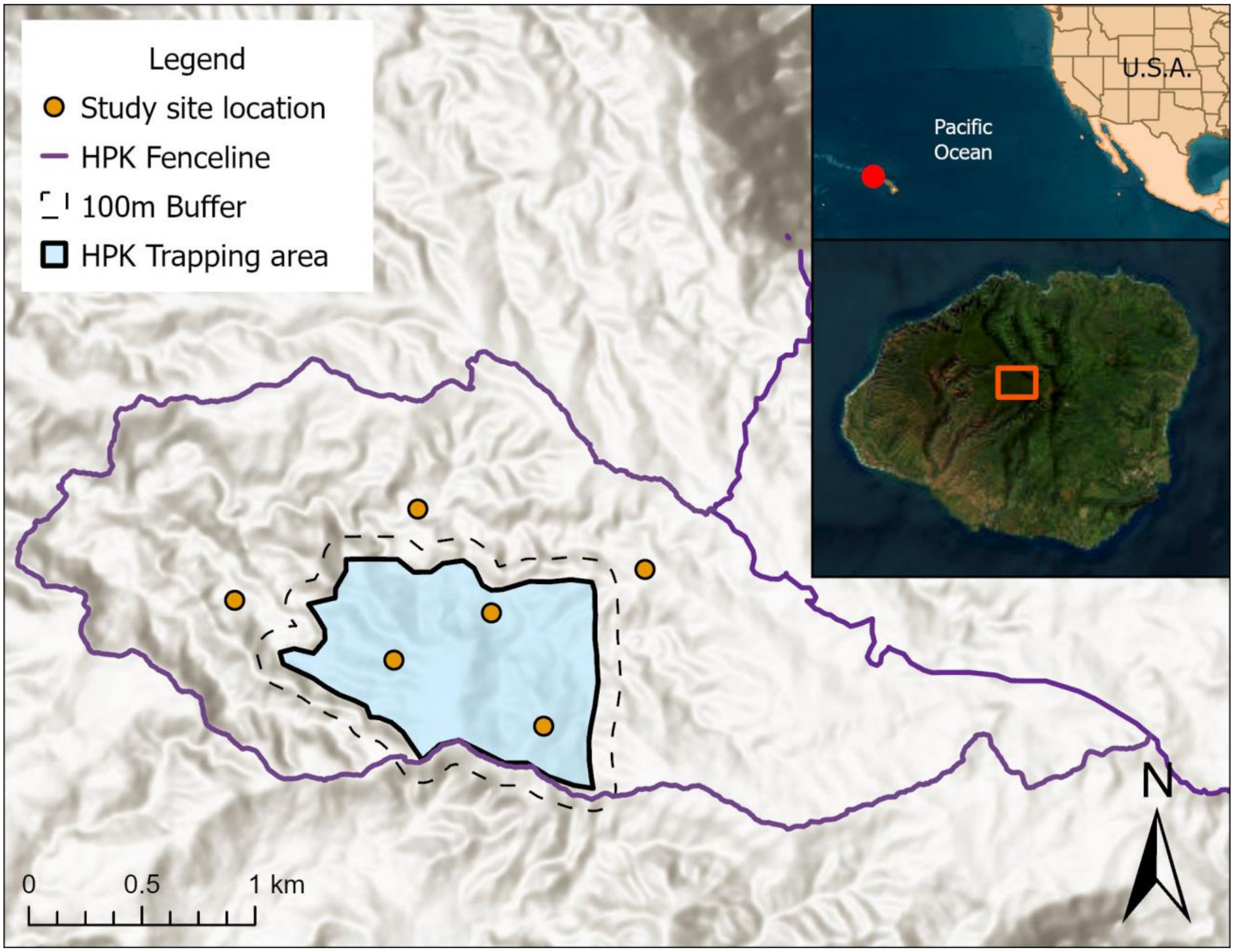

Figure 2.1. The study location (Halepa‘akai) in the Alaka‘i Wilderness (Kaua‘i, Hawai‘i, U.S.A.) where forest regeneration studies occurred in the presence and absence of rat trapping. The purple line shows the fencing that excludes non-native ungulates, and the blue area shows the rodent control area. Orange dots indicate the six sites where fruit density, seed rain and seedling emergence were measured; three sites are located within the rodent trapping plot and three sites located outside of the trapping plot.

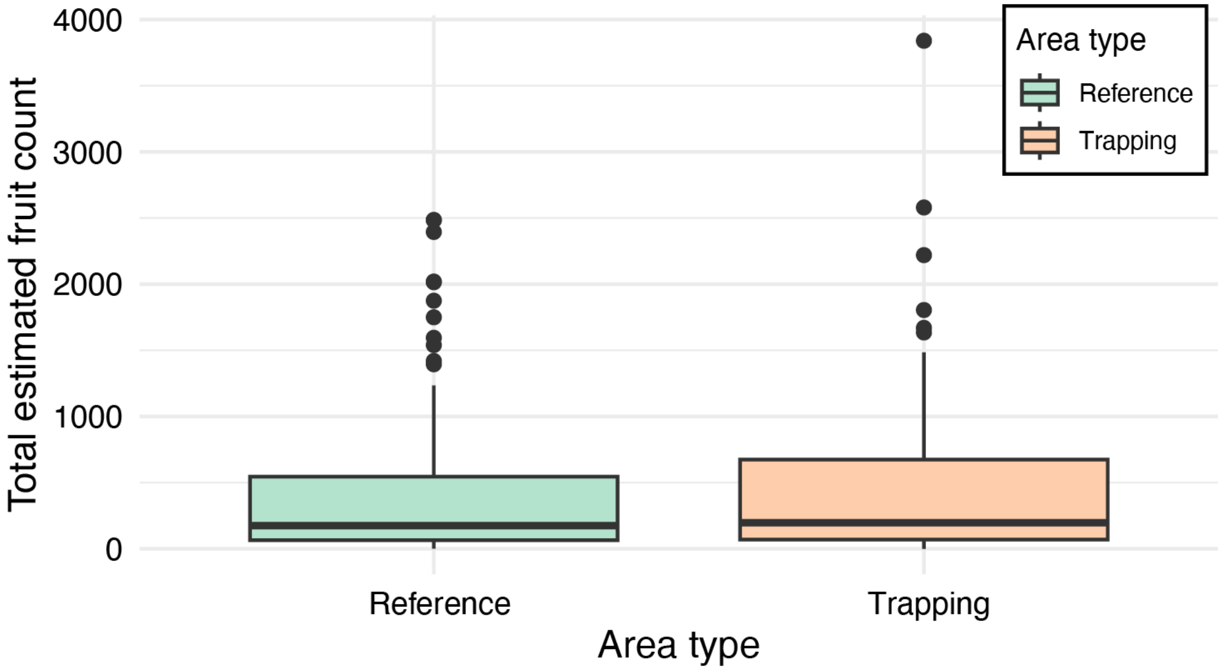

Figure 2.5. Boxplots showing the relationship between mean fruiting density in rat trapping and references areas in the Halepaʻa kai study area on Kauaʻi, Hawaiʻi (U.S.A.).

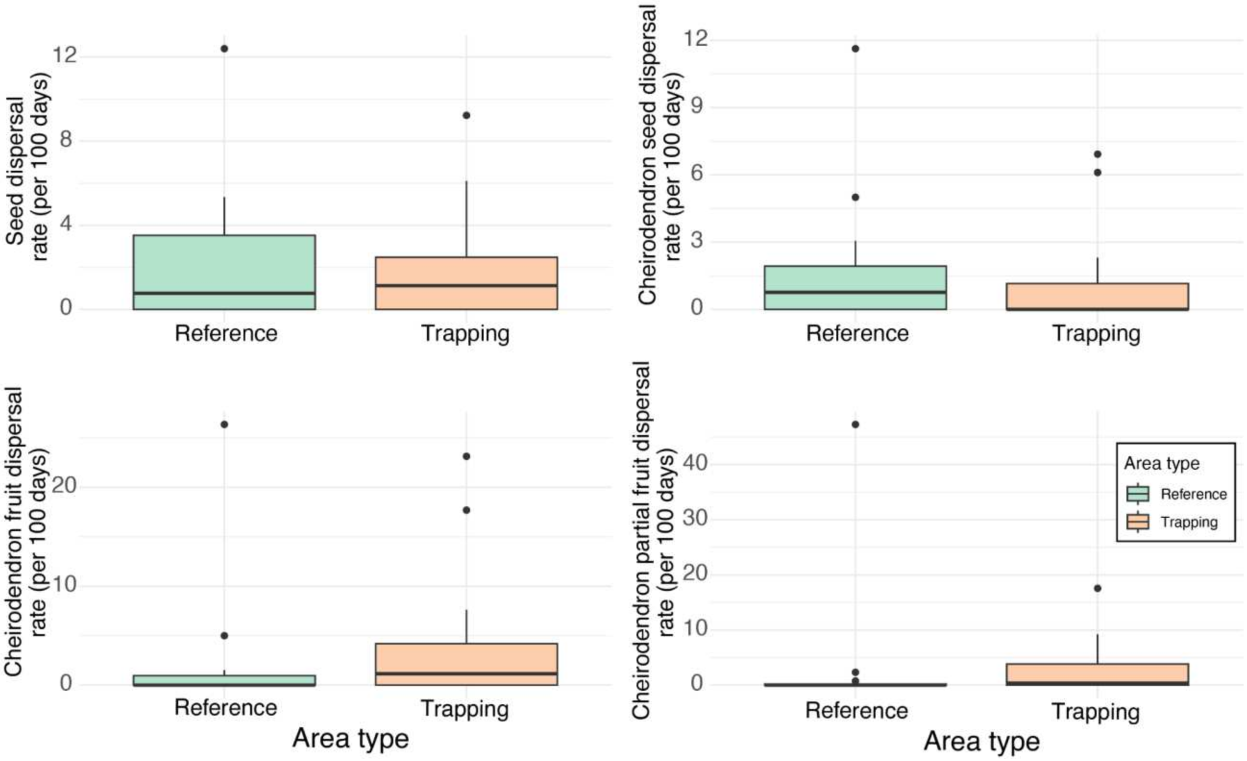

Figure 2.6. Boxplots showing relationships between seed, fruit, and partial fruit dispersal rates from seed rain traps in sites with rat trapping and references sites in the Halepaʻa kai study area on Kauaʻi, Hawaiʻi (U.S.A.).

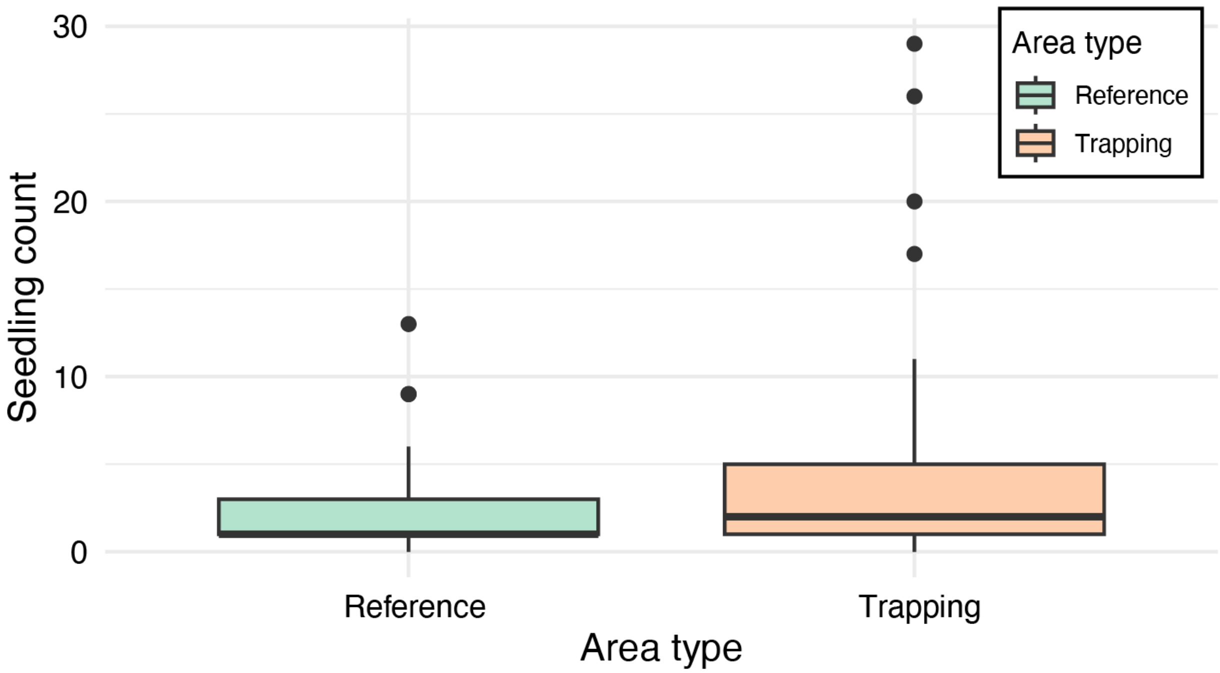

Figure 2.7. Boxplots showing the relationship between seedling emergence in rat trapping and reference sites in the Halepaʻa kai study area on Kauaʻi, Hawaiʻi (U.S.A.).

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APPENDIX

Table 1.1. Focal bird species, and major life history characteristics, used to evaluate the effect of rat control on body condition and demography. *The average weight for male Kauaʻi ʻAmakihi is unknown. Weight provided is the average weight of an after-hatch year bird with sex unknown. **No information on mean nest height exists for Kauaʻi ʻElepaio. Data was taken from information on Hawaiʻi ʻElepaio (*Chasiempis sandwichensis*). ***Mass for males is not available. Weight provided is for after hatch year birds with males and females combined. These data were extracted from Birds of North America accounts (Lepson 2020, Lindsey et al. 2020, Snetsinger et al. 2020, VanderWerf 2020, Van Riper & Van Balen 2020)

Species	 **Kauaʻi ʻAmakihi**	 **ʻAnianiau**	 **Kauaʻi ʻElepaio**	 **Warbling White-Eye**
Scientific Name	*Hemignathus kauaiensis*	*Hemignathus parvus*	*Chasiempis sclateri*	*Zosterops japonicus*
Family	Fringillidae	Fringillidae	Monarchidae	Zosteropidae
IUCN Status	Vulnerable	Vulnerable	Vulnerable	Least Concern
Native / Introduced	Native	Native	Native	Introduced
Diet	Insects, grubs, caterpillars, nectar, berries, and fruit	Arthropods, nectar, rarely fruit	Arthropods	Variety of insects, fruit, nectar

Avg. Weight (Male)	16.9g	10g	12.9g*	11.25g
Avg. Clutch Size	2.5	3.04	2	3
Avg. Nest Height	5.6 m	6 m	Extremely variable, 6.2-12.0 m**	Variable, 3.27-5.89 m
Foraging `Habitat	Crown, and bark foraging, trunks and limbs of large trees of ‘ōhi‘a and other large trees. Also feeds among leaves and flowers	Flowers, outer canopy foliage, twigs of ‘ōhi‘a and koa, and various shrubs, fern fronds	Highly variable. Uses wide variety of plant species and substrates	All vegetation at all heights and densities, particularly in subcanopy of forest

Table 1.3. Model comparison and descriptive statistics for top models for top models predicting sex. Top models are models that were within 2 AICc of the lowest AICc model. * No models were within 2 AICc of the intercept only model for Kaua‘i ‘Elepaio.

Species	Distance	Term	Estimate	Standard Error	95% CI (low)	95% CI (high)	AICc
Kaua‘i ‘Amakihi	150	(Intercept)	-0.3042	0.3488	-1.0060	0.3743	77.14
		Rodent Control	-0.0739	0.0473	-0.1735	0.0147	77.14
		(Intercept)	-15.1073	9.9039	-35.6041	3.8537	77.56
		Julian Date	0.0007	0.0005	-0.0002	0.0016	77.56
		(Intercept)	-13.4587	10.1100	-34.2754	6.0080	77.61
		Rodent Control	-0.0683	0.0478	-0.1683	0.0219	77.61
		Julian Date	0.0006	0.0005	-0.0003	0.0015	77.61
		(Intercept)	-0.6678	0.2750	-1.2260	-0.1411	77.63
	300	(Intercept)	-0.2063	0.3626	-0.9322	0.5028	76.22
		Rodent Control	-0.0298	0.0167	-0.0652	0.0011	76.22
		(Intercept)	-12.1570	10.2136	-33.1174	7.5825	77.04
		Rodent Control	-0.0266	0.0168	-0.0622	0.0047	77.04
		Julian Date	0.0005	0.0005	-0.0004	0.0015	77.04
		(Intercept)	-15.1073	9.9039	-35.6041	3.8537	77.56
		Julian Date	0.0007	0.0005	-0.0002	0.0016	77.56
		(Intercept)	-0.6678	0.2750	-1.2260	-0.1411	77.63
‘Anianiau	150	(Intercept)	-0.3054	0.3522	-1.0149	0.3797	60.09
		Malaria (Positive)	-1.3041	0.8509	-3.2770	0.2148	60.09
		(Intercept)	-0.5947	0.3114	-1.2281	0.0024	60.67
	300	(Intercept)	-0.3054	0.3522	-1.0149	0.3797	60.09
		Malaria (Positive)	-1.3041	0.8509	-3.2770	0.2148	60.09
		(Intercept)	-0.5947	0.3114	-1.2281	0.0024	60.67

Kaua‘i ‘Elepaio*	150 + 300	(Intercept)	-0.5261	0.2020	-0.9300	-0.1357	140.58
Warbling White-eye	150	(Intercept)	-9.2330	5.6785	-20.6107	1.7614	194.80
		Julian Date	0.0004	0.0003	-0.0001	0.0009	194.80
		(Intercept)	-0.5836	0.1714	-0.9258	-0.2521	195.11
		(Intercept)	-10.3074	5.7971	-21.9340	0.9050	195.93
		Malaria (Positive)	0.3716	0.3792	-0.3766	1.1170	195.93
		Julian Date	0.0004	0.0003	-0.0001	0.0010	195.93
		(Intercept)	-0.6642	0.2080	-1.0823	-0.2639	196.68
		Malaria (Positive)	0.2587	0.3686	-0.4722	0.9788	196.68
		(Intercept)	-9.1221	5.6836	-20.5090	1.8836	196.75
		Rodent Control	0.0097	0.0268	-0.0433	0.0620	196.75
		Julian Date	0.0004	0.0003	-0.0001	0.0009	196.75
	300	(Intercept)	-9.2330	5.6785	-20.6107	1.7614	194.80
		Julian Date	0.0004	0.0003	-0.0001	0.0009	194.80
		(Intercept)	-0.5836	0.1714	-0.9258	-0.2521	195.11
		(Intercept)	-10.3074	5.7971	-21.9340	0.9050	195.93
		Malaria (Positive)	0.3716	0.3792	-0.3766	1.1170	195.93
		Julian Date	0.0004	0.0003	-0.0001	0.0010	195.93
		(Intercept)	-9.2353	5.6790	-20.6132	1.7607	196.66
		Rodent Control	0.0044	0.0094	-0.0142	0.0229	196.66
		Julian Date	0.0004	0.0003	-0.0001	0.0009	196.66
		(Intercept)	-0.6642	0.2080	-1.0823	-0.2639	196.68
		Malaria (Positive)	0.2587	0.3686	-0.4722	0.9788	196.68

Table 1.4. Model comparison and descriptive statistics for top models predicting body condition. Top models are models that were within 2 AICc of the lowest AICc model. * The null model for ANIA had an AICc score of 144.66, making it a similarly competitive model to all top models in this table and indicating that there is no strong evidence that these models are explaining differences in body condition for this species.

Species	**Distance (m)**	**Fixed Effect**	**Estimate**	**Standard Error**	**95% CI (low)**	**95% CI (high)**	**AICc**
Kaua'i 'Amakihi	150m	Intercept	52.55	14.42	24.30	80.81	283.39
		Temperature	-1.41	0.55	-2.50	-0.33	
		Malaria (Positive)	0.84	0.41	0.03	1.65	
		Intercept	53.59	14.87	24.44	82.74	283.94
		Temperature	-1.42	0.56	-2.52	-0.33	
		Malaria (Positive)	0.82	0.42	-0.01	1.65	
		TWI	-0.32	0.95	-2.18	1.53	
		Intercept	48.19	14.54	19.69	76.69	285.24
		Temperature	-1.24	0.56	-2.33	-0.14	
		Intercept	51.06	14.63	22.40	79.73	285.29
		Sex(M)	-0.28	0.40	-1.06	0.50	
		Temperature	-1.35	0.56	-2.45	-0.25	
		Malaria (Positive)	0.84	0.42	0.02	1.65	
	300m	Intercept	52.55	14.42	24.30	80.81	283.39
		Temperature	-1.41	0.55	-2.50	-0.33	
		Malaria (Positive)	0.84	0.41	0.03	1.65	
		Intercept	53.17	14.89	23.99	82.35	284.11
		Temperature	-1.42	0.56	-2.52	-0.32	
		Malaria (Positive)	0.84	0.42	0.01	1.66	
		TWI	-0.18	0.90	-1.94	1.58	

		Intercept	48.19	14.54	19.69	76.69	285.24
		Temperature	-1.24	0.56	-2.33	-0.14	
		Intercept	51.06	14.63	22.40	79.73	285.29
		Sex(M)	-0.28	0.40	-1.06	0.50	
		Temperature	-1.35	0.56	-2.45	-0.25	
		Malaria (Positive)	0.84	0.42	0.02	1.65	
‘Anianiau *	150m	Intercept	9.65	0.17	9.31	9.98	143.27
		Malaria (Positive)	-0.70	0.34	-1.38	-0.03	
		Intercept	11.51	1.37	8.83	14.19	143.35
		Malaria (Positive)	-0.76	0.35	-1.44	-0.09	
		TWI	-0.72	0.53	-1.75	0.31	
		Intercept	18.80	11.42	-3.58	41.19	144.93
		Temperature	-0.35	0.44	-1.21	0.51	
		Malaria (Positive)	-0.62	0.36	-1.33	0.09	
		Intercept	21.86	11.39	-0.47	44.19	144.98
		Temperature	-0.40	0.43	-1.24	0.45	
		Malaria (Positive)	-0.67	0.36	-1.38	0.04	
		TWI	-0.75	0.52	-1.78	0.28	
		Intercept	24.55	11.12	2.76	46.34	145.11
		Temperature	-0.58	0.43	-1.42	0.26	
	300m	Intercept	9.65	0.17	9.31	9.98	143.27
		Malaria (Positive)	-0.70	0.34	-1.38	-0.03	
		Intercept	10.61	1.67	7.33	13.89	144.41
		Malaria (Positive)	-0.71	0.35	-1.39	-0.03	
		TWI	-0.38	0.66	-1.68	0.91	

		Intercept	18.80	11.42	-3.58	41.19	144.93
		Temperature	-0.35	0.44	-1.21	0.51	
		Malaria (Positive)	-0.62	0.36	-1.33	0.09	
		Intercept	24.55	11.12	2.76	46.34	145.11
		Temperature	-0.58	0.43	-1.42	0.26	
Kaua‘i ‘Elepaio	150m	Intercept	47.47	11.02	25.87	69.07	411.70
		Temperature	-1.30	0.43	-2.14	-0.47	
		Intercept	50.04	11.39	27.71	72.37	412.59
		Temperature	-1.36	0.43	-2.20	-0.51	
		TWI	-0.45	0.53	-1.49	0.58	
	300m	Intercept	47.47	11.02	25.87	69.07	411.70
		Temperature	-1.30	0.43	-2.14	-0.47	
		Intercept	50.26	11.28	28.16	72.36	411.79
		Temperature	-1.34	0.43	-2.18	-0.51	
		TWI	-0.69	0.62	-1.91	0.54	
		Intercept	49.33	11.31	27.17	71.49	413.65
		Temperature	-1.29	0.43	-2.13	-0.44	
		Malaria (Positive)	-0.29	0.28	-0.84	0.27	
		TWI	-0.86	0.65	-2.12	0.41	
Warbling White-eye	150m	Intercept	45.69	7.89	30.23	61.15	548.94
		Temperature	-1.24	0.30	-1.82	-0.65	
		TWI	-0.75	0.45	-1.63	0.13	
		Intercept	42.45	7.76	27.24	57.67	549.79
		Temperature	-1.19	0.30	-1.77	-0.60	
		Intercept	35.69	8.82	18.41	52.98	550.15
		Temperature	-1.16	0.30	-1.74	-0.58	

		Canopy Density	0.10	0.04	0.02	0.19	
		TWI	-0.96	0.45	-1.85	-0.08	
	300m	Intercept	42.45	7.76	27.24	57.67	549.79
		Temperature	-1.19	0.30	-1.77	-0.60	
		Intercept	44.50	7.91	29.00	60.00	550.19
		Temperature	-1.21	0.30	-1.80	-0.63	
		TWI	-0.56	0.49	-1.52	0.39	
		Intercept	41.54	7.80	26.25	56.83	551.77
		Sex(M)	-0.26	0.23	-0.70	0.19	
		Temperature	-1.15	0.30	-1.74	-0.55	

Figure 1.2. Goodnature A24 rat trap with plastic blocker attached. These traps were used to control rats in the treatment plots. Each plastic blocker was secured via zip ties to the opening of the trap to prevent non-target kills. Photo property of KFBRP.

Figure 1.3. Tracking tunnels were used to measure relative rat abundance in control and treatment plots. Relative abundance was measured by tracking the presence or absence of rat footprints using a track pad (a), which was baited with peanut butter (b) and placed on the forest floor (c). Photos property of KFBRP.

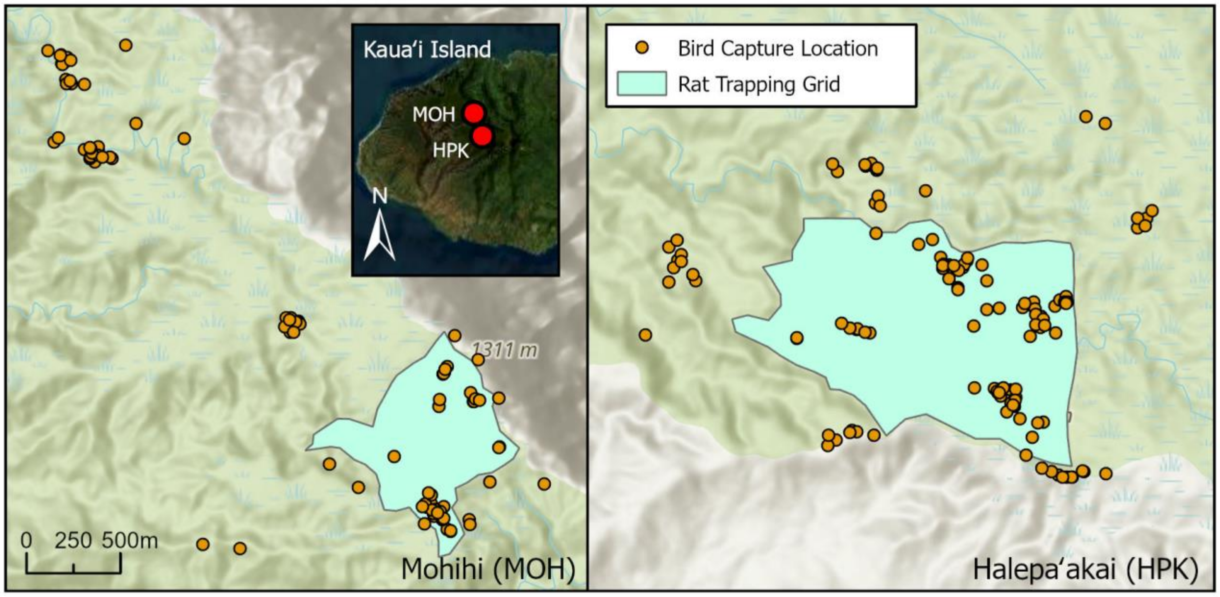

Figure 1.4. Orange circles mark the capture locations of birds for this study. The solid green indicates the extent of the grid containing rodent traps on the landscape. Birds were captured in the Alaka‘i Wilderness Preserve on Kaua‘i Hawai‘i.

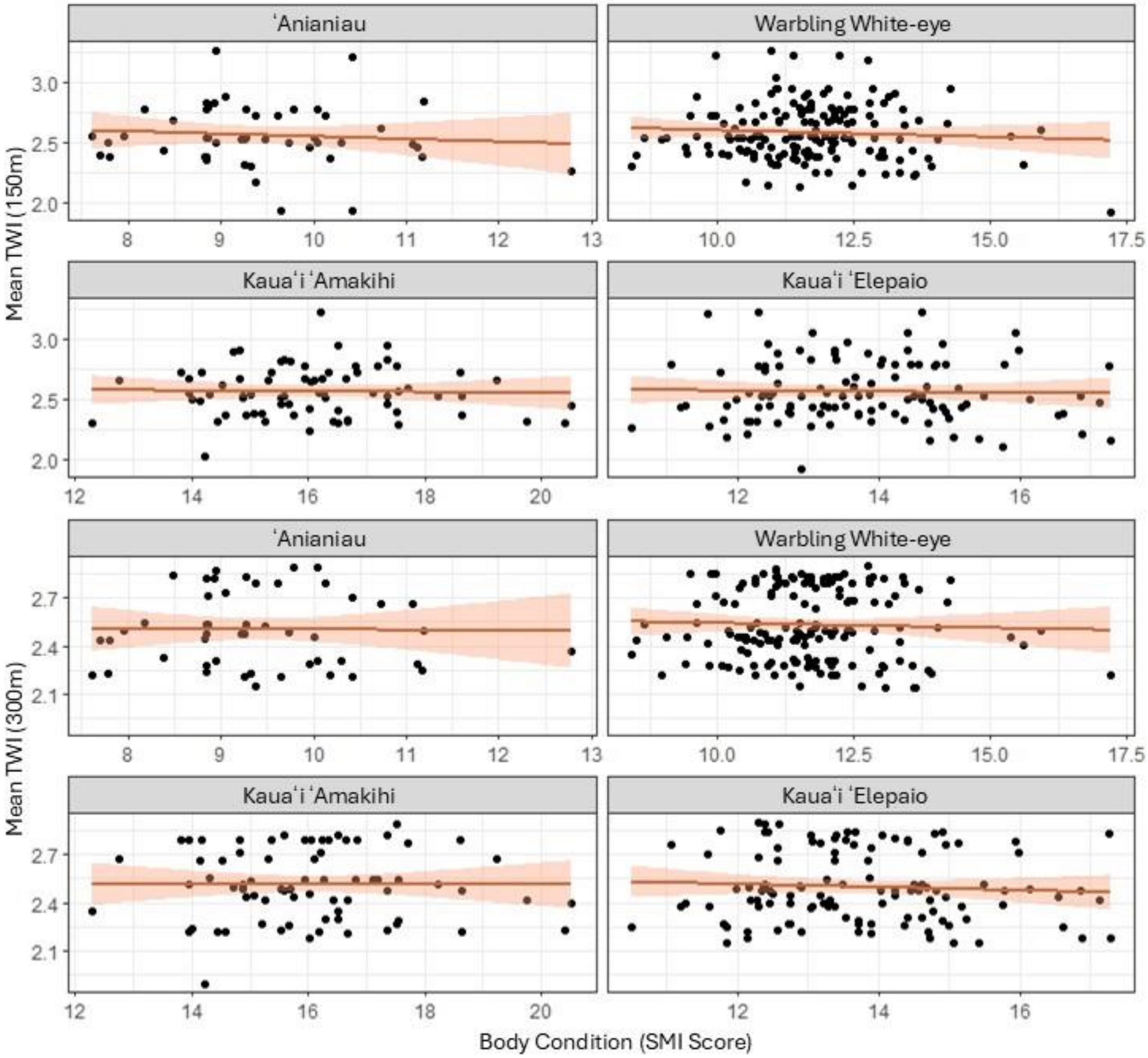

Figure 1.8. Relationship between body condition (SMI Score) and the average topographic wetness index (TWI) surrounding the area of a birds capture location at 150m and 300m for four focal bird species in the Alakaʻi Wilderness Preserve, Kauaʻi, Hawaiʻi. The solid lines represent the linear trend between body condition and temperature, with shaded areas indicating the 95% confidence intervals.

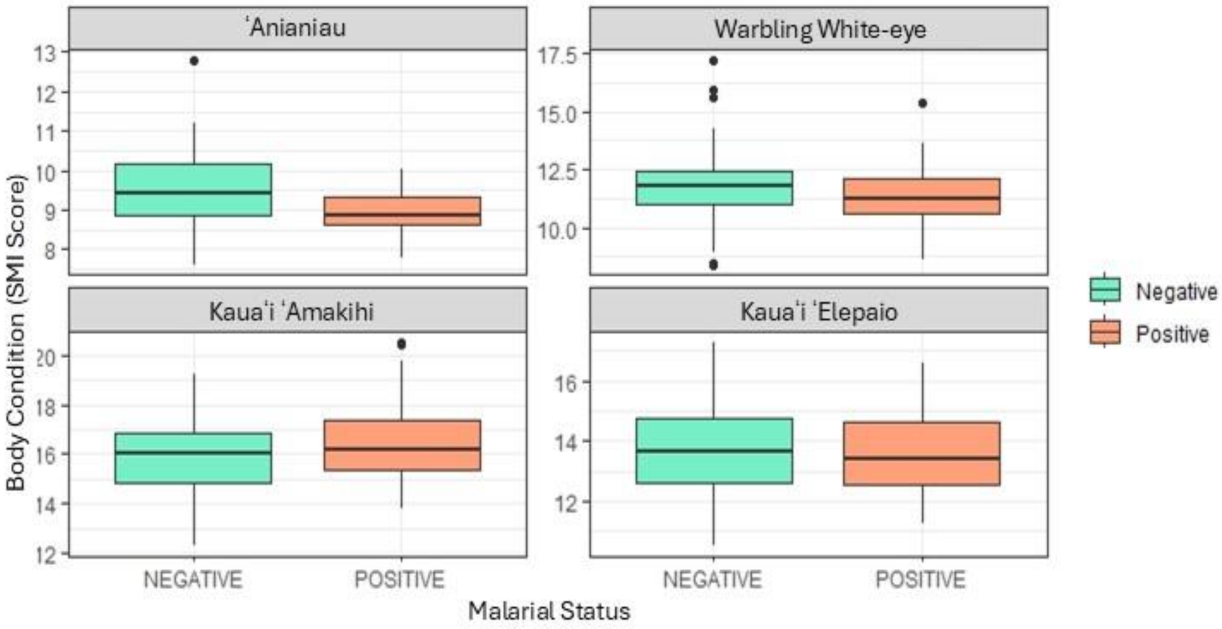

Figure 1.9. Relationship between body condition (SMI Score) and malarial infection status for four bird species in the Alakaʻi Wilderness Preserve, Kauaʻi, Hawaiʻi. Birds were captured and tested for malarial and presence with blood samples. Birds were diagnosed as either negative or positive for malarial infection.

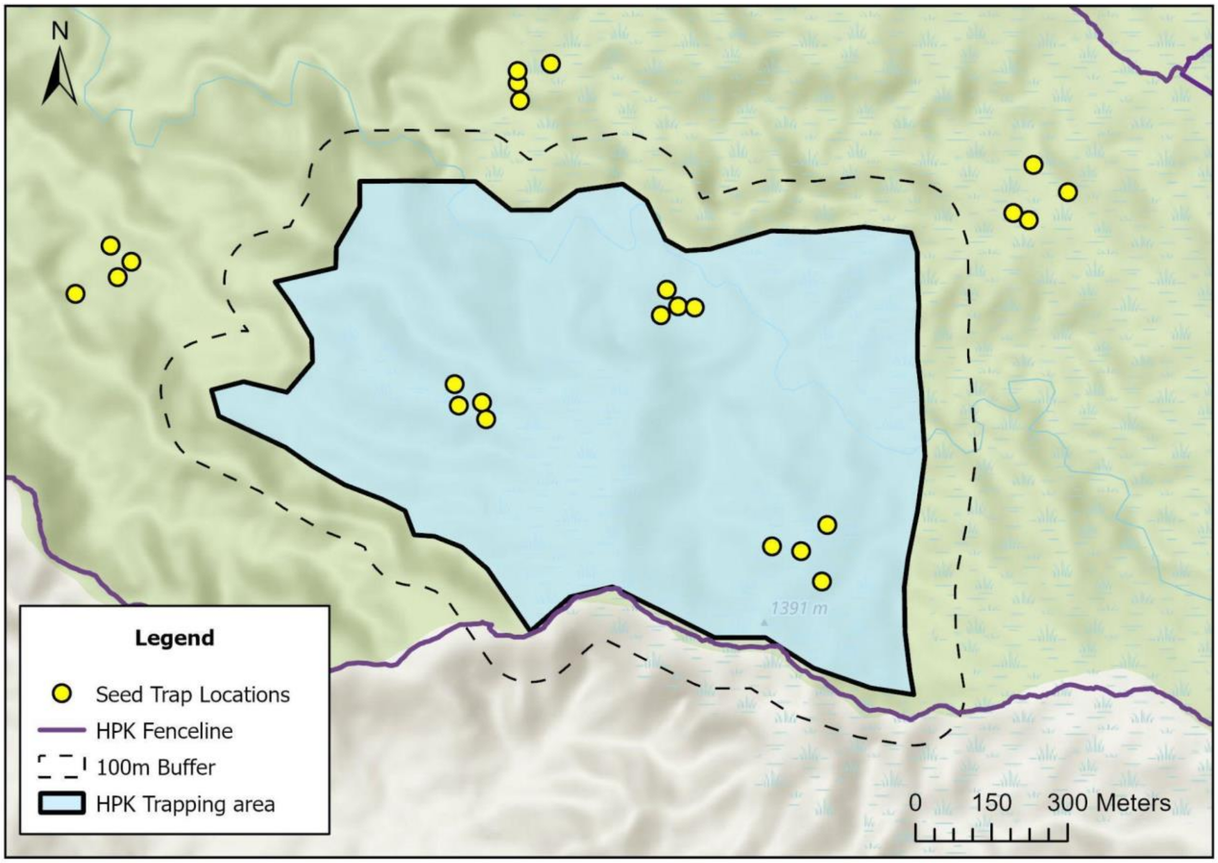

Figure 2.2. Four seed rain traps were placed within each of the six sites established to assess forest regeneration in the presence and absence of rodent control on Kauaʻi, Hawaiʻi.

Figure 2.3. Example of a seed rain trap that was used to assess seed rain in the presence and absence of rodent control in Kaua‘i, Hawai‘i. Seed traps consisted of 1m diameter mesh baskets with a silkscreen. Traps were hung from trees in the understory to collect seed rain in the forest.

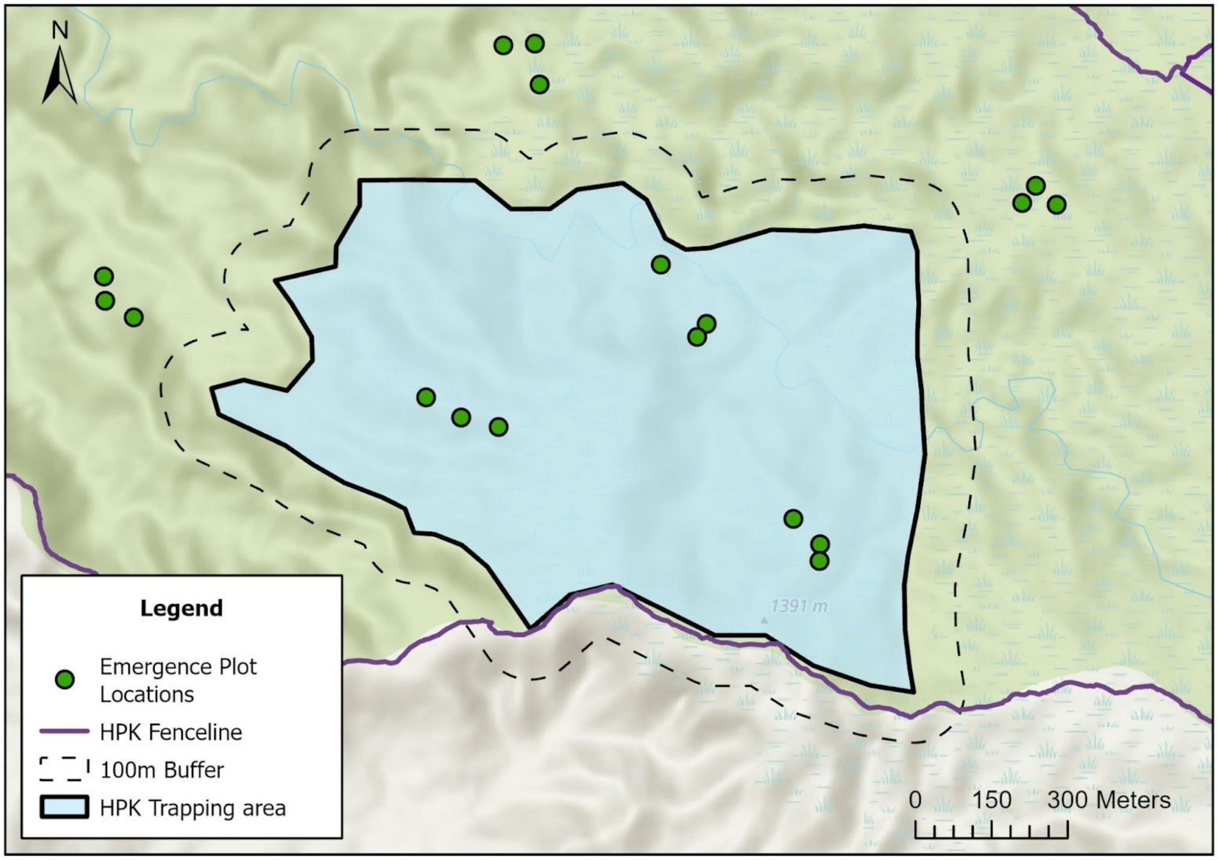

Figure 2.4. Three emergence plots were established at each of the six sampling sites within and outside the rodent control trapping area on Kauaʻi.