POPULATION DYNAMICS AND HABITAT USE OF THE PUEO (HAWAIIAN SHORT-EARED OWL; *ASIO FLAMMEUS SANDWICHENSIS*)

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ABSTRACT

Short-eared owls (*Asio flammeus*) are a globally distributed species inhabiting four continents and numerous island systems spanning tropical and temperate latitudes. Across the species range, short-eared owls are expected to follow global macroecological patterns in movement strategies where island populations are more resident, and experience expanded niches. To date, most studies exploring short-eared owl movement originate from North America and Europe and further research exploring these patterns throughout the species range is needed. The need for further research is highlighted by range-wide population declines of short-eared owls over the last 40 years that have increased concern for the persistence of the species. In Hawaiʻi, managers suspect population declines of the endemic short-eared owl subspecies, the pueo (*A. f. sandwichensis*), which is classified by the state of Hawaiʻi as endangered on the island of Oʻahu. In my study I was curious how the pueo population has changed over the last decade and how pueo are moving through time and space. To assess pueo population dynamics throughout Hawaiʻi, I used community science data collected over the last ten years to estimate trends in pueo occupancy, or the probability that a given site is occupied by at least one pueo. Occupancy dynamics are reflective of underlying changes in population size and the vital rates driving occupancy dynamics such as site colonization, extinction, and persistence provide insight temporal dynamics of the species distribution. To explore pueo spatial ecology further, I captured and banded five adult pueo, and attached VHF transmitters to four of the five, to track individual movements on the island of Oʻahu. I found some no evidence of small regional decline in pueo occupancy probability over the last decade. Statewide pueo occupancy probability ($\hat{\psi}$) averaged 0.19 ± 0.01 SE with an estimated rate of change ($\hat{\lambda}$) during 2011-2020 of 0.98 ± 0.01 SE, showing a slight annual decrease in occupancy. In contrast to studies of nominate short-eared owls in western North America, site turnover ($\hat{\tau}$), or the probability that a site occupied in one year was unoccupied in the previous year, was consistently low among years at 0.06 ± 0.01 SE providing evidence that the pueo are less nomadic. Following the movements of individual pueo tagged with VHF transmitters, I observed consistently use of both grassland and wooded habitats. The VHF tagged pueo roosted mainly on elevated perches in wooded habitats, as opposed to the short-eared owls in North America and Eurasia that are commonly described as open-habitat specialists typically roosting on the ground in open habitats. These results suggest that wooded areas should also be considered for conservation of the subspecies and that pueo in Hawaiʻi may exhibit an expanded niche compared to continental owls. Further, repeat sightings of tagged individuals in subsequent years indicates that individual pueo tend to occupy the same site from year to year, providing additional support of a more resident population in Hawaiʻi than short-eared owls in North America. Overall, I present evidence of slight declines in pueo occupancy, however, trends appear stable over the last decade. The models presented in this study are not predictive and factors affecting pueo occurrence and vital rates remain relatively unknown. Further research should work to identify drivers of occupancy dynamics in pueo. With the use of community science data and VHF transmitters I present findings exploring the spatial ecology of pueo, suggesting that pueo exhibit different movement ecology strategies in Hawaiʻi. My small sample size precludes broad conclusions and further work should include the use of longer-lived GPS transmitters deployed at more sites throughout Hawaiʻi.

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CHAPTER 1
GLOBAL INTRODUCTION

Raptors are experiencing global declines and higher levels of threat than birds in general (McClure et al. 2018). In particular, forest dependent, range restricted, island endemic, non-migratory, and tropical raptors appear to be at greatest risk of extinction (McClure et al. 2018, 2020, Pizzarello and Balza 2020). Knowledge of population trends and basic species ecology are necessary to identify and address drivers of decline. However, this information is lacking for many raptor species globally. Because of this, common raptor conservation research priorities include examining population trends and better understanding basic species ecology (McClure et al. 2018).

Short-eared owls (*Asio flammeus*) represent one species that requires more research to better understand population trends and basic ecology. The global distribution of short-eared owls spans four continents, with populations found in temperate, tropical, continental, and island systems. The majority of research on the species focuses on the nominate subspecies (the subspecies for which the specific epithet is repeated; *A. f. flammeus*) found throughout North America and Europe. The nominate subspecies is well known for its nomadic nature where individuals wander across the landscape and do not consistently use the same sites from year to year (Village 1987, Johnson et al. 2017, Tseng et al. 2017). The ultimate reasons for nomadic movement strategies in short-eared owls remains unknown but nomadic movements to new sites are probably an adaptation to patchily distributed and dynamic resources (Newton 2006, Teitelbaum and Mueller 2019, Teitelbaum et al. 2020).

Movement and habitat use strategies, however, vary through time and space (Van Horne 2002). Broadly, avian migration strategies have been shown to vary among species with latitude and seasonality, with more resident or non-migratory species found closer to the tropics (Somveille 2016). Few studies have explored within-species variation in movement strategies, but populations on island systems have been shown to experience niche expansion, and movement strategies have been shown to vary with, age, sex, and breeding status (Van Valen 1965, Wheat et al. 2017, Sayol et al. 2018, Stroud 2021). Given their global distribution throughout temperate, tropical, continental, and island systems with resident and migratory populations, the short-eared owl is a good candidate for further research regarding intraspecific variation in movement strategies.

Globally, short-eared owls are considered Least Concern but population trends indicate widespread declines, and the species is listed regionally in many parts of its range (Booms et al. 2014, BirdLife International 2015). Drivers of decline are not well understood but survival is likely impacted by a combination of factors, including predation, food availability, disease, as well as anthropogenic drivers (Lockie 1955, Clark 1975, Bluhm and Ward 1979, Holt 1992, T. M. Work and Hale 1996, Keyes and Gahbauer 2016, Wiggins et al. 2020). Anthropogenic drivers of decline include collision with vehicles and structures (e.g. fences and communication towers), secondary rodenticide poisoning, and habitat loss and fragmentation (Siers et al. 2019, Wiggins et al. 2020).

Studies exploring topics of population dynamics or movement ecology range-wide are inherently vast in scale, logistically difficult, and must instead rely on repeated independent studies across the species range (Morrison 2001, Van Horne 2002). In Hawaiʻi, the endemic Hawaiian short-eared owl subspecies (pueo; *A. f. sandwichensis*) represents a population of conservation concern likely to experience different population dynamics and interact differently with the environment than short-eared owls in North America and Europe, owing to biogeographical differences between the systems. Pueo play an important role as one of the only native apex predators, a role they share with the ʻio (*Buteo solitarius*) on the island of Hawaiʻi only. In addition to their ecological importance pueo are regarded as an ʻaumakua, or incarnation of an ancestor, and their presence is valued by Hawaiians and other Hawaiʻi residents alike (Hawaiʻi Department of Land and Natural Resources 2005). The need to increase our understanding of pueo ecology to improve management efforts and reduce extinction risk is highlighted by suspected population declines, their ecological role, and cultural importance (Hawaiʻi Department of Land and Natural Resources 2005). This thesis presents novel analyses that are both of scientific interest in the global context of the species and valuable to conservation in Hawaiʻi. In chapter one I estimate pueo population dynamics over the last decade, and in chapter two I investigated the habitat use of pueo on the island of Oʻahu with the use of VHF transmitters attached to pueo.

CHAPTER 2

POPULATION DYNAMICS OF THE PUEO (*ASIO FLAMMEUS SANDWICHENSIS*) OVER THE LAST DECADE, INFORMED WITH COMMUNITY SCIENCE

ABSTRACT

Short-eared owls (*Asio flammeus*) have undergone range-wide population declines over the last 40 years, increasing the concern for the continued existence of the species, and reigniting efforts to monitor short-eared owl populations to identify and inform conservation actions. Efforts to monitor short-eared owl occupancy trends, a metric reflective of underlying abundance, in Western North America most recently have suggested that declines have stabilized regionally. In Hawaiʻi, population declines are suspected of the endemic short-eared owl subspecies (pueo, *A. f. sandwichensis*). However, no previous research has explored pueo population trends. In this study I set out to estimate pueo population trends over the last decade. I applied a dynamic occupancy model to community science (eBird) data collected from 2011 to 2020 to estimate probabilities of site colonization and extinction, informing an estimate of the rate of change of the probability of pueo occupancy in Hawaiʻi. Overall, pueo were rare on the landscape with an average occupancy probability ($\hat{\psi}$) of 0.19 ± 0.01 SE over the ten-year period. Site colonization ($\hat{\gamma}$) and extinction ($\hat{\varepsilon}$) probabilities were uninformed in the top model. In general, site colonization probabilities were lower than site extinction probabilities at 0.01 (95% CI: 0.01–0.03), and 0.08 (95% CI: 0.04–0.15) respectively. Owing to higher site extinction probabilities, the statewide population showed a slight decrease, but overall trends remained relatively stable with an annual rate of change ($\hat{\lambda}$) of 0.98 ± 0.01 SE over the past decade. In contrast to studies in western North America, site turnover ($\hat{\tau}$), a parameter reflective of spatial species distribution dynamics among years, was consistently low at 0.06 ± 0.01 SE. Low site turnover probabilities indicate a population that is occupying the same sites from year to year and provides evidence that pueo are less nomadic than short-eared owls in western North America. These models represent the first attempt to quantify population dynamics of pueo in the state of Hawaiʻi and provide occupancy estimates that are reflective of underlying changes in abundance during the study period. These models, however, are not able to predict future estimates and further research should work towards building predictive models to quantify species extinction risk. Site colonization and extinction parameters were uninformed in the top

model and provide no insight into the factors driving site colonization and extinction probabilities. Future studies should work to identify the factors driving colonization and extinction to provide insight into conservation actions aimed at maximizing site colonization and minimizing site extinction.

INTRODUCTION

Short-eared owls (*Asio flammeus*) are a globally distributed species inhabiting every continent except Australia and Antarctica (Wiggins et al. 2020). The species is subdivided into ten subspecies with the nominate subspecies (the subspecies for which the specific epithet is repeated; *A. f. flammeus*) the most widespread throughout North America and Eurasia (Holt et al. 1999, Dickinson 2003). Evidence of widespread and sustained declines of the North American and European short-eared owl populations have been documented over the last 40 years (Booms et al. 2014, BirdLife International 2015, BirdLife International 2016). The most recent evidence from Western North America, however, indicate that populations there may have stabilized in the short-term (Meyers et al. 2020). Trends for the nominate subspecies have only been estimated in North America and Europe, excluding the portion of the subspecies range in Asia (Booms et al. 2014, BirdLife International 2015).

Population trends are less clear for the nine other short-eared owl subspecies, but downward global trends are cause for concern (BirdLife International 2016). Of the nine subspecies, six are range restricted island residents and seven are found in tropical latitudes where they may be more likely to be declining, further highlighting the need to study these populations (McClure et al. 2018, 2020, Pizzarello and Balza 2020). One island endemic subspecies, the pueo (*A. f. sandwichensis*) is found only in the Hawaiian archipelago. Current pueo population trends remain unknown; however, suspected declines led the state of Hawaiʻi to list the pueo as endangered on the island of Oʻahu (Hawaii Department of Land and Natural Resources 2015, NatureServe 2021). Preliminary efforts estimated the Oʻahu population size in 2018 but no research to date has explored temporal trends (Cotin and Price 2018).

Population estimates at large spatial scales utilizing expert observers are often prohibitively costly to complete. Increasingly, a big data approach of using large and growing community science databases to fill data gaps and monitor population dynamics has met with great success (Sullivan et al. 2009, 2014, Walker and Taylor 2017, Callaghan et al. 2018, Horns et al. 2018). eBird is one such rapidly growing community science database with more than 700 million observations available to answer a plethora of scientific inquiry ranging from migration to population dynamics (Sullivan et al. 2009, La Sorte et al. 2016, Walker and Taylor 2017).

In many cases direct population estimates may be impossible to generate, but relative metrics may be used to reflect population dynamics without directly estimating population size.

Occupancy, or the probability that a site is occupied by the species of interest, represents an alternative to abundance models that has successfully utilized community science data to explore population dynamics (MacKenzie et al. 2003, MacKenzie and Nichols 2004, Miller et al. 2016, Callaghan et al. 2018, Fink et al. 2020, Meyers et al. 2020). The goal of this chapter was to explore pueo population dynamics over the last decade using community science data accessed from eBird (http://www.ebird.org) to inform a dynamic occupancy model.

METHODS

I explored site-occupancy dynamics of pueo in the state of Hawaiʻi from 2011 to 2020 using community science observations from the eBird basic dataset (MacKenzie and Nichols 2004, MacKenzie et al. 2017). The eBird platform allows users to enter bird sightings from a birding occasion in checklists along with accompanying observation (sampling event) information including location, protocol (core protocols: stationary, travelling, incidental, and historical), and checklist effort (kilometers travelled while birding, time spent birding, number of observers). Once submitted the checklists are passed through a series of data quality filters and unusual observations are flagged for review by regional experts for eventual inclusion or exclusion from the eBird basic dataset (Sullivan et al. 2009, 2014). I downloaded the eBird basic dataset and applied filters to partially standardize checklist effort (Johnston et al. 2020). I then gathered and joined land-cover class and elevation environmental data, summarized within a 1.5 km buffer (~7 km^2) around each checklist location, to each checklist. Finally, data were filtered and formatted to meet the assumptions of the dynamic occupancy (colonization-extinction) model and fit to this model using the R package unmarked (MacKenzie et al. 2003, Fiske and Chandler 2011). All data processing and analyses were done using R (Version 4.0.3; R Core Team 2020) and AWK (Version 5.1.0).

eBird Data Filtering and Preparation

I downloaded the complete eBird basic dataset and used the R package auk, calling the program AWK (Version 5.1.0), to extract, process, and filter the eBird Basic Data set text files (Strimas-Mackey et al. 2018). I filtered the checklists to only those collected on land in the state of Hawaiʻi, USA between the years of 2011 and 2020 (Figure 2.1). Duplicate checklists, those that were shared between observers during the same birding occasion and shared the same sampling event data, were eliminated by retaining only one unique record per "sampling event identifier." I further retained only those checklists that were collected under the stationary or travelling protocols and that had been marked as complete (where birding was the primary purpose and all bird species identified by sight or sound were recorded). Checklists reporting extreme effort (collected over a distance of greater than five kilometers, five hours, or with more than ten observers) were excluded to partially standardize effort (Johnston et al. 2020).

I prepared data for use in the dynamic occupancy model by creating detection histories by site. Sites were defined using the latitude and longitude coordinates of each checklist rounded to the nearest 0.1°. Using rounded latitude and longitude values effectively lumped checklists collected within about one kilometer of each other as the same site. Sites were retained for analysis if they had at least two visits during a single year to inform the detection process. In cases where sites were visited more than 10 times per year, I subsampled to a maximum of 10 visits to limit imbalances in the number of repeat visits per site (MacKenzie et al. 2017). To maximize the detection rate, I further restricted checklists to those collected during peak activity periods, excluding checklists collected when the sun was greater than 60° above the horizon, roughly corresponding to the middle third of the day (Figure 2.2, Calladine et al. 2010).

Environmental and Survey Effort Covariates

I used the 20 m resolution Carbon Assessment Hawai‘i land-cover product (Jacobi et al. 2017) and an elevation raster at 1 km resolution from Amatulli et al. (2018) as environmental covariates. Environmental data were summarized within a buffer of 1.5 km around each checklist location. The buffer scale corresponds roughly to the size of a full (95%) pueo home range (see chapter three) as well as accounts for the nature of eBird data collection where observers may submit travelling checklists (MacKenzie and Nichols 2004, Strimas-Mackey et al. 2020). Land-cover data were summarized as the proportion of the buffer falling within each land-cover class (PLAND). Given that tall vegetation can reduce the likelihood of detection, I summed the proportion of open land-cover classes (agriculture, barren, grassland, and wetland) for use as a detection covariate (Luther 2020). To avoid overparameterizing the model, I summed the proportion of land-cover classes thought to be positively correlated with pueo occupancy (grassland, shrubland, wetland, and agriculture) for use as an occupancy covariate (Aitchison 1982, Miller et al. 2016, Cotin and Price 2018, Luther 2020). Median values and the standard deviation were calculated within each buffer for elevation. I mean-centered and standardized elevation, and land-cover covariates prior to modeling.

When submitting checklists, eBird users are prompted to enter data describing effort including time of day, distance traveled (km), duration (min), and number of observers. I converted time of day to sun position (degrees relative to the horizon) rather than hours after midnight to be both more biologically relevant and better reflect the bimodal peak in detections during morning and evening hours when the sun is low relative to the horizon. Sun position was calculated using the R package suncalc (Thieurmel and Elmarhraoui 2019). An additional observation covariate, list length (the number of species observed during each checklist) has been shown to account for inter-observer variation but is not automatically included in checklist data (Horns et al. 2018). I calculated list length for each checklist by counting the number of times the unique sampling event ID appeared in the data. Checklists were grouped by island and, in the case of low sample sizes, islands were grouped with their nearest neighbors. The islands of Molokaʻi, Lānaʻi, and Kahoʻolawe, and Maui were grouped into Maui Nui. There were no checklists submitted on the island of Niʻihau (Figure 2.1).

Principal component analysis (PCA) of checklist effort covariates was used to account for covariate variation more parsimoniously and account for collinearity among covariates (Abdi and Williams 2010). Checklist effort covariates for the PCA were *a priori* identified as relevant to the detection process. Covariates used in the detection PCA included sun position when checklist was started, distance (km), duration (min), list length, and number of observers. Top principal components explaining > 90% of cumulative variation were retained for model fitting.

Dynamic Occupancy Modelling

To estimate changes in occupancy over time I used the hierarchical colonization and extinction dynamic occupancy model in the R package unmarked (MacKenzie et al. 2003, Fiske and Chandler 2011). The dynamic occupancy model estimates four parameters, detection (p), initial year occupancy (ψ_i), site colonization (γ) and site extinction probabilities (ε). The model estimates site occupancy in the initial year and then estimates rates of site colonization and extinction for subsequent years (the probability than an occupied site is unoccupied in a subsequent season, and the probability than an unoccupied site is occupied in a subsequent season, respectively). In all years, repeat visits to each site were used to estimate the detection process and account for imperfect detection. Rates of site colonization and extinction can therefore be used to estimate annual occupancy rates and standard errors for each season.

I began by fitting the global model with all parameters fully informed with all *a priori* candidate covariates. Detection covariates included the proportion of open land-cover, top principal components (PCs) of checklist effort, and year as a factor. Initial occupancy covariates included median elevation, island, and the summed proportion of grassland, shrubland, wetland,

and agriculture. Site colonization and extinction parameters were informed with island and year. I assessed the fit of the global model using a MacKenzie and Bailey (2004) goodness-of-fit (GOF) test with 1000 simulations in the R package AICcmodavg (Mazerolle 2020). The MacKenzie-Bailey GOF test also estimates the variance inflation factor ($\hat{c}$), a measure of overdispersion, to further assess model fit and adjust error estimates for overdispersion.

I selected the best model in a multistep process where I compared candidate models one parameter at a time using the R package MuMIn (MacKenzie et al. 2017, Barton 2020). I began by selecting the top detection covariates by comparing candidate models with all combinations of detection covariates where the initial occupancy, colonization, and extinction parameters fully informed and covariates were not changed. At the next step, I removed detection covariates that were not included in the best model and compared all combinations of initial occupancy covariates. The process was repeated for the colonization and extinction parameters simultaneously. The estimate of $\hat{c}$ was counted as a modeled parameter and candidate models were ranked by quasi Akaike information criterion (QAIC). Smoothed annual occupancy estimates ($\hat{\psi}_t$) were used to calculate annual rates of change in occupancy ($\hat{\lambda}_t$) by dividing the subsequent occupancy estimate by the previous (Equation 2.1). Site turnover ($\hat{\tau}$), or the probability that an occupied site in a given year was unoccupied in the previous, was calculated using equation 2.2 (Nichols et al. 1998, Green et al. 2019).

Equation 2.1.

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t}$$

Equation 2.2.

$$\tau_t = \frac{\gamma_{t-1}(1 - \psi_{t-1})}{\gamma_{t-1}(1 - \psi_{t-1}) + (1 - \varepsilon)\psi_{t-1}}$$

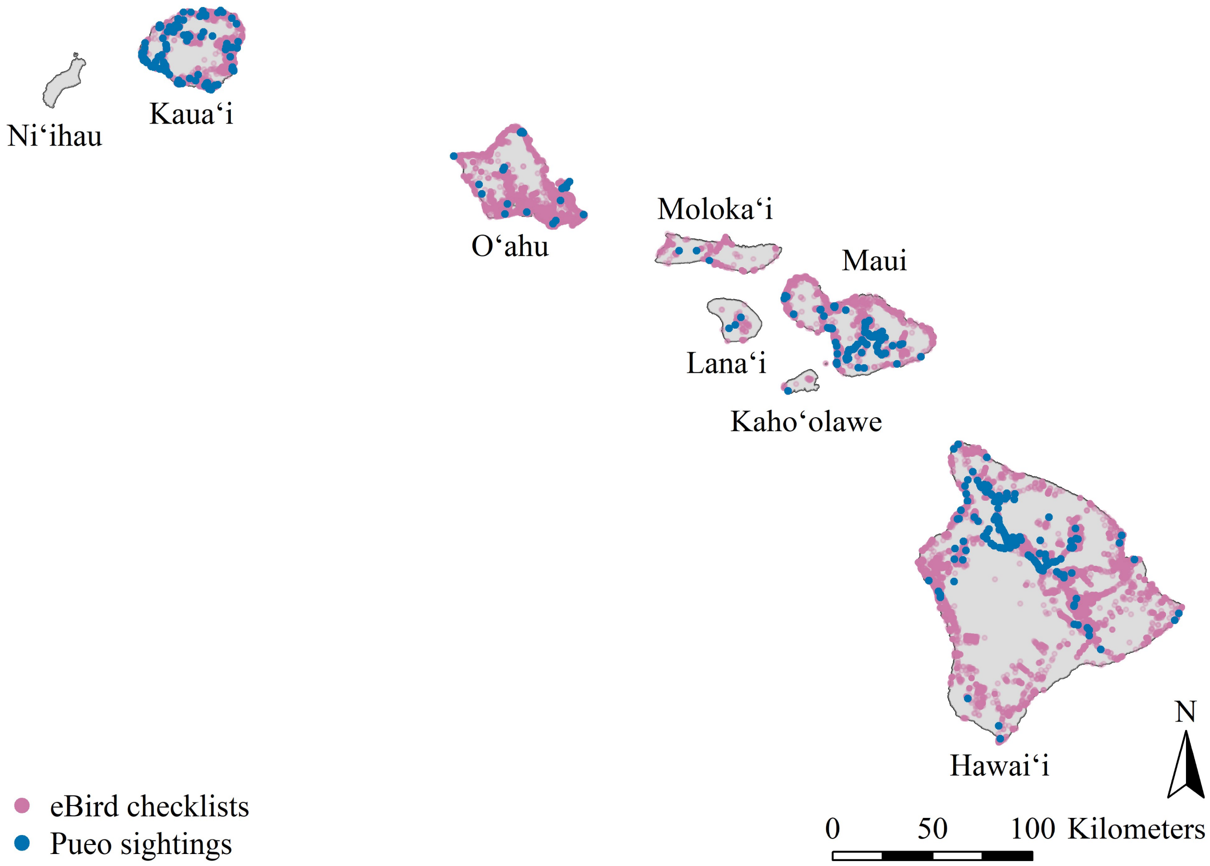

Figure 2.1. Map of eBird checklists submitted in the state of Hawai‘i between 2011 and 2020. Blue dots represent pueo detections and pink dots are non-detections.

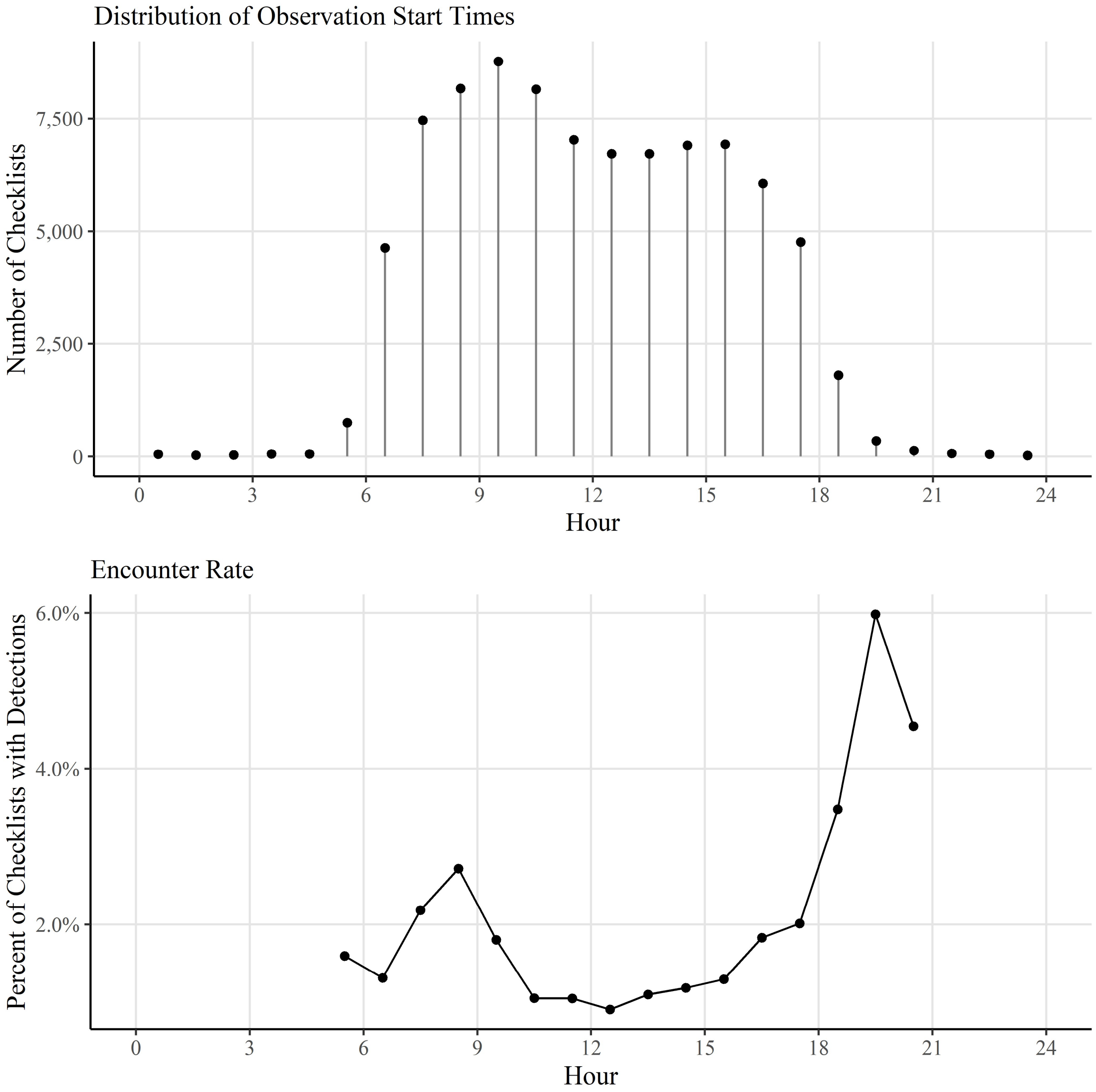

Figure 2.2. Distribution of eBird checklist start times and pueo encounter rates (the proportion of checklists with pueo detections) per hour of eBird checklists submitted in the state of Hawai‘i between 2011 and 2020.

RESULTS

After filtering, a total of over 32,700 eBird checklists collected at 1,877 sites were used for analysis. An average of 3,277 ± 1,138 SD checklists were collected per year at an average of 593 sites ± 181 SD. Individual sites were visited an average of 17.5 times each over the ten-year period. A total of 555 pueo detections were recorded at 208 sites. Pueo were detected annually an average of 36 times ± 15 SD with an average annual encounter rate, or the percentage of checklists with a pueo detection, of 5.9% ± 1.2 SD and average naïve annual occupancy rate of 5.9% ± 1.2 SD. An average of 353 ± 131 SD sites were visited in consecutive years with an annual naïve site colonization rate of 4.1% ± 0.9 SD and extinction rate of 3.9% ± 1.1 SD.

The global model with all covariates showed significant lack of fit ($P = 0.02$); however, the estimated variance inflation factor was greater than one ($\hat{c} = 3.03$), indicating that lack of fit was due to overdispersion. The variance inflation factor was then counted as a modeled parameter and used to adjust standard errors of fitted parameters, post-hoc accounting for overdispersion in the model, and allowing me to proceed with model selection using QAIC (Richards 2008).

The top detection model included the proportion of open habitat in the 1.5 km buffer around the checklist location and the first two PCs of checklist effort covariates (Table 2.1). The first two PCs of checklist effort covariates explained > 99% of variation. Detection correlated positively with the first PC and negatively with the second PC. The first PC is strongly positively correlated with checklist duration (1.00) and the second PC is strongly positively correlated with sun position when the checklist was started (1.00), suggesting that pueo detection probabilities are positively correlated with observer effort, and more likely when the sun is low on the horizon (Appendix A). Weights for detection models including year were small (< 1%) providing evidence that the probability of detection did not vary by year (Table 2.1).

At the initial year occupancy step of model selection, the top model was explained by island group, median elevation, and the summed grassland, shrubland, wetland, and agriculture land-cover cover covariate (Table 2.1). With all other covariates held at their mean values, initial year occupancy estimates ($\hat{\psi}_i$) by island were 0.72 (95% CI: 0.42–0.90), 0.40 (95% CI: 0.13–0.74), 0.04 (95% CI: 0.00–0.55), and 0.01 (95% CI: 0.00–0.11) for Kaua‘i, Maui Nui, O‘ahu, and Hawai‘i Islands, respectively (Figure 2.3). Initial occupancy was positively correlated with elevation (Figure 2.4) and the summed proportion of land-covers (Figure 2.5).

Table 2.1. Model selection table of a dynamic occupancy model of pueo fit with eBird observations in the state of Hawaiʻi from 2011-2020. Top models were chosen by comparing candidate models one parameter at a time, starting with detection (p), initial occupancy (ψ_i), then site colonization (γ) and extinction (ε). Detection covariates included the proportion of open land-cover, the first two principal components (PCs) of checklist effort covariates, and year. Initial occupancy covariates included island, median elevation (m), and the summed proportion of grassland, shrubland, wetland, and agriculture land-cover (pland) summarized with 1.5 km of the checklist site. Colonization, and extinction covariates included island and year. The column *K* indicates the number of parameters in the model.

Model					***K***	**QAIC**	**ΔQAIC**	**Weight**
Detection								
$p \sim$	open	PC1	PC2		44	1177.2	0.0	0.85
$p \sim$	open	PC1			43	1180.8	3.6	0.14
$p \sim$	open	PC1	PC2	year	48	1186.8	9.6	0.01
$p \sim$	open	PC1		year	47	1189.9	12.7	0.00
$p \sim$					35	1294.8	117.6	0.00
Initial Occupancy								
$\psi_i \sim$	island	elevation	pland		44	1177.2	0.0	0.94
$\psi_i \sim$	island		pland		43	1183.0	5.8	0.05
$\psi_i \sim$	island	elevation			43	1187.6	10.4	0.01
$\psi_i \sim$	island				42	1197.0	19.8	0.00
$\psi_i \sim$					38	1204.2	27.0	0.00
Site Colonization and Extinction								
$\gamma \sim$		$\varepsilon \sim$			16	1145.1	0.0	0.53
$\gamma \sim$		$\varepsilon \sim$	island		30	1145.3	0.2	0.47
$\gamma \sim$	island	$\varepsilon \sim$			34	1155.1	10.0	0.00
$\gamma \sim$		$\varepsilon \sim$	island	year	34	1158.8	13.7	0.00
$\gamma \sim$		$\varepsilon \sim$		year	16	1159.4	14.3	0.00

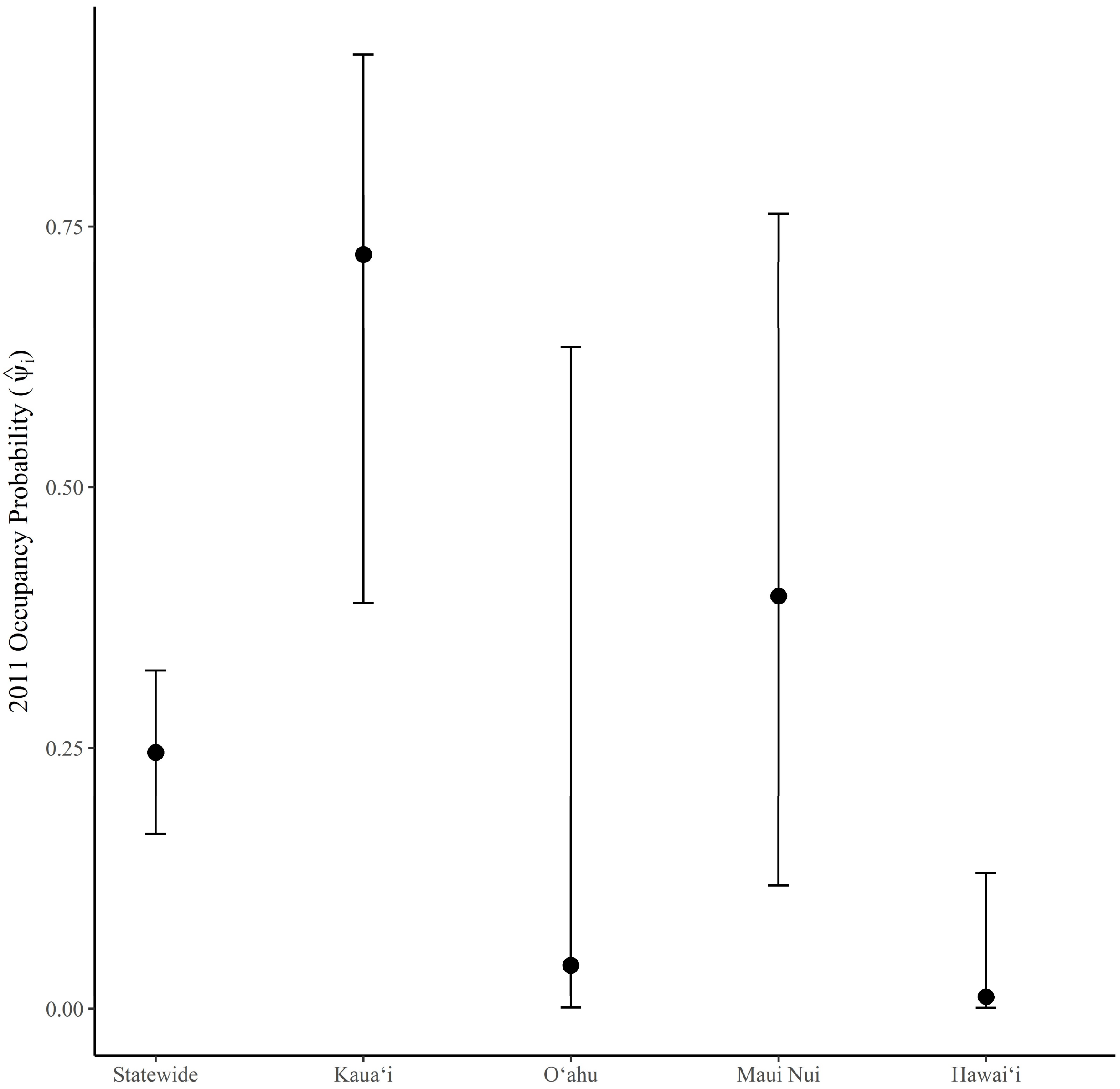

Figure 2.3. Occupancy ($\hat{\psi}_i$) rates with 95% confidence intervals by island in the year 2011 from the initial season occupancy estimate in a dynamic colonization and extinction model of pueo in the state of Hawai‘i between 2011 and 2020 fit with eBird observations.

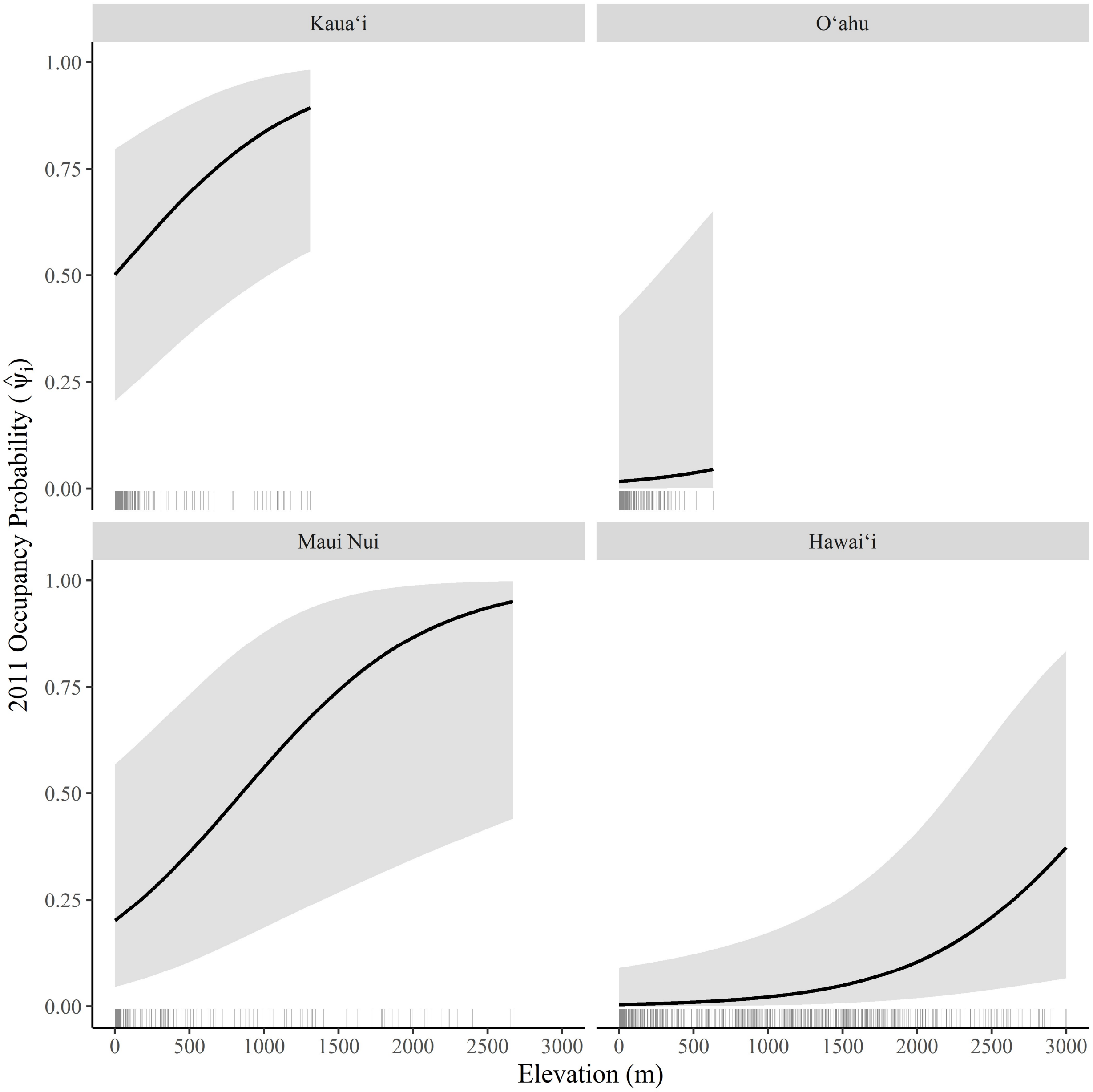

Figure 2.4. Occupancy ($\hat{\psi}_i$) rates with 95% confidence intervals by island over a range of elevation (m) in the year 2011 from the initial season occupancy estimate in a dynamic colonization and extinction model of pueo in the state of Hawai‘i between 2011 and 2020 fit with eBird observations. Grey ticks at the base of each panel indicate the elevational distribution of eBird sites used in analysis.

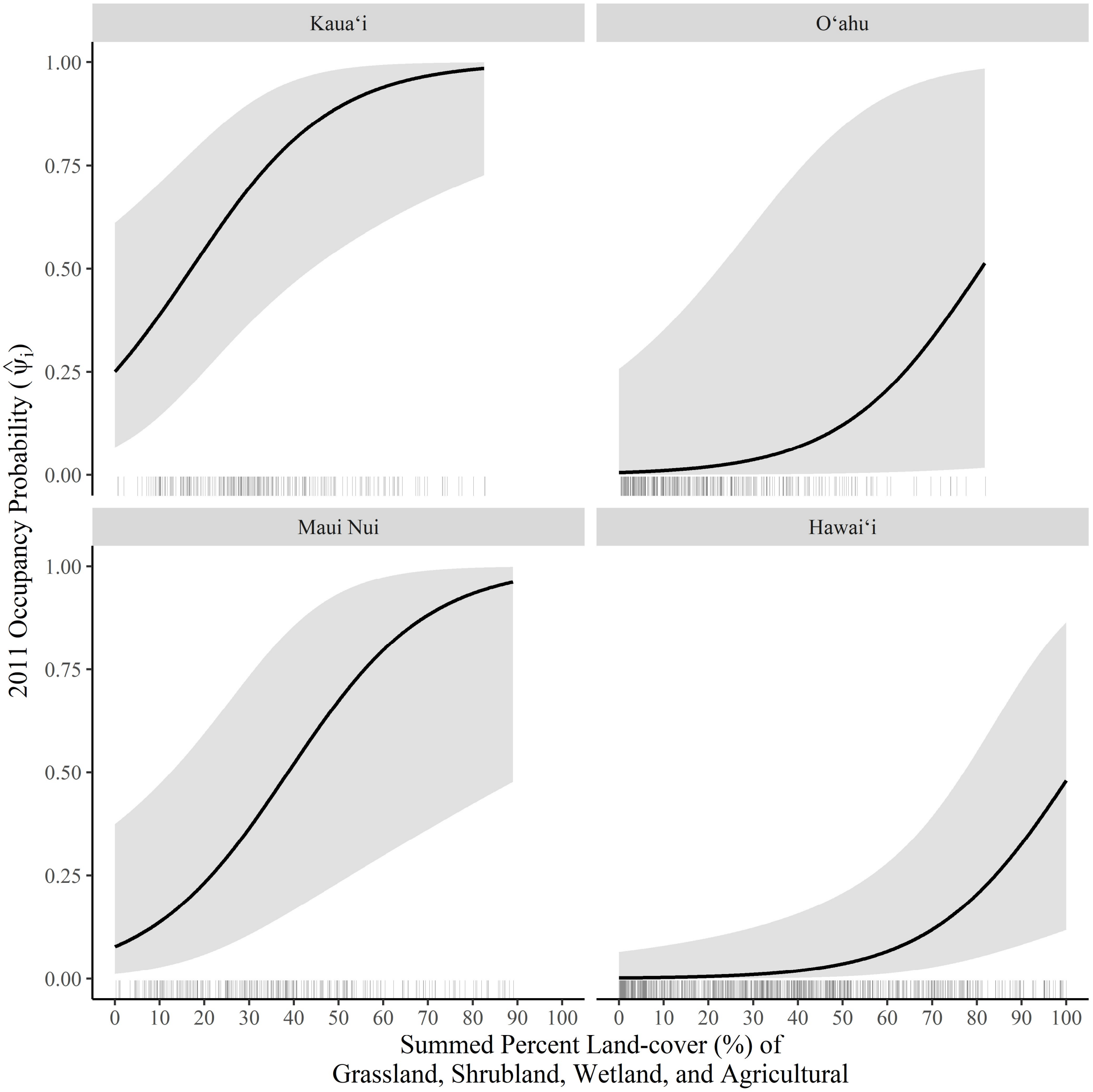

Figure 2.5. Occupancy ($\hat{\psi}_i$) rates with 95% confidence intervals by island over a range of the summed proportion of grassland, shrubland, wetland, and agriculture land-cover classes (PLAND) summarized within a 1.5 km buffer of checklists locations in the year 2011. Predicted curves are from the initial season occupancy estimate in a dynamic colonization and extinction model of pueo in the state of Hawai‘i between 2011 and 2020 fit with eBird observations. Grey ticks at the base of each panel indicate the PLAND distribution of eBird sites used in analysis.

The top model informing site colonization and extinction rates was best explained by island, accounting for 98% of model weights (Table 2.1). Model weights provide evidence that site colonization and extinction parameters are more island dependent than time dependent. It should be noted, however, that the inclusion of categorical covariates significantly increases the number of model parameters (*K*), which QAIC uses to penalize candidate models. Site colonization rates were highest for the island of Hawaiʻi and lowest for Maui Nui. Site extinction rates were highest on the island of Oʻahu and lowest for the island of Kauaʻi (Figure 2.6). Colonization and extinction confidence intervals overlap for all islands except for Hawaiʻi where site extinction rates appear to be slightly higher than colonization rates. The final model predicted a mean annual occupancy estimate of 0.19 ± 0.01 SE (Figure 2.7). The annual occupancy rate of change ($\hat{\lambda}$) for the state was 0.98 ± 0.01 SE (Figure 2.8).

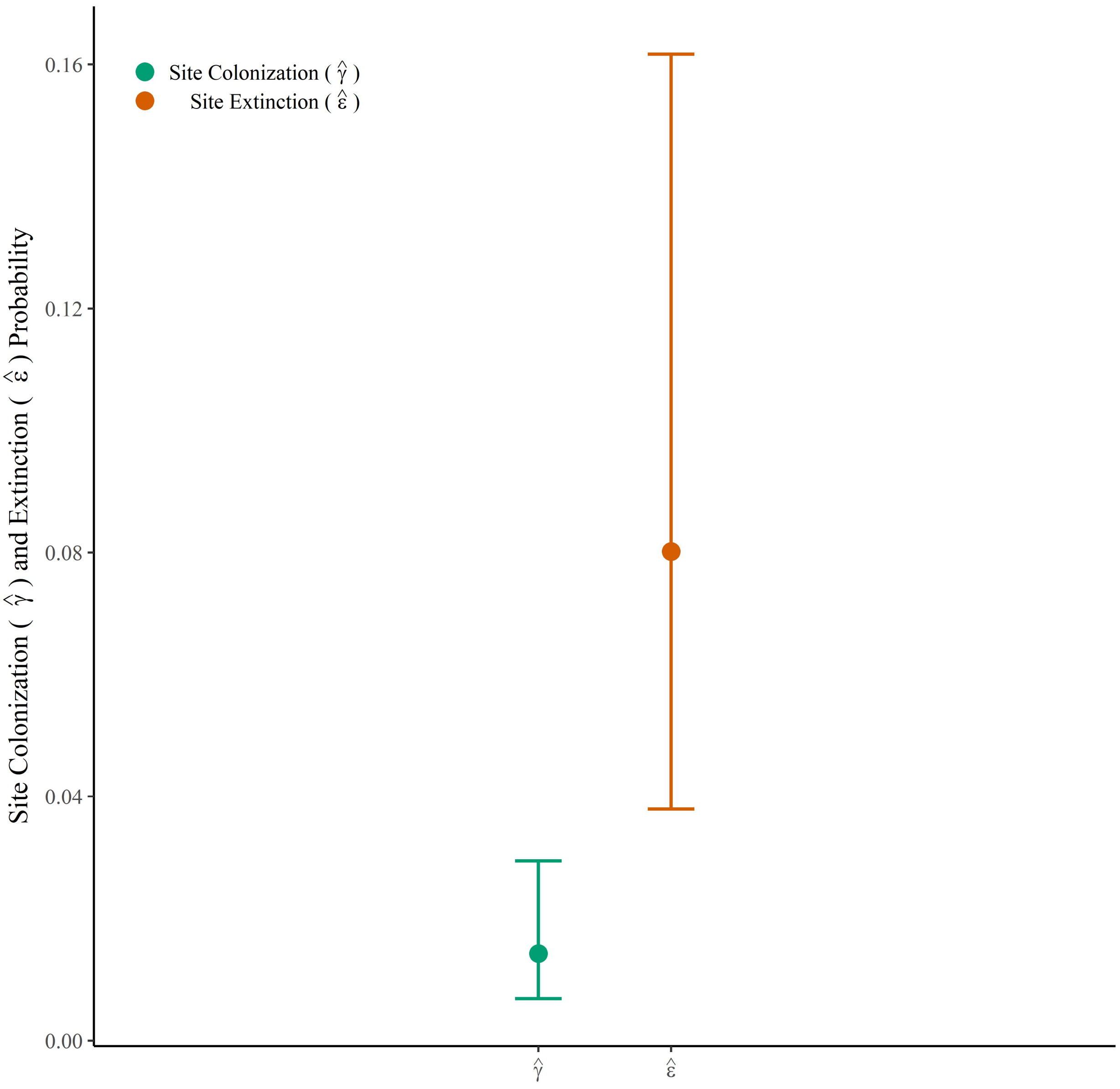

Figure 2.6. Estimated site colonization ($\hat{\gamma}$) and extinction rates ($\hat{\varepsilon}$) with 95% confidence intervals during the years 2011 to 2020 from a dynamic colonization and extinction model fit with eBird observations of pueo in the state of Hawai‘i.

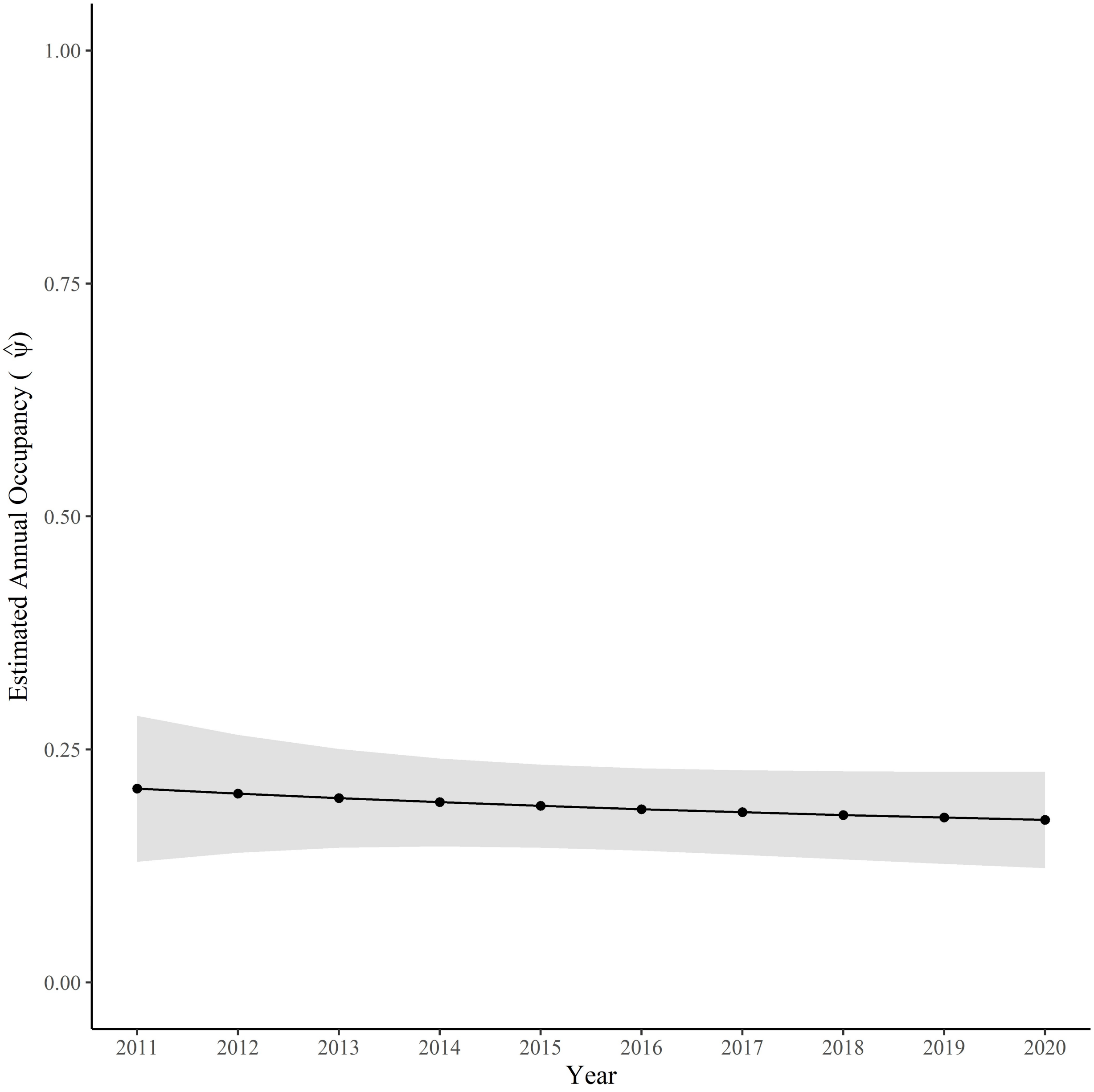

Figure 2.7. Estimated occupancy ($\hat{\psi}$) rates with 95% confidence intervals during the years 2011 to 2020 from a dynamic colonization and extinction model fit with eBird observations of pueo in the state of Hawaiʻi.

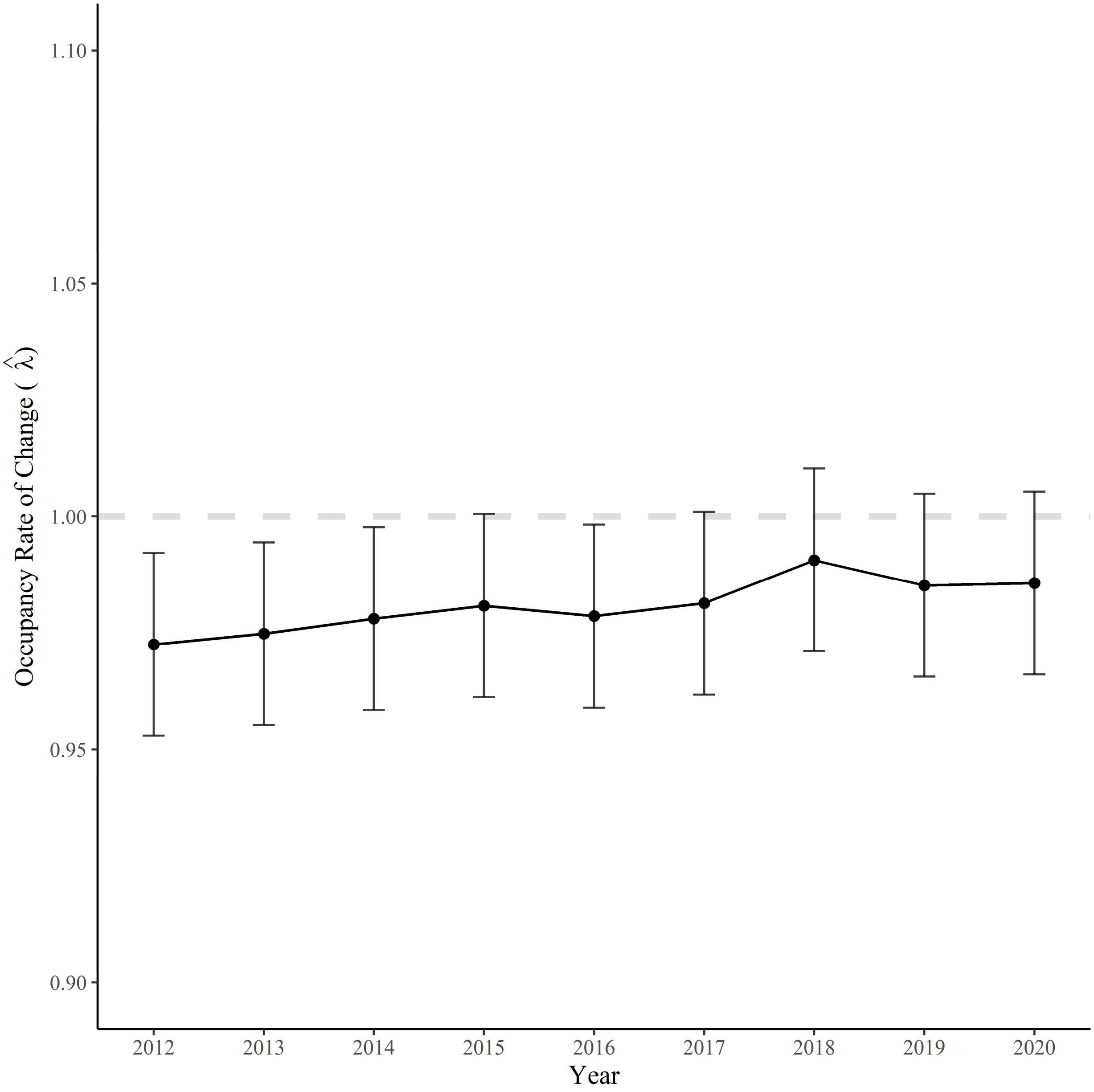

Figure 2.8. Estimated annual rate of change ($\hat{\lambda}$) in the proportion of occupied sites with 95% confidence intervals during the years 2011 to 2020 from a dynamic colonization and extinction model fit with eBird observations of pueo in the state of Hawaiʻi. A rate of 1 indicates no change, below 1 indicates decline, and above 1 indicates growth.

DISCUSSION

Pueo occupancy in the state of Hawaiʻi showed a slight decrease over the last ten years. The rate of change ($\hat{\lambda}$) averaged 0.98 ± 0.01 SE, indicative of a slight decline ($\hat{\lambda} < 1$, where 1 indicates no change), but $\hat{\lambda}$ overall is near 1 indicating that declines were small. Predicted site colonization probabilities were lower than predicted site extinction, driving the overall decrease in occupancy; however, although site colonization and extinction estimates differed, both were relatively low, leading to a slow rate of change where most sites that were occupied in one year, remained occupied in the following. Site colonization and extinction parameters were uninformed in the top model and inference is limited about factors driving this pattern. The second-best site colonization and extinction model with a nearly identical QAIC score as the top model included island as an extinction covariate indicating that island explains at least some variation in site extinction probabilities, but not enough to offset the QAIC penalty for additional covariates.

Site colonization and extinction parameters can provide important insight into the mechanisms driving changes in occupancy and underlying abundance. Uncertainty surrounding factors driving pueo site colonization and extinction probabilities warrant further investigation, especially given the state protected status of pueo. Site colonization and extinction parameters estimate changes in occupancy in sequential years that are either due to birth, and immigration or death, and emigration, respectively. Drivers of decline and causes of mortality are not well understood but pueo are likely impacted by a combination of factors including predation by invasive mammals, food availability, disease, as well as anthropogenic factors such as habitat loss, heavy machinery, car strikes, secondary poisoning, and barbed-wire fences (Lockie 1955, Clark 1975, Holt 1992, W. M. Work and Hale 1996, Keyes 2011, Booms et al. 2014, Siers et al. 2019, S. Bell, University of Hawaiʻi at Mānoa, personal communication). The ground nesting habit of pueo likely increases the vulnerability of their nests to a number of threats including invasive mammals and human disturbance (Hawaiʻi Department of Land and Natural Resources 2015). Further research should attempt to quantify and explore how these factors relate to site colonization and extinction to identify drivers of decline and outline conservation actions that can be taken to maximize the populations vitality rates.

Statewide, pueo occupied a relatively low proportion of sites over the last ten years (0.19) and occupancy varied relatively little over time (maximum of 0.21 in 2011 and a minimum of

0.17 in 2020). Average statewide occupancy estimates are similar to rates reported for the nominate short-eared owl subspecies in western North America, although differences in study design obscure direct comparisons (Miller et al. 2016, Meyers et al. 2020). Regional occupancy trends in western North America appear stable as well (Meyers et al. 2020). Although regional occupancy trends are stable in western North America, high annual variation exists sub-regionally within US states (Meyers et al. 2020). This pattern is reflected in high turnover ($\hat{\tau}$) estimates for the population where few sites are consistently occupied from year to year (Meyers et al. 2020). The large annual variation by sub-region coupled with regional stability, and high turnover indicates a large annual variation in the spatial distribution of the population, as would be expected for nomadic species (Nichols et al. 1998, Newton 2006, Green et al. 2019). If the population of pueo in Hawaiʻi were similarly nomadic I would expect a similar pattern of site colonization and extinction probabilities that show strong sub-regional and annual patterns. In contrast to this expectation, the top site colonization and extinction model did not include sub-region (island), or year, and turnover was very low, indicating that pueo are less nomadic than their nominate cousins. Although this model provides evidence against nomadism in pueo, further research with the use of marked individuals is necessary to rule out the possibility that although sites are consistently occupied among years, the individuals occupying those sites are changing. In chapter two of this thesis, I recorded banded pueo utilizing the same site for multiple years, further supporting these findings, however, more research is needed with more banded pueo across the island chain and additionally future research should explore within year movements.

Initial (2011) occupancy rates were highest on Kauaʻi and Maui Nui where pueo were relatively common on the landscape, and lowest on Oʻahu and the island of Hawaiʻi where pueo were comparatively rarer. Contrary to expectations, pueo occupancy was equally as low on Hawaiʻi island as it was on Oʻahu where the population is listed as endangered by the state. Although occupancy estimates are similar for both islands Hawaiʻi island is nearly seven times larger than Oʻahu and after taking into account island size, Hawaiʻi island would be expected to account for more occupied area than Oʻahu. Factors surrounding the lower-than-expected initial occupancy estimate for Hawaiʻi island are unknown, but, could be explained by limiting factors such as the amount of available habitat. Future research should identify and quantify the amount of available habitat by island, paying particular attention to Hawaiʻi island.

In agreement with other studies, evidence from this study suggests that elevation is an important predictor of occupancy (Miller et al. 2016, Cotin and Price 2018, Luther 2020, Meyers et al. 2020). I found an overall positive correlation with initial occupancy and elevation. Luther (2020) also found a positive relationship with pueo occupancy and elevation in their study on Maui, however, in western North America Meyers et al. (2020) found nominate short-eared owls to be more likely to occupy lower elevation sites. Potential explanations include correlation of land-cover classes with elevation, reduced human disturbance at higher elevations, or climatic niche. In fact, Meyers et al. (2020) found short-eared owls were most likely to occupy sites with lower summer temperatures, suggesting that temperature is potentially a limiting factor at lower elevations in Hawaiʻi. If temperature is a driving factor this could be potentially troublesome for pueo as temperatures increase in Hawaiʻi with climate change; however, more research is needed to explore the factors driving this relationship.

In this model I accounted for pueo-land-cover associations by including a covariate of the summed proportion of land-cover classes *a priori* identified as likely to be significant correlated with occupancy. As expected, this covariate was positively correlated with the probability of occupancy, indicating that the land-cover classes of grassland, shrubland, wetland, and agriculture are important for pueo. The amalgamation of land-cover classes, however, obscures nuance that may exist in relationships between pueo occupancy and the individual components of the combined covariate. Future studies should work to add nuance to pueo occupancy and land-cover composition relationships (Greenacre 2020, Greenacre et al. 2021).

Overdispersion was present in our model but was accounted for by inflating standard errors with the variance inflation factor use of QAIC for model selection (Richards 2008). Although post-hoc accounting for overdispersion effectively solves issues of model fit due to overdispersion, future use of Bayesian methods would allow more flexibility in changing distributional assumptions of modeled parameters or adding random effects to deal with issues of overdispersion. The use of Bayesian methods would also facilitate forecasting future colonization and extinction dynamics under different climate change scenarios with more realistic results than other species distribution models (Nordén et al. 2020).

Overall, I provide evidence of a slight decrease in pueo occupancy over the last ten years. It should be noted, however, that temporal trends in occupancy are generally sensitive to underlying trends in abundance but often underestimate the rate of change (MacKenzie and

Nichols 2004, Wauchope et al. 2019). Occupancy may underestimate the rate of change because the number of individuals at a site can decrease without changing the occupancy status of the site, resulting in occupancy tending to estimate the rate of change more conservatively than direct abundance models (Wauchope et al. 2019). For this reason, I recommend that population-wide pueo occupancy trends are monitored on a regular basis to develop long-term models and assess the risk of continued, low-rate declines to the subspecies continued existence. I further suggest that community science data are sufficient for monitoring broad trends while more structured studies may be necessary to detect finer scale trends and test hypotheses (Sullivan et al. 2009, Miller et al. 2016, Horns et al. 2018).

Population connectivity among islands remains unstudied and may help inform the significance of individual island sub-populations to the subspecies in general. In this study I found evidence that pueo populations exhibit less spatiotemporal variation than short-eared owls in western North America and propose that this is due to a less nomadic population. Future research should test this with the use of satellite transmitters or genetics to explore both within island and among island movements at seasonal and annual temporal scales (MacKenzie and Nichols 2004).

CHAPTER 3

HABITAT USE AND ACTIVITY PATTERNS OF PUEO (HAWAIIAN SHORT-EARED OWL; *ASIO FLAMMEUS SANDWICHENSIS*) ON OʻAHU, HAWAIʻI

ABSTRACT

Short-eared owls (*Asio flammeus*) are considered nomadic grassland specialists in temperate and continental systems, which represent much of their global range. However, across a species' range individuals and populations adopt different habitat use strategies as a mechanism to persist in different environments. Thus, short-eared owls in tropical and island systems may exhibit different behaviors than temperate and/or continental systems. In Hawaiʻi the endemic short-eared owl subspecies, the pueo (Hawaiian short-eared owl: *A. f. sandwichensis*) inhabits an extremely different ecosystem composed of isolated subtropical islands. It is expected that pueo use habitat differently than their continental counterparts, yet no study to date has explored the movements and habitat use of pueo. Here, I aimed to identify habitats associated with specific behaviors as well as describe activity patterns of pueo throughout the day and night. In this study I captured five pueo on the island of Oʻahu, Hawaiʻi and fit four pueo with very high frequency (VHF) transmitters to document their habitat use and behavior during diurnal, crepuscular, and nocturnal periods. I recorded sufficient data for analyses of two of the four VHF tagged pueo. I found that grasslands were used largely for hunting and wooded patches were used for roosting. Pueo were most often observed foraging from perches. In contrast with short-eared owls in North America and Europe, I observed pueo roosting almost exclusively on elevated perches in trees rather than directly on the ground in grassy areas. Activity levels peaked during crepuscular and nocturnal periods and roosting was most common during diurnal periods. Despite the small sample size, the results of my study describe, for the first time, the habitat use and activity patterns of pueo with VHF transmitters. The results highlight the importance of both grassland and wooded areas for pueo, and indicate the importance of studying globally distributed species across their entire range. Although more research is needed to make broader conclusions, the data suggest that wooded areas play an important role in the conservation of pueo on the island of Oʻahu and likely across the entire archipelago.

INTRODUCTION

Short-eared owls (*Asio flammeus*) are a globally distributed species, with ten subspecies dispersed among all continents except Australia and Antarctica, and many islands (Wiggins et al. 2020). Short-eared owls are often described as vagrant, grassland specialists that wander nomadically across vast expanses of open habitat (Calladine et al. 2012, Booms et al. 2014, Johnson et al. 2017). Across their global distribution the bulk of published literature originates from the nominate subspecies (the subspecies for which the specific epithet is repeated; *A. f. flammeus*) found throughout North America and Eurasia, with few studies on the nine other short-eared owl subspecies (Holt et al. 1999, Dickinson 2003). Nominate short-eared owls exhibit facultative migration on a continental scale with most owls showing little to no site-fidelity during the breeding and non-breeding seasons (Novak and Ross 2016, Johnson et al. 2017). During the breeding season nominate short-eared owls appear to maintain stable home ranges followed by long distance, generally southward, migration with occasional stopovers (Johnson et al. 2017). During the non-breeding season, some individuals maintain stable home ranges while others wander nomadically across large areas (Novak and Ross 2016, Johnson et al. 2017, Tseng et al. 2017).

Seasonal migration and nomadism have been observed for the nominate subspecies, but movement and habitat use strategies are likely to vary across a species range as a mechanism to persist in different environments (Van Horne 2002). Conditions predicting the occurrence of a species change through space and time; thus, movement patterns of individuals in one area may not hold true at another location or time where environmental conditions are different (Van Horne 2002). With globally distributed species, such as short-eared owls, it is not feasible to conduct single large-scale studies that account for variation in movement and habitat use patterns across the full range of environmental conditions where a species exists. Therefore, individual studies repeated in different geographical areas are essential to characterize species movement and habitat use patterns throughout their distribution (Wiens and Rotenberry 1981, Morrison 2001, Van Horne 2002, Gaston 2003). Variation in movement strategies and habitat use also tend to be most prominent at the edges of a species range (Van Horne 2002). In this context, to enhance our knowledge of short-eared owl spatial ecology more research is needed with greater representation of populations outside of North America and Eurasia.

Across the global distribution of short-eared owls there are a few resident populations, defined as populations that occupy the same area throughout the entire year, inhabiting island systems quite unlike the vast continental grassland systems where they have been most frequently studied. Resident island populations are found in the Greater Antilles, Galápagos, Malvinas (Falklands), and Hawaiian Islands (Wiggins et al. 2020). In Hawaiʻi the resident and endemic subspecies of short-eared owl is known as the pueo (Hawaiian short-eared owl; *A. f. sandwichensis*). Pueo are found on all of the main Hawaiian Islands. Across the archipelago pueo play an important role, both ecologically as one of two native apex terrestrial predators in Hawaiʻi, and culturally appearing in moʻolelo (stories) and as ʻaumakua (ancestral guardians). Pueo are currently listed as endangered on the island of Oʻahu by the state of Hawaiʻi (Hawaii Department of Land and Natural Resources 2015). Despite playing important ecological and cultural roles, this ground-nesting raptor remains understudied and relatively little is known about its basic ecology, including movement ecology.

Few studies have evaluated the movement and habitat use strategies of island endemic short-eared owls. In Hawaiʻi, no studies to date have explored pueo movement and habitat use patterns. Incidental observations indicate that pueo appear to use a more diverse range of habitats to meet their needs throughout their life cycle compared with their continental counterparts. For instance, nests and hunting behaviors have been observed in wetlands, grasslands, agricultural lands, and even high-elevation native forests (Cotin et al. 2018). Furthermore, pueo appear to show an extended breeding season with breeding occurring from November through July (Cotin et al. 2018, A. Wang, Hawaiʻi Division of Forestry and Wildlife, personal communication).

Short-eared owls, inclusive of pueo, are well known for their crepuscular and diurnal activity and pueo are often described as a crepuscular, or even on occasion diurnal, species (Berger 1981, Mikkola and Willis 1983, Pratt et al. 1987, NatureServe 2021). Studies of short-eared owls tagged with transmitters, however, have documented extended nocturnal activity (Calladine et al. 2010, Calladine and Morrison 2013). In Hawaiʻi, observational studies and eBird data show activity peaks during the crepuscular hours (Cotin et al. 2018). However, these data do not extend into nocturnal hours and pueo nocturnal activity remains unstudied.

VHF transmitters attached to individuals are commonly used to study movement and habitat use patterns, especially for lighter species where GPS technology is still too heavy for safe use (Powell 2000, Calladine and Morrison 2013, Tseng et al. 2017). VHF transmitters emit very high frequency (VHF) radio waves that can be picked up with a receiver and a hand-held or car-mounted directional antenna to physically find and resight a tagged individual repeatedly over the lifespan of the transmitter. As a result, the behavior of the individual can be assessed at the time of sighting, allowing study of the individual's use of habitat as it relates to behavior.

The aim of my study was to, for the first time, investigate habitat use related to specific behaviors and to explore pueo activity patterns throughout the day. To achieve this goal, I captured and tagged pueo with VHF transmitters and tracked the movements of pueo within their home ranges. I assessed habitat use of individuals for specific behaviors including hunting and roosting as well as described home range composition. I used behavioral notes from pueo resights to explore activity patterns during diurnal, crepuscular, and nocturnal periods. Based on these results, I discuss the importance to the conservation of pueo in Hawaiʻi.

METHODS

Study Site

This study initially took place on the islands of Oʻahu and Maui, with a focus on military-managed and agricultural lands. Specific trapping sites were selected in areas where preliminary surveys identified frequent pueo use and land access was granted (Cotin and Price 2018, Luther 2020). Three field sites were identified, including one site on U.S. Navy-managed lands at the Joint Base Pearl Harbor Hickam Lualualei Annex (JBPHH-LA; 21°25'47.6"N 158°9'12.0"W; ~15 m elevation) on the west (leeward) side of Oʻahu, a second site on agricultural lands in central Oʻahu (21°32'34.5"N 158°03'35.7"W; ~250 m elevation), and a third site on the southern flank of mount Haleakalā on the island of Maui (20°40'33.3"N 156°23'52.4"W; ~450 m elevation; Figure 3.1). Despite substantial effort and consistently observing pueo, no pueo were captured from the central Oʻahu or Maui field sites; all captures occurred on the leeward side of Oʻahu.

The JBPHH-LA field site is located in the center of the Lualualei Valley on the east side of the Waiʻanae Range, Oʻahu, Hawaiʻi (Figure 3.1). Lualualei is the largest valley on the island of Oʻahu and the landscape is composed of a broad and flat, u-shaped valley floor surrounded on three sides by steep ridges and bounded by the ocean on the fourth. The land-cover is a mosaic of kiawe woodland, mowed grassland, agriculture, and suburban housing. Under the Köppen climate classification scheme the climate is considered tropical savanna with a dry summer and the area receives roughly 60 cm of rainfall annually (Chen and Chen 2013, Giambelluca et al. 2013). Trapping efforts occurred within the 700 ha JBPHH-LA VLF (very low frequency) Antenna Field located in the center of the valley at a mean elevation of 16 m (0−33 m) in an area that included maintained (mowed) grassland, kiawe woodland, and small developments (see Table 3.1 for land-cover class descriptions).

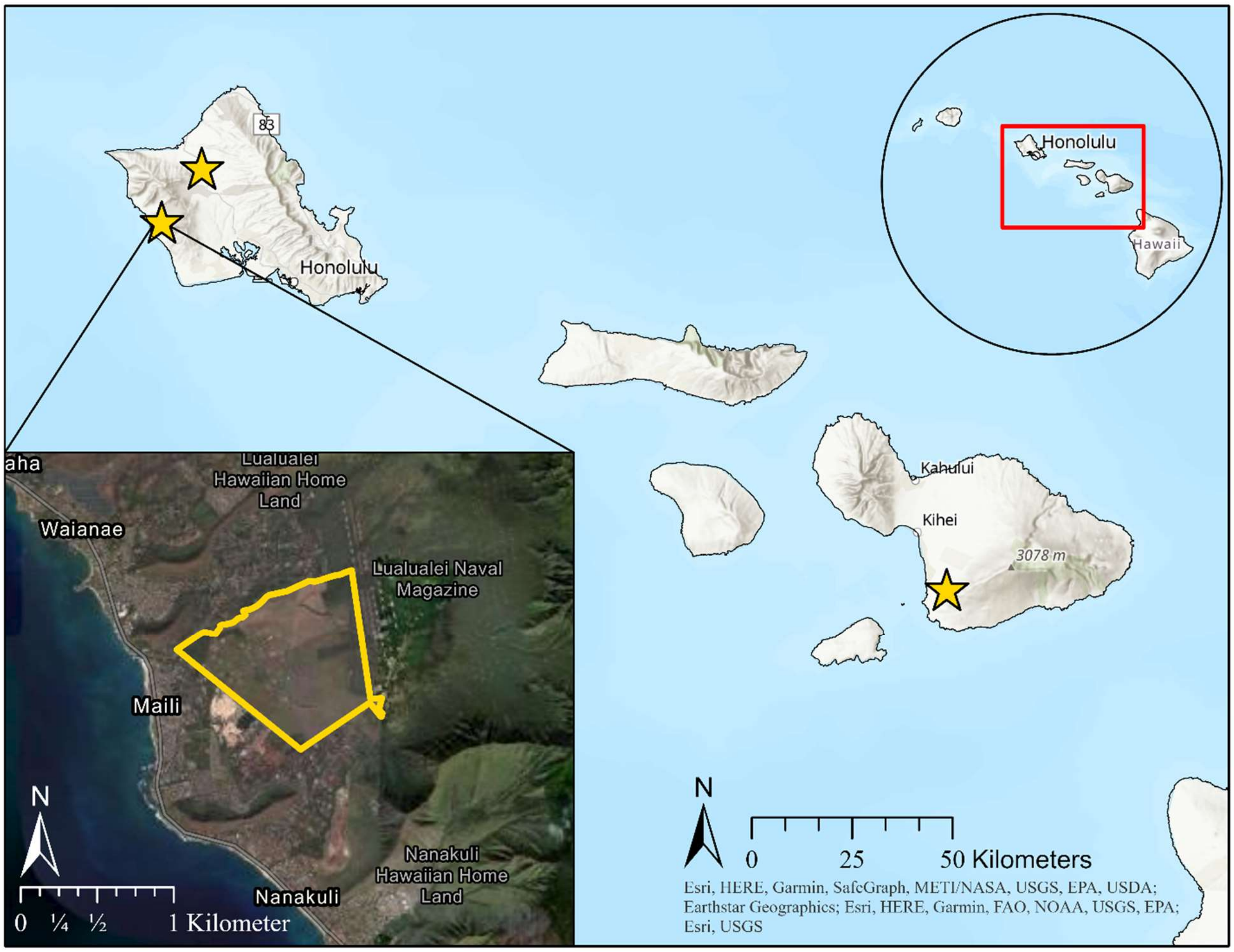

Figure 3.1. Yellow stars indicate field sites where I attempted to capture pueo on the islands of O‘ahu and Maui, Hawai‘i, USA. An inset of the Joint Base Pearl Harbor Hickam Lualualei Annex (JBPHH-LA) on the island of O‘ahu is included, showing the site where pueo were successfully captured for this study.

Table 3.1. Description of land-cover categories digitized at the Joint Base Pearl Harbor Hickam Lualualei Annex, O‘ahu, Hawai‘i, USA.

Land-cover Type	**Description**
Grassland	Buffelgrass (*Cenchrus ciliaris*) dominated grassland either maintained at a height of about 20 cm height through regular mowing or not maintained at a height of about 40 cm
Kiawe Woodland	Wooded overstory dominated by mature common kiawe (*Prosopis pallida*) and understory dominated by unmaintained buffelgrass
Wetland	Fresh and saltwater wetlands dominated by California grass (*Urochloa mutica*) and saltwort (*Batis maritima*), respectively
Urban	Urbanized lands including housing, parks, parking lots, etc.
Agricultural	Lands used for the production of row crops
Water	Open water in ponds, ditches etc.
Developed	Other developed lands, including quarries

Capture Methods

Pueo trapping sessions were conducted during crepuscular periods known to have peak activity, starting about 2 hours before sunset and ending before midnight from February 2019 through October 2019 (Cotin et al. 2018). Pueo were captured using a dome shaped bal-chatri trap baited with a mouse (*Mus musculus*; Bird and Bildstein 2007). A bal-chatri trap consists of a cage covered with many monofilament nooses baited with a prey item inside. An interested pueo will attempt to capture the prey, landing on the trap where its feet become ensnared in the nooses. Captured pueo were outfitted with an alpha-numeric colored visual identification band and a United States Geological Survey aluminum Federal Bird Band (3.2g total). Recognizing that there may be impacts related to transmitter attachment, care was taken to tailor the harness design to specifically fit pueo following expert guidance (Barron et al. 2010, B. Milsap, J. Pagel, United States Fish and Wildlife Service, and J. Penniman, Maui Nui Seabird Recovery Project, personal communication). Pueo were outfitted with a VHF transmitter (American Wildlife Enterprises 8.7g backpack AWE-Q) using a backpack-style harness constructed with 3/16-inch Teflon ribbon (Bally Ribbon Mills, 2g). A small piece of neoprene was attached to the underside of transmitters to make the fit more comfortable (Figure 3.2). The total weight of the transmitter, harness, and band was about 14g representing 4.7% of the average weight of tagged pueo (299g).

For each captured individual, several biometric measurements were collected using a wing rule and calipers accurate to the nearest 1 mm including unflattened wing chord, tail, and metatarsal length, and body mass to the nearest 0.1 g using an electronic scale (Appendix B). A few drops of blood were collected from the brachial vein and stored on FTA cards (Flinders Technology Associates) for future genetic analyses. Individuals were sexed and aged by plumage characteristics (Martínez-Climent et al. 2002). The banding, tagging, and morphometric process lasted up to three hours and individuals were released in the same location they were trapped. After release, tagged individuals were observed for at least 30 minutes to observe that they resumed normal activities. All activities took place under appropriate federal, state, and institutional permits (Bird Banding Lab permit no. 24137; Hawai‘i Department of Forestry and Wildlife Scientific Collecting Permit no. WL19-10; University of Hawai‘i Institutional Animal Care and Use Committee protocol no. 18-2752; and University of Hawai‘i Institutional Biosafety Committee protocol no. 18-11-949-01).

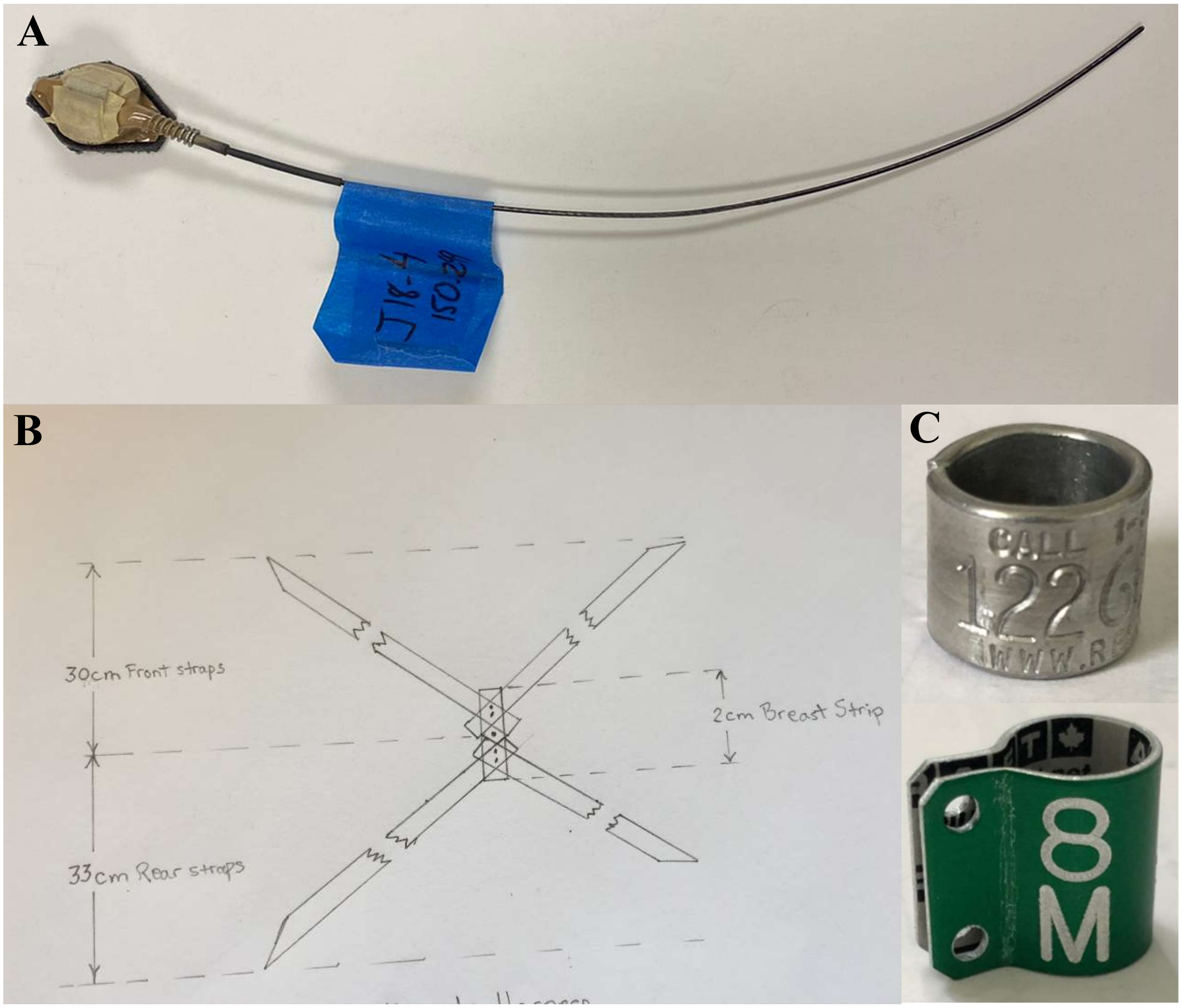

Figure 3.2. (A) American Wildlife Enterprises backpack AWE-Q VHF transmitter; (B) backpack-style harness design tailored to pueo (B. Milsap, J. Pagel, United States Fish and Wildlife Service; J. Penniman, Maui Nui Seabird Recovery Project, personal communication); and (C) aluminum federal and visual identification bands used to tag and band pueo in 2019 on the island of O‘ahu, Hawai‘i, USA.

Tracking Methods

VHF tagged pueo were resighted using a 3-element yagi antenna on at least three different days per week over the lifespan of the transmitters. Sequential resight locations were collected at least half an hour apart. Upon resighting, I recorded the location of the tagged pueo, and conducted behavioral observations for 5-10 minutes. I observed the individual with a spotting scope or binoculars either before they were alerted to my presence or from the greatest distance possible to minimize behavioral response to observer presence. Behavior at the time of resighting was classified as either flying, hooting, hunting, patrolling, agonostic, wing-clapping, courtship flight, roosting, or unknown (Table 3.2). Additional data were collected during each resight including time of day, general habitat notes (e.g. perch substrate), visually estimated perch height, and weather data. Weather metrics included temperature and windspeed measured with a Kestrel 5000 Environmental Meter, precipitation (none, slight, steady, or heavy), and percent cloud cover.

Land-cover types were assigned to each resight location using the Spatial Join tool in ArcGIS Pro 2.7. Land-cover types were digitized from satellite imagery using manual interpretation (Table 3.1, Esri 2021). General habitat notes from the field at the time of observation as well as subsequent field visits were used to inform land-cover types derived from satellite data.

Table 3.2. Description of behaviors (Clark 1975, Wiggins et al. 2020).

Behavior	**Description**
Flying	Exact behavior unknown, seen in flight likely transiting between locations
Hooting	Perched and hooting
Hunting	Diving for prey, flying with facial disk concentrated below, kiting, perched and active with eyes open, facial disk rounded and ear tufts down
Patrolling	Exaggerated wing beats high over body displaying the under-wing
Agonistic	Flying fast and directly at intruder, pulling up and presenting talons
Wing-clap	Defensive wing-clap display while flying low
Courtship flight	Male ascends by flying in small circles to a desired height (30-150 m), hangs in wind or flies forward on fanned wings and tail, give courtship song, followed by shallow stoop with about 5-10 wing-claps under trunk of body. Female usually perches below giving call. Male performs several bouts before descending to ground with wings in positive dihedral position, rocking side to side
Perched – roosting	Eyes closed, relaxed facial disk and ear-tufts, and wings tucked near body
Unknown	Behavior is unknown (e.g. unable to observe directly, or disrupted behavior upon relocation)

Data Analysis

Resight data were analyzed with the program R (Version 4.0.3) using the packages adehabitatHR, sp, and rgeos, to estimate pueo home ranges and describe habitat use (Calenge 2006, Bivand et al. 2013, Bivand and Rundel 2020, R Core Team 2020). Home ranges can be estimated using several techniques ranging from simple minimum convex polygons to more complex parametric kernel density estimates (KDE; Worton 1989) or mechanistic models such as the Brownian bridge movement model (BBMM; Horne et al. 2007). Kernel home range estimation methods were most appropriate for the data in this study given our small sample size and resight frequency (Kernohan et al. 2001). KDE home ranges were built using the package adehabitatHR (Calenge 2006). Classic KDEs also assume independent relocations. Relocations can be considered independent when the focal individual has had sufficient time to traverse its home range between relocations.

KDEs are used to estimate a three-dimensional probability density function. When applied to home ranges, a KDE describes the spatial utilization distribution of a tagged individual and can be interpreted as the relative probability of finding an animal in any part of its home range at any given moment (Powell 2000). KD home range estimates are built by placing a kernel, or three-dimensional bump, around each resight location with a peak over the resight location and decreasing in height with distance from the resight location. The kernels overlap and create an estimate of the utilization distribution.

The width of the kernel placed around each resight location is controlled by the smoothing parameter, h. Two common methods are used for selecting an h-value; the reference method (h_{ref}) and the least squares cross validation method (LSCV). The h_{ref} method selects h based on the variance of the relocations and was developed for normal unimodal distributions. In contrast, the LSCV method selects an h-value based on minimizing the estimated measure of error and is more appropriate for use with multimodal distributions (Worton 1989, 1995, Horne and Garton 2006, Fieberg 2007). In this study I created home range estimates beginning with the LSCV method and then visually inspected the output for severe under or oversmoothing. Home range estimates were fit using h_{ref} if the LSCV method failed to converge or the LSCV output showed obvious smoothing issues (Seaman and Powell 1996, Blundell et al. 2001, Huck et al. 2008).

To assess differences in habitat use by behavior, I used a Pearson’s Chi-square test to compare land-cover class use while hunting and while roosting for all individuals with >40 resights pooled. Low count categories were lumped or excluded, or a Fisher’s exact test was used when the data failed to meet the minimum expected count assumptions of a Pearson’s Chi-square test (Kim 2017). Activity patterns were assessed by grouping resights into two behavioral states, inactive (roosting), or active (any behavior other than roosting). Resight times were grouped into three time periods, diurnal, crepuscular, and nocturnal. Crepuscular periods were defined as the time period when the sun was between 0° and 18° below the horizon. Sun position was calculated for each resight location and time using the suncalc package in R (Thieurmel and Elmarhraoui 2019). A Pearson’s Chi-square test was used to compare activity and time period for all individuals with >40 resights pooled, and in the case of low counts, a Fisher’s exact test was used. If results from a pooled Chi-square or Fisher’s exact tests were significant, a Fisher’s exact post-hoc analysis was conducted (Shan and Gerstenberger 2017).

RESULTS

A total of 85 trapping sessions were conducted over a 7-month period from February 2019 through February 2020 for a total of approximately 1300 person hours. During this period, I captured and banded a total of 5 pueo (2 adult females, 1 subadult female, 2 adult males) from the JBPHH-LA site, and VHF transmitters were attached to all owls except for one adult female (Table 3.3). VHF tagged individuals were then tracked and resighted for an average of 53 days until the tags failed, or the individual died (Table 3.3). I recorded an average of 26 resight locations per individual; however, due to a harness failure (adult male) and one mortality (subadult female), two individuals were tracked over a relatively shorter period. An additional 2 fledglings of unknown sex were hand-captured at nests incidentally discovered in March of 2020. One fledgling was banded and released and the second was released without bands because it was too young to be banded.

An adult male tagged with a VHF transmitter on 11th of February 2019 was able to destroy the harness and the transmitter was recovered 7 days later. Owls in general are well known to be hard on transmitters due to their mobile necks and hooked bills allowing them to access tags and harnesses in ways that other species cannot. The adult male has subsequently been resighted in the same area exhibiting normal behavior. A subadult female, tagged on 29th of April 2019, was found dead 23 days later on the 22nd of May 2019 in an open field in close proximity to a communications tower (21°25'12.7"N 158°08'49.2"W). The individual was observed alive the previous night putting time of death late May 21st or early May 22nd, 2019. The body was collected and transferred to Dr. Thierry Work at the United States Geological Service National Wildlife Health Center Honolulu Field Station for necropsy. Necropsy results indicate trauma as the likely cause of death. Apparent cause of death coupled with the location of the body near the communication towers indicate that collision with the tower or guy wires likely resulted in death. Some feather loss was noted under both wings near the harness strap.

The remaining two tagged pueo, an adult male and adult female, were tracked and resighted for an average of 90 days, until the internal batteries of the VHF transmitters became too weak to emit a signal (Table 3.3). I recorded an average of 46 resight locations for these two individuals. Resight locations were recorded between the hours of 0500 Hawaiʻi Standard Time (HST) and 2300 HST. At the time of resight, I observed individuals using land-cover classes including developed (*n* = 25), grassland (*n* = 41), kiawe woodland (*n* = 22), and urban (*n* = 4;

Table 3.4). Only one individual was observed using urban areas in the town of Māʻili about 1.5 km from its roost site. Kernel density home range estimates were generated for these two individuals with an average 50% core area of 1.12 km^2 and an average 95% full area of 5.57 km^2 (Figure 3.3). Land-cover composition of home ranges are reported in Table 3.4. Single occasion forays to new locations up to 4.5 km away from the full home ranges were recorded four times and in all cases the individual returned to their home range within a day.

Table 3.3. Pueo tagged and banded from the 11th of February 2019 to the 25th of March 2020 at the Joint Base Pearl Harbor Hickam Lualualei Naval Annex on O‘ahu, Hawai‘i, USA.

Federal Band Number	**Color Band**	**Age**	**Sex**	**Capture Date**	**Duration (days)**	**No. of Resight Locations**	**Fate**
1155-51121	Green 7C	Adult	M	11 Feb. 2019	7	7	Harness Failure
1155-51122	Green 7K	Adult	M	22 Feb 2019	103	50	Battery Failure
1155-51123	Green 7N	Adult	F	20 Mar. 2019	77	42	Battery Failure
1155-51124	Green 7D	Subadult	F	29 Apr. 2019	23	6	Mortality
1155-51125	Green 7E	Adult	F	18 Oct. 2019	No Transmitter	NA	NA
1226-11160	Green 8B	Juvenile	Unk	25 Mar. 2020	No Transmitter	NA	NA

Table 3.4. Home range size estimates (core and full) and within home range land-cover type compositions for two pueo tagged and tracked from the 11th of February 2019 to the 5th of June 2019 at the Joint Base Pearl Harbor Hickam Lualualei Naval Annex on O‘ahu, Hawai‘i, USA.

Federal Band Number (VID)	**Age**	**Sex**	**Land-cover Class**	**Core Area[a] ha (%)**	**Full Area[b] ha (%)**
1155-51122	Adult	Male	Agriculture	2.9 (2%)	20.2 (3%)
(Green 7K)			Developed	12.9 (9.6%)	88.7 (12%)
			Grassland	77.9 (58.1%)	330.1 (44%)
			Kiawe Woodland	34.2 (25.5%)	116.0 (15%)
			Urban	4.3 (3%)	139.7 (19%)
			Water	1.2 (1%)	58.1 (8%)
			Wetland	0.5 (<1%)	1.2 (<1%)
—			**Total:**	134.0 ha	753.9 ha
1155-51123	Adult	Female	Agriculture	0.0 (0%)	9.4 (3%)
(Green 7N)			Developed	9.5 (16.2%)	18.3 (5%)
			Grassland	49.2 (84%)	266.3 (74%)
			Kiawe Woodland	0.0 (0%)	50.3 (14%)
			Urban	0.0 (0%)	12.2 (3%)
			Water	0.0 (0%)	1.7 (<1%)
			Wetland	0.0 (0%)	1.2 (<1%)
			Total:	58.7 ha	359.4 ha

[a] Core kernels represent the 50th percentile of the kernel density home range estimate.

[b] Full kernels represent the 95th percentile of the kernel density home range estimate.

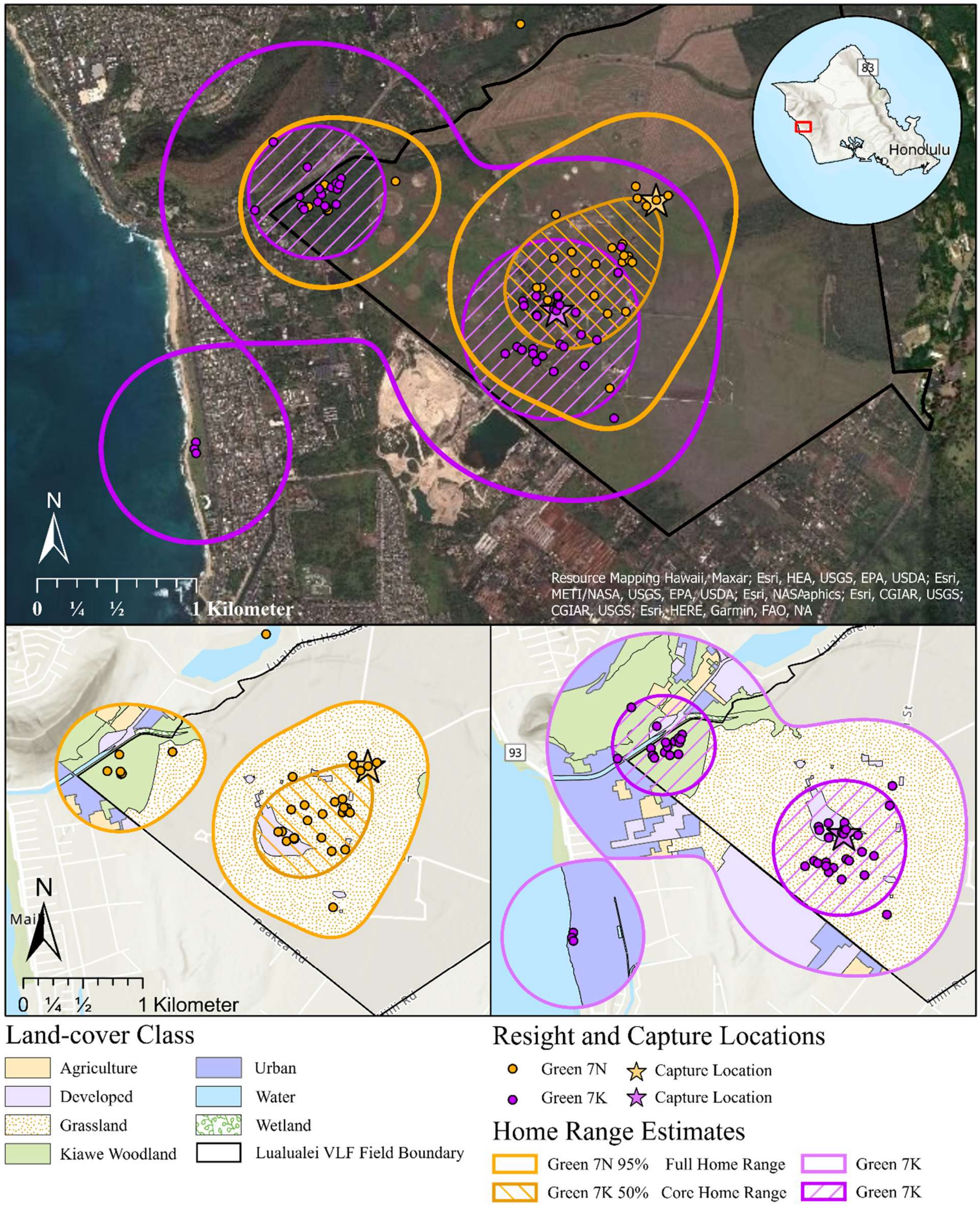

Figure 3.2. Capture and resight locations with full (95%) and core (50%) home range estimates of two pueo (Green 7N – adult female; Green 7K – adult male) captured at the Joint Base Pearl Harbor Hickham Lualualei Annex, Oʻahu, Hawaiʻi, USA and resighted with VHF transmitters from the 11th of February 2019 until the 5th of June 2019.

Behaviors observed at the time of resight included roosting (*n* = 34), hunting (*n* = 32), agonistic (*n* = 2), calling (*n* = 2), flying (*n* = 1), and unknown (*n* = 21; Figure 3.4). Individuals were observed hunting both aerially (*n* = 4) and from perches (*n* = 28) including the ground (*n* = 19), trees (*n* = 5), and streetlights (*n* = 4). I observed individuals roosting both perched in trees (*n* = 29) and on the ground (*n* = 5). Few resights were recorded in urban areas (*n* = 4) and the urban land-cover class was excluded from analysis, leaving developed, grassland, and kiawe woodland land-cover classes. Using a Pearson's chi-square test I found land-cover class use was significantly associated with behavior for the two individuals with >40 resight locations pooled ($P < 0.01$; $\chi 2 = 43.7$). A post-hoc analysis indicated that hunting behaviors were more often observed in grassland (83%) than developed (14%) or kiawe woodland (3%) land-cover classes. Roosting individuals were more often observed in developed areas (53%) in comparison to kiawe woodland (44%) or grassland (3%; Table 3.5). The unknown behavior category showed no significant association with land-cover class, indicating that the frequency of unknown observations was not related to land-cover (Table 3.5).

I recorded resights most often during diurnal periods (*n* = 46) followed by crepuscular (*n* = 27), and nocturnal (*n* = 19) time periods (Figure 3.5). Using a Fisher's exact test, I found that time period was significantly associated with activity for the two individuals with >40 resight locations pooled ($P < 0.01$). A post-hoc analysis indicated that the proportion of resights of active individuals was highest during nocturnal (70%) and crepuscular (63%) periods and lowest during diurnal periods (15%; Table 3.6). The unknown behavior category showed no significant association with time period, indicating that the frequency of unknown observations was not related to time of day (Table 3.6).

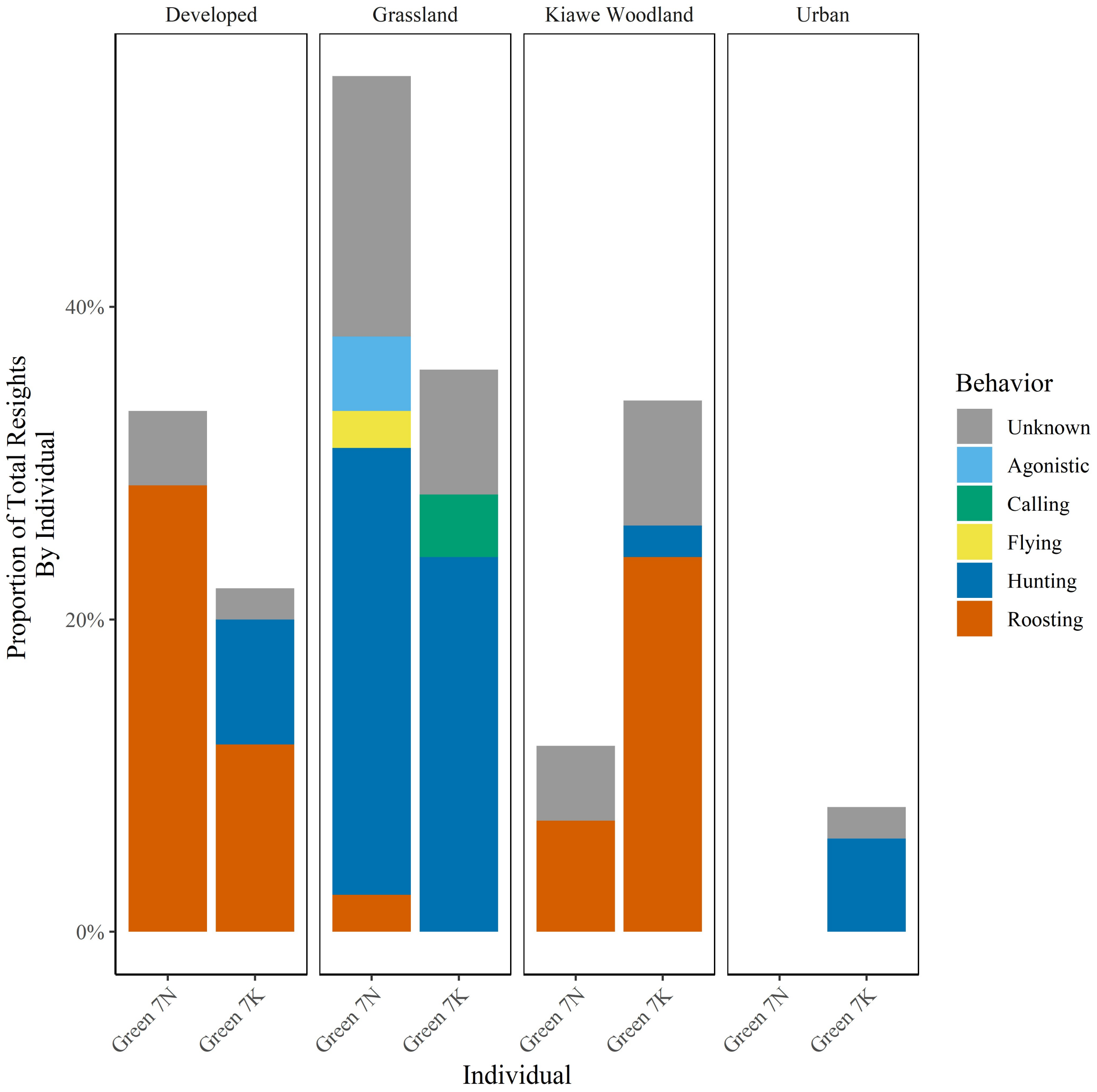

Figure 3.3. The proportion of resights in different land-cover classes broken down by behavior at the time of resight of two pueo (Green 7N – adult female; Green 7K – adult male) captured at the Joint Base Pearl Harbor Hickham Lualualei Annex, Oʻahu, Hawaiʻi, USA and resighted with VHF transmitters from the 11th of February 2019 until the 5th of June 2019.

Table 3.5. Table of *P*-values from a Fisher's exact post-hoc analysis of hunting and roosting behaviors by land-cover class of two pueo tagged and tracked from the 11th of February 2019 to the 5th of June 2019 at the Joint Base Pearl Harbor Hickam Lualualei Naval Annex on O'ahu, Hawai'i, USA. Samples sizes are in parentheses and asterisks indicate significance.

	Developed	**Grassland**	**Kiawe Woodland**
Hunting	0.02 (4)*	<0.01 (24)*	<0.01 (1)*
Roosting	< 0.01 (18)*	<0.01 (1)*	<0.01 (15)*
Unknown	0.10 (3)	0.30 (11)	0.77 (6)

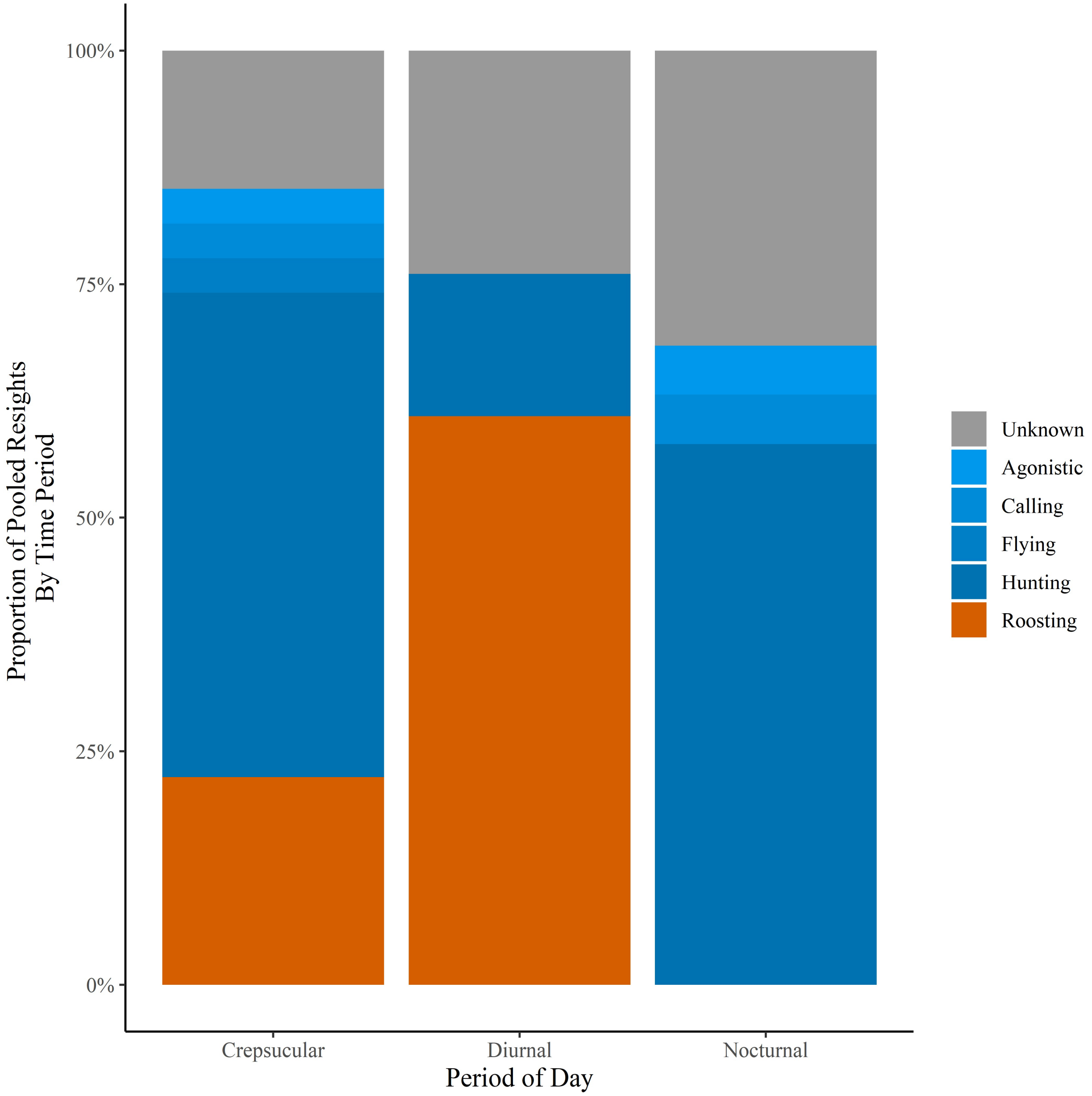

Figure 3.4. Proportion of resights of active (blue: agonistic, calling, flying, or hunting) or inactive (orange: roosting) of two tagged pueo at the Joint Base Pearl Harbor Hickham Lualualei Annex, Oʻahu, Hawaiʻi, USA and resighted with VHF transmitters from the 11th of February 2019 until the 5th of June 2019.

Table 3.6. Table of *P*-values from a Fisher's exact post-hoc analysis of activity throughout crepuscular, diurnal, and nocturnal time periods of two pueo tagged and tracked from the 11th of February 2019 to the 5th of June 2019 at the Joint Base Pearl Harbor Hickam Lualualei Naval Annex on O'ahu, Hawai'i, USA. Samples sizes are in parentheses and asterisks indicate significance.

	Crepuscular	**Diurnal**	**Nocturnal**
Inactive	0.10 (6)	<0.01 (28)*	<0.01 (0)*
Active	0.01 (17)*	<0.01 (7)*	0.01 (13)*
Unknown	0.29 (4)	1.0 (11)	0.36 (6)

DISCUSSION

Short-eared owls are typically considered open habitat specialists, utilizing grasslands, shrublands, and agricultural areas almost exclusively, but my resight data from VHF tagged owls in Hawaiʻi allowed me to document consistent use of forested and wooded developed areas in addition to grasslands. Although I am unable to make broad population inference due to the small sample size of this study, these findings hint at a more diverse range of habitat used by pueo than their continental counterparts. Antillean short-eared owls native to the islands of Hispaniola and Cuba in the Caribbean (*A. f. domingensis*) have also been known to inhabit tropical and montane forest edges, and mangroves (Wiley 1986, Wiley et al. 2010, Enríquez 2015). Habitat use and niche expansion of populations on island systems may be attributed to impoverished species richness releasing island residents from inter-specific competition while increasing intra-specific competition (Van Valen 1965, MacArthur et al. 1972, Alcover and McMinn 1994, Sayol et al. 2018). The short-eared owl is a good candidate for further research of this phenomenon in raptors owing to their global distribution throughout temperate, tropical, continental, and island systems with resident and migratory populations throughout.

The two tagged pueo at JBPHH-LA field occupied adjacent territories throughout the duration of the study and home range estimates built for the two individuals showed considerable overlap at the full and core use areas (95% and 50% contours, respectively). The two individuals were observed using the same areas, including even the same specific trees, for roosting consistently throughout the study period. At one point the two pueo were observed roosting in the same tree as a barn owl. Conspecific communal roost sites are well documented in the literature for the species, at least during the non-breeding season, and our observations appear consistent with our two pueo (Clark 1975, Bosakowski 1986, 1989, Schneider 2003, Vrezec 2016). Home range overlap of the two was also evident in grassland areas used for hunting nearby, however, the owls defended hunting patches and when one individual encroached on the hunting territory of the other a fight would ensue. On occasion if an individual began hunting before the other, they would attempt to hunt in adjacent hunting territories only to be chased out when the owner left their roost.

Hunting and roosting behaviors were significantly associated with land-cover class use for these two individuals, with hunting occurring mostly during crepuscular and nocturnal periods in grassland, and diurnal roosting in kiawe woodland and developed areas. Calladine and

Morrison (2013) and Tseng et al. (2017) also noted differential habitat use during diurnal roosting and nocturnal hunting of VHF tagged short-eared owls in Scotland and Taiwan, respectively. Strikingly, one individual (male) was found occasionally leaving the JBPHH-LA area, flying approximately 1.5 km over the town of Māʻili, to hunt in a busy urban beach park. The individual was only observed using this area after dark and with night vision equipment I was able to observe the individual hunting cockroaches on the ground near the public restrooms. During one observation I resighted the pueo hunting from a perch in a palm tree in the beach park.

Unlike other short-eared owl subspecies that typically roost on the ground in open fields and occasionally on perches (Clark 1975, Bosakowski 1986, 1989, Enríquez 2015, Tseng et al. 2017), I found that pueo roosted diurnally mostly in kiawe woodland and developed areas, on branch perches between 2−5 m high. The developed areas being used for roosting by the two pueo consisted of an abandoned military housing project with mature ornamental trees throughout. Nominate short-eared owls have been known to use wooded areas for roosting when deep snow covers ground roosting sites, but this behavior appears to be relatively rare in continental populations (Bosakowski 1986). Grasslands in the JBPHH-LA are composed largely of mowed fields maintained for fire risk management through regular mowing by the U.S. Navy. Although patches of undisturbed grassland do exist in the study area, mowing activities over a large portion of the fields may be driving the pueo to seek roosting sites in wooded areas and this pattern may not hold for pueo in other areas with less anthropogenic disturbance. Nonetheless the consistent use of wooded areas for roosting hint that wooded ecosystems may represent an important component of pueo habitat.

Mowing activities at the JBPHH-LA site have the potential to impact pueo in several ways. Regular disturbance of the grassland could be influencing the use of wooded areas for roosting. Further, agricultural mowing is known to destroy nests (Arroyo and Bretagnolle 1999, Stanton et al. 2018, Sviridova et al. 2020), but also represents a threat to chicks that disperse from the nest prior to fledging. However, studies have also shown that habitat management through fire, mowing, or seasonal grazing conducted at an appropriate time of year may be required to maintain grasslands of a suitable height for short-eared owl nesting (Herkert et al. 1999, Dechant et al. 2001). Nominate short-eared owls also tend to prefer hunting in habitat with less structure (height < 30 cm and lower density) with more forb cover than roost sites (Weller et al. 1955, Novak and Ross 2016, Ting and Washburn 2017). Overall, more research is needed to understand how mowing or other forms of disturbance by heavy machinery may impact short-eared owls.

In my study, I found that the majority of pueo hunting observations took place from perched positions, rather than on-the-wing. Short-eared owls, however, are often observed hunting on the wing, and they are well-known for this characteristic behavior. Previous studies have even described short-eared owls in North America as hunting largely on the wing and rarely from perched positions (Clark 1975, Village 1987). Bosakowski (1989) later suggested that hunting from perches plays a more significant role than previously thought, and proposed that perch-hunting could be the primary form of hunting, noting the regularity with which they observed short-eared owls in New Jersey hunting from perches such as fence posts. In agreement with Bosakowski I found that tagged pueo were most often hunting from perched positions with hunting on the wing relatively rare. Bosakowski and others have described perch hunting as mostly occurring from elevated locations such as wooden fence posts, power lines, or elevated hills (Martínez et al. 1998, Keyes 2011). I did observe pueo hunting from elevated perches including streetlights more often than hunting on the wing, however, the majority of hunting resights were of pueo hunting from ground perches. Previous studies, however, based inference on observational studies of unmarked birds and may have overemphasized the prevalence of hunting on the wing and from elevated perches due to ease in which individuals are observed on the wing and perched in elevated locations in comparison to a ground perch.

Activity levels of the two tagged pueo were correlated with the period of day. Active behaviors, including hunting, agonistic, callings, and flying, peaked during crepuscular and nocturnal periods while roosting peaked during diurnal periods. Neither of the pueo were observed roosting during nocturnal periods, and were only infrequently observed active during diurnal periods; however, pueo, and short-eared owls in general, are well-known for their diurnal activity and have even occasionally been described as diurnal in the literature (Berger 1981, Mikkola and Willis 1983, Pratt et al. 1987, NatureServe 2021). This behavior is likely overstated, maybe owing to the novelty of observing an owl during the day. The results of this study, eBird observations, and others suggest that short-eared owls are most active during crepuscular periods with activity likely continuing throughout the night (Erkinaro 1973, Clark 1975, Bosakowski 1986, 1989, Calladine et al. 2010, Calladine and Morrison 2013).

Although effective for short-term, smaller spatial scale studies, VHF utility is limited by battery life and transmission range for long term and regional scale studies. Annually and regionally, it is still unclear how far and how frequently pueo are moving, whether through seasonal migration or dispersal within or among islands. In a similar study on the wintering grounds in Taiwan of VHF tagged nominate short-eared owls researchers noted that owls used roosting and hunting sites for a few days before abandoning them in search of another site at an average distance of 3.25 km from the former (Tseng et al. 2017). No regional movements were observed of VHF tagged pueo tracked in my study, over longer periods of time. Four cases of forays outside of the study area (<4.5 km) were recorded but the individuals returned to their home ranges within a day and forays were isolated events. Our tracking efforts did coincide with breeding at the site when individuals are less likely to move out of the area, however, neither of the two tagged pueo bred that year and therefore were not attached to a nest site.

Short-eared owls in general are highly volant and capable of inter-island movements. In the Galápagos researchers found evidence for interisland movements by the endemic Galápagos short-eared owl (*A. f. galapagoensis*) over distances similar to those found in Hawaiʻi (Schulwitz et al. 2018). Pueo have also been observed breeding on the island of Kahoʻolawe during annual rodent irruptions and conspicuously absent from the island when rodent abundance is low, suggesting regular movement to and from the island (J. Bruch, Kahoʻolawe Island Reserve Commission, personal communication). At the JBPHH-LA field site, however, I have consistently resighted VID tagged pueo in the same territories for two consecutive years after banding. This hints that at least some of the population may be largely resident in Hawaiʻi, and further research is needed to explore movement patterns over longer periods of time and at more sites with the use of solar powered GPS devices.

CHAPTER 4

SUMMARY

This thesis represents one of the first attempts to explore the population status of pueo, the endemic short-eared owl of Hawaiʻi, across their range and I report the first successful use of transmitters to study pueo movement. My goal was to answer questions about population dynamics and habitat use directly relevant to the conservation of pueo through the lens of global theory. I present evidence that the Hawaiian short-eared owl population has been relatively stable for the last ten years, and present other findings that hint at suspected broader patterns of niche expansion and more resident population.

Short-eared owls provide an interesting challenge when studying population dynamics, owing to their low rates of occupancy across broad landscapes and even lower rates of detection. Furthermore, populations of short-eared owls in North America appear to be extremely vagrant and rarely occupy the same areas from year to year, frustrating efforts to monitor short-eared owl populations there (Booms et al. 2014, Johnson et al. 2017, Meyers et al. 2020). In Hawaiʻi, I found that trends of pueo occupancy appear relatively stable over the last ten years at the statewide scale, although there is evidence of a slow decline. More research is needed to build predictive models that can help assess pueo extinction risk as well as identify factors driving occupancy dynamics over time. Strong differences were found in occupancy between islands with estimates lowest for Oʻahu and Hawaiʻi island. The relatively low pueo occupancy estimate on the island of Oʻahu is in line with expectations given that pueo are listed as an endangered species on the island of Oʻahu by the state of Hawaiʻi. Curiously, occupancy estimates are equally as low for the island of Hawaiʻi and raises concerns for the continued existence of pueo on Hawaiʻi island. More research is needed to better understand why occupancy estimates are so low for Hawaiʻi island in particular and occupancy trends for the island remain unknown.

While modelling population dynamics, I found rates of site-specific colonization and extinction were not strongly season or island dependent and site turnover is much lower compared to estimates generated for short-eared owls in western North America (Meyers et al. 2020). This evidence suggests that the pueo population is less spatially dynamic from year to year than short-eared owls in western North America. I propose that this pattern can be explained by a less nomadic and migratory population in Hawaiʻi, potentially due to more consistent resource availability across seasons, expanded diet, limited competition with other raptor species, among others. I present further evidence with the use of VHF transmitters hinting that, at least in the short-term, pueo are maintaining home ranges over longer periods of time than nomadic populations in Eurasia and North America (Johnson et al. 2017, Tseng et al. 2017). Resights of tagged and banded birds in their same home ranges up to two years after their transmitters died provides some support, although this deserves more careful study with longer lasting GPS transmitters. I suggest that differences in ecological strategies represent a case of intraspecific variation that is reflective of broad biogeographic patterns where niche expansion on island systems and more stable climates drive more resident populations (Newton 2006, Somveille 2016, Stroud 2021).I further found that the VHF tagged pueo in this study are consistently using wooded habitats for roosting, a behavior that has previously been described as unusual for the species. I recommend that wooded areas be considered for conservation purposes as potential habitat for pueo when planning for land-disturbance or development.

APPENDIX A

PUEO DETECTION PROBABILITIES

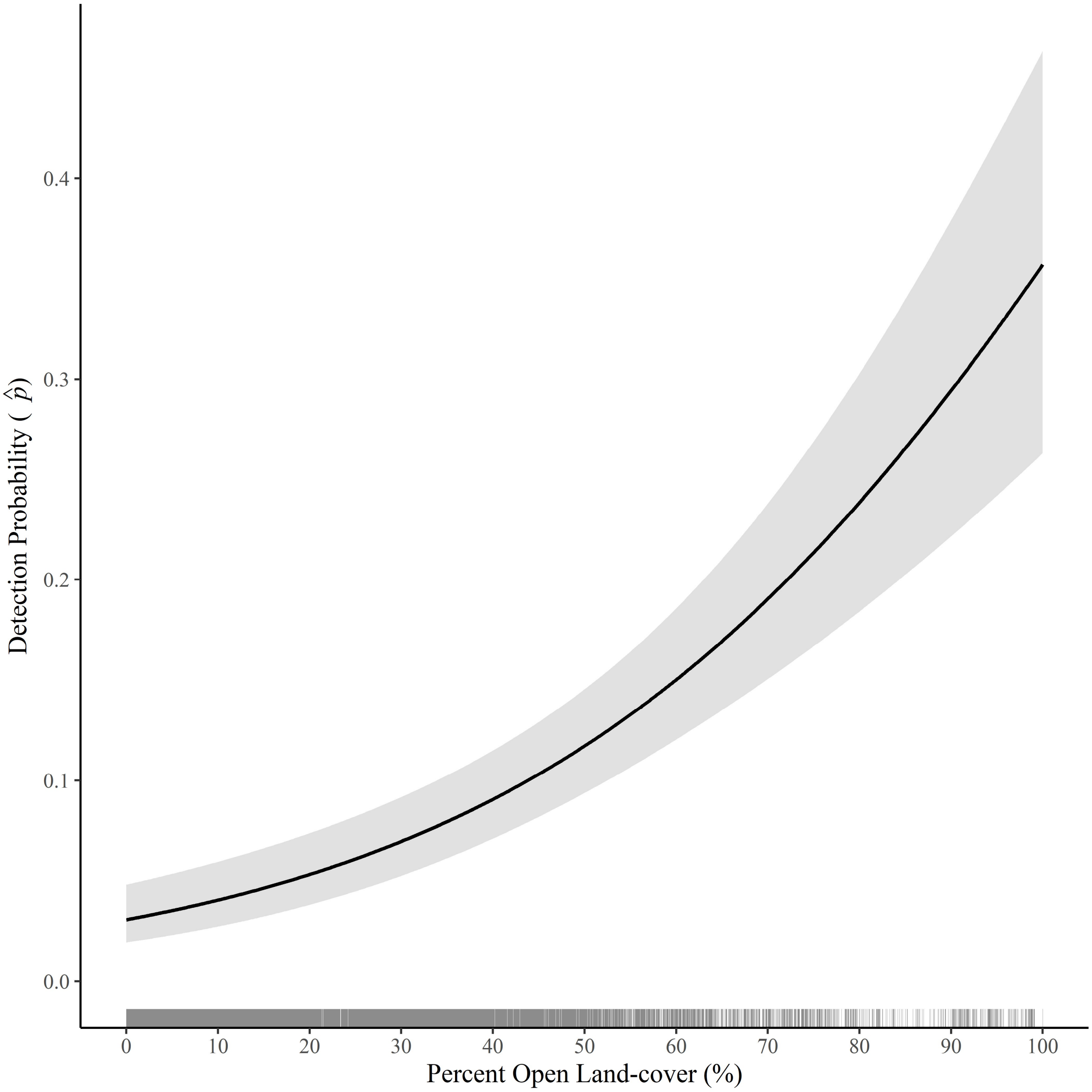

Figure A.1. Detection probabilities (p) with 95% confidence intervals as the proportion of open land-cover in a 1.5 km radius around the checklist location increases. Estimates generated from a dynamic colonization and extinction model of pueo in the state of Hawai‘i between 2011 and 2020 fit with eBird observations.

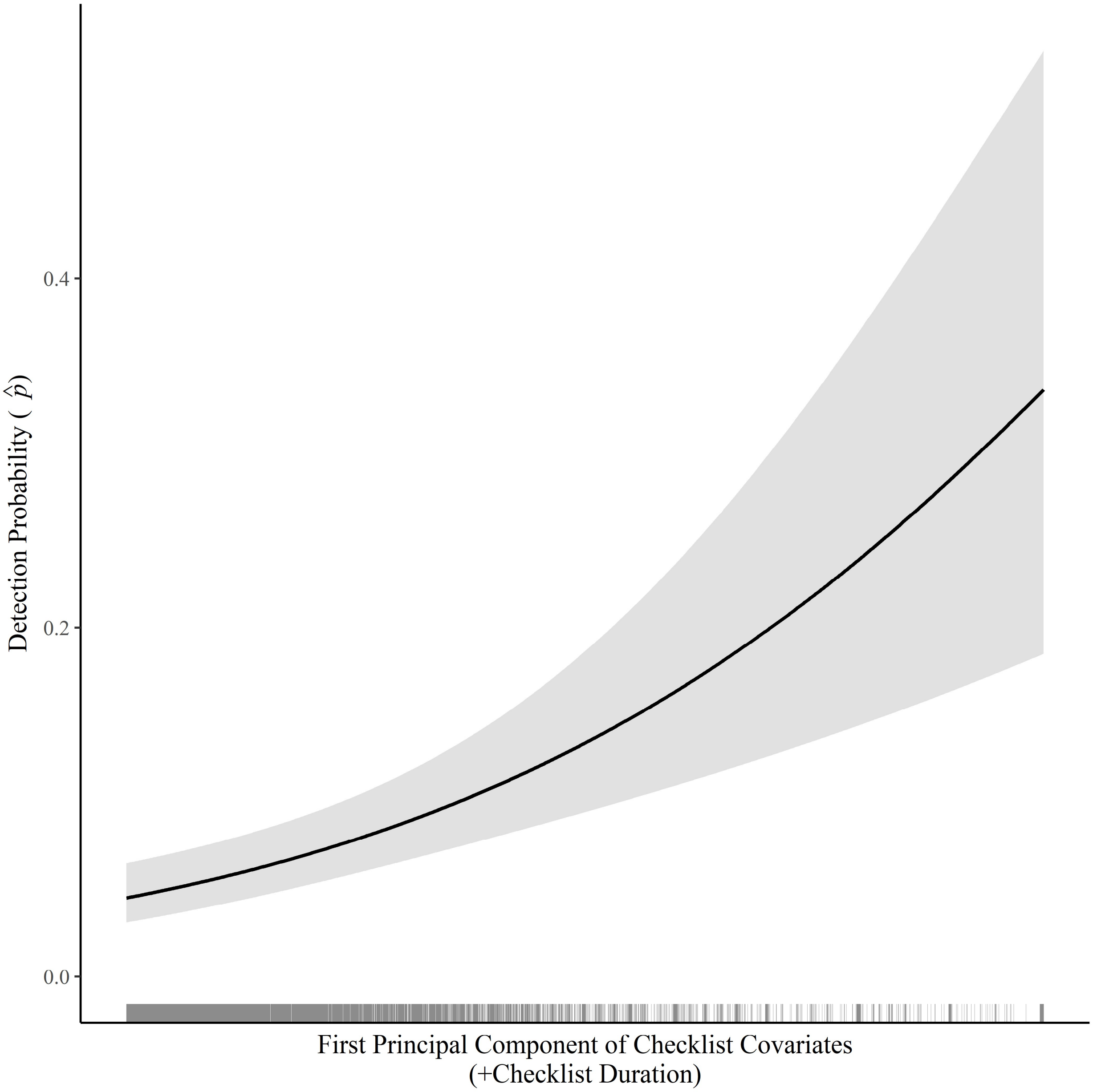

Figure A.2. Detection probabilities (*p*) with 95% confidence intervals as the first principal component of checklist effort covariates increases. The principal component is strongly positively correlated with checklist duration (min). Estimates generated from a dynamic colonization and extinction model of pueo in the state of Hawai‘i.

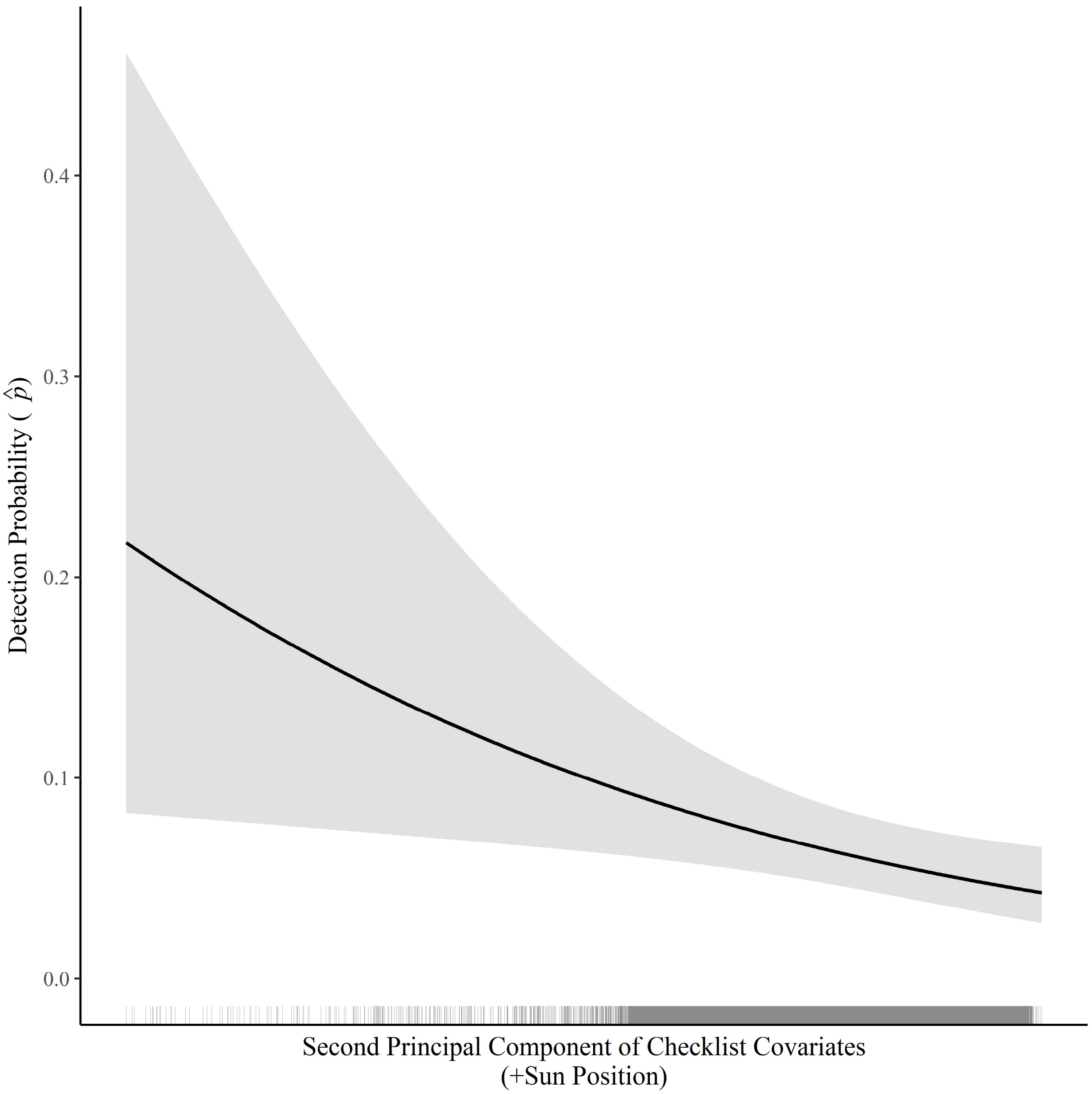

Figure A.3. Detection probabilities (*p*) with 95% confidence intervals as the second principal component of checklist effort covariates increases. The principal component is strongly negatively correlated with the time checklist began and strongly positively correlated with the number of species observed (list length). Estimates generated from a dynamic colonization and extinction model of pueo in the state of Hawai‘i.

APPENDIX B

PUEO MORPHOMETRICS

Table B.1. Morphometric data collected from pueo tagged and banded from the 11th of February 2019 to the 25th of March 2020 at the Joint Base Pearl Harbor Hickam Lualualei Naval Annex on O‘ahu, Hawai‘i, USA.

Federal Band Number	Color Band	Age	Sex	Mass (g)	Unflattened Wing Chord (mm)	Tail Length (mm)	Metatarsal Length (mm)
1155-51121	Green 7C	Adult	M	296	298	146	51.9
1155-51122	Green 7K	Adult	M	328	287	145	47.2
1155-51123	Green 7N	Adult	F	255	283	130	44.0
1155-51124	Green 7D	Subadult	F	290	320	152	44.5
1155-51125	Green 7E	Adult	F	303	324	152	46.5
1226-11160	Green 8B	Juvenile	Unk	307	NA	NA	46.0

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