BREEDING ECOLOGY AND MANAGEMENT OF PUEO (HAWAIIAN SHORT-EARED OWL, *ASIO FLAMMEUS SANDWICHENSIS*)

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ABSTRACT

Short-eared Owls (*Asio flammeus*) are an appropriate study species for understanding intraspecific variations in life-history traits in raptors due to their global distribution across continental and island systems at a variety of latitudes. In Hawaiʻi, little is known about the ecology of Pueo (Hawaiian Short-eared Owls, *A. f. sandwichensis*), but populations are thought to be in decline and are state-listed as endangered on Oʻahu. While studies of other Short-eared Owl subspecies serve as a starting point for creating conservation plans for Pueo, initial research has indicated differences in diet, habitat use, and movement ecology of Pueo versus continental Short-eared Owls. Given these differences, further regional studies from Hawaiʻi are necessary to ensure management actions adequately address the needs of Pueo. In Chapter 2 of this study, I investigated the breeding ecology of Pueo using a collaborative approach to combine results from targeted nest-searching at two focal study sites on Oʻahu with incidental reports of Pueo nests across the Hawaiian Islands. In Chapter 3 I used these results to draft management recommendations to minimize disturbance to breeding Pueo. At our focal study sites, I found that Pueo select sites with greater vegetation height and density than the surrounding environment for nesting, but that these same vegetation characteristics do not necessarily correlate to increased nest survival. The diet of breeding Pueo was relatively diverse and contained more bird prey when compared to that of North American and European Short-eared Owls. However, diet did not differ significantly among breeding Pueo pairs. Across both focal study sites and incidental observations, Pueo nest initiation spanned November through July, with a peak in February and March. Pueo breeding habitat ranged from non-native dry grasslands at low-elevation to high-elevation native wet forest, showing a marked increase in breeding habitat diversity compared to North American and European Short-eared Owls. Our results establish a basis for informing Pueo conservation in Hawaiʻi, including recommendations towards reducing different types of nest disturbance and data to inform spatial and temporal nest buffers. State-wide management actions must account for the expanded breeding season and diversity of breeding habitat types of Pueo.

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CHAPTER 1

GLOBAL INTRODUCTION

Globally, raptors have a greater proportion of threatened and declining species than other avian groups (McClure & Rolek, 2020). Understanding basic aspects of a species' ecology and threats to their survival is critical to forming effective conservation actions, but this research is lacking for many threatened and endangered raptor species, especially in island endemic and tropical species (McClure et al., 2018). Addressing these knowledge gaps in basic life history is a top research priority for many raptor species, especially those in particularly vulnerable systems (McClure et al., 2018).

One such species that requires more research to inform conservation and management actions is the Short-eared Owl (*Asio flammeus*), a raptor with a global distribution of ten subspecies on both continental and island systems across a variety of latitudes (Wiggins et al., 2020). Although Short-eared Owls are not considered threatened on the IUCN Red List, their global population trend is decreasing and regional studies show evidence of long-term population declines (BirdLife International, 2016). Despite their wide range, most research has focused on the nominate subspecies (*A.f. flammeus*) in North America and Europe. In these systems, they are known to be grassland specialists, where breeding habitat use and phenology are tied strongly to the population dynamics of their primary prey, small mammals (Clark, 1975; Korpimaki & Norrdahl, 1991). Thus, a major conservation concern for Short-eared Owls in North America is the loss of large tracts of native grasslands that serve as their primary breeding and foraging habitat (Booms et al., 2014). However, since few studies have looked at the habitat use and breeding ecology of other Short-eared Owl subspecies, particularly for island sub-species, it is unknown whether these conservation concerns and subsequent management recommendations are the same across the global distribution.

Breeding ecology and population dynamics may vary dramatically across a wide spatial scale. In species with a wide range, the differences in biogeography can lead to different interspecific interactions, climate conditions, and prey population dynamics in each region, resulting in intraspecific variation within a broadly distributed species (Blondel, 1985; Lambrechts & Dias, 1993; Van Valen, 1965; Wiggins et al., 1998). Given their global distribution across island and continental systems in both temperate and tropical regions, Short-

eared Owls serve as a good candidate for investigating intraspecific variation in breeding ecology.

Pueo, or the Hawaiian Short-eared Owl (*A. f. sandwichensis*), are the only native raptor that breeds on all of the main Hawaiian Islands (Hawai'i Department of Land and Natural Resources, 2005). Pueo are thought to originate from the North American population *A. f. flammeus* and appear relatively recently in the fossil record in Hawaiʻi. Resident populations are believed to have established on the islands around the same time as the arrival of Polynesians (approximately 1000 A.D.) and the introduction of the Pacific Rat (*Rattus exulans*), providing a reliable rodent food source (Hawai'i Department of Land and Natural Resources, 2005; Olson & James, 1982). Population trends are poorly understood, but on Oʻahu they are noted to be in decline and are state-listed as endangered (Hawaiʻi Department of Land and Natural Resources, 2005). As with mainland Short-eared Owls, Pueo seem to be threatened by habitat loss, the effects of which are exacerbated by the already restricted land area of the island system (Hawai'i Department of Land and Natural Resources, 2005). Other threats include collisions with vehicles, bioaccumulation of pesticides and rodenticides, and introduced non-native predators such as feral dogs (*Canis lupus famliaris*), feral cats (*Felis domesticus*), and Indian mongoose (*Herpestes auropunctatus*) (Bell et al., 2021; Hawai'i Department of Land and Natural Resources, 2005). In addition to their ecological importance as one of the only endemic raptor species in Hawaiʻi (the other being ʻIo (Hawaiian Hawk, *Buteo solitarius*), Pueo are a species of cultural significance as ʻaumakua, or ancestral guardians, to native Hawaiians, and appear often in moʻolelo (histories), oli (chants), and kaʻao (legends).

Given their declining populations, and significance in Hawaiian culture and history, land and natural resource managers across the state are eager for recommendations on how to reduce negative impacts to Pueo and manage habitats for their continued survival and abundance. For example, many managers are interested in predicting the likelihood of Pueo utilizing their land for breeding, or when and how to perform potentially destructive activities (i.e. clearing vegetation or digging earth) in order to minimize disturbance to Pueo nests. However, while incidental observations of Pueo breeding have been documented, no targeted study examining Pueo breeding ecology has been conducted to date, resulting in little data to answer these basic management questions. This thesis examines the breeding and foraging ecology of Pueo,

provides findings that contextualize the potential for intraspecific variation of this globally distributed species, and directly informs management activities in Hawai‘i. In chapter two I present analyses of state-wide Pueo breeding habitat use and phenology studies, including Pueo nest site selection, nest survival, and breeding diet from select study sites. In chapter three I contextualize these analyses into management recommendations that can be applied throughout the state of Hawai‘i.

CHAPTER 2

REPRODUCTIVE ECOLOGY OF PUEO

ABSTRACT

Short-eared Owls (*Asio flammeus*) are a globally distributed species known to depend strongly on intact grasslands and small mammal populations for breeding habitat and diet. However, this understanding of their breeding ecology is based primarily on research of the nominate subspecies (*A.f. flammeus)* found in North America and Europe; few studies exist outside this mainland range. Consequently, our understanding of how Short-eared owl breeding ecology may vary biogeographically is limited and results in a lack of data to inform regional conservation needs. Pueo (*A.f.sandwichensis*) are the Hawaiian subspecies of Short-eared Owl and the only endemic raptor species known to breed across all the main Hawaiian Islands, but otherwise little information exists on their breeding ecology. To address this knowledge gap, I collected data on breeding Pueo nest site selection, nest success, diet, and other breeding parameters from two focal study sites on O‘ahu, and supplemented our data with incidental reports of Pueo nests and chicks from across the state. At the focal study sites on O‘ahu, I searched for nests during the 2020–2022 breeding seasons and collected nest-site characteristic data to investigate the relationship between habitat characteristics and nest site selection and nest success. Using a binomial logistic regression model, I found that taller vegetation height and greater visual obstruction readings (VOR) were the top predictors of Pueo nest site selection. However, these same metrics did not translate to increased nest survival. Our logistic exposure model for nest survival showed that nests initiated earlier in the season and with higher percent vegetation cover had higher daily nest survival rates. Breeding Pueo diet included a variety of rodent, bird, and insect species, but diet composition did not vary significantly between different breeding pairs. State-wide nesting observations served to inform our understanding of the diversity of Pueo breeding phenology and habitat; the nesting season across all islands spans from November through July, and breeding habitats ranged from coastal vegetation on nearby atolls to high elevation native wet forest. However, despite this wide variety of breeding habitat type, Pueo nests tended to be found in areas of tall, dense vegetation, corroborating our site-specific nest site selection results.

INTRODUCTION

As top predators and "charismatic megafauna", raptors serve as biological indicators of ecosystem health and biodiversity (Bildstein, 2001; Sergio et al., 2006). Despite their ecological and cultural importance, 52% of raptor species globally are experiencing population declines, and even for species listed as "Least Concern" by the IUCN, 38% are in decline (McClure et al., 2018). World-wide, raptors are threatened by habitat fragmentation and loss, environmental contaminants, and direct mortality caused by anthropogenic factors (Bildstein et al., 1998; Grande et al., 2018). Assessments of factors that impact reproductive success and breeding ecology are necessary to understand population trajectories and ultimately to mitigate threats to raptors, especially given that their lower fecundity and longer generation time makes them more susceptible to anthropogenic impacts, such as habitat loss or human persecution, relative to other bird species (Bennett & Owens, 1997; Owens & Bennett, 2000).

However, raptors tend to be difficult to study and conserve due to their relatively low densities and large home ranges, dispersal and migration across long distances, and often elusive behavior and breeding locations (Donázar et al., 2016; Newton, 2010). These challenges sometimes result in a lack of basic life history understanding for certain species. Indeed, current research on raptors is biased towards a few species, with only 10 species accounting for one-third of all research worldwide (Buechley et al., 2019). Raptors with small geographic ranges, such as tropical and island endemics, are particularly underrepresented in research efforts despite having higher risks of extinction due to their restricted ranges and vulnerability on islands (Buechley et al., 2019; Ferrer-Sanchez & Rodrıguez-Estrella, 2015). Given the increased threats and heightened vulnerability for island and tropical raptor species, studies that fill basic knowledge gaps of their life history and ecology are necessary to address global raptor conservation needs and to investigate how biogeographic variation may influence various aspects of life history.

Some aspects of life history are likely to differ for raptors in island versus continental systems or across a latitudinal gradient, necessitating focused regional studies (Wiggins et al., 1998). For example, the globally distributed Barn Owl (*Tyto alba*) diet varies across their range with the proportion of rodents in their diet varying significantly with latitude, elevation, and island versus mainland geographies (Romano et al., 2020). However, this is one of the few examples of global biogeographical patterns in raptor niche variation due to both the low number

of raptors with a global distribution, and the abundance of data required to look at trends from all areas of their range. For species that are found on both continental and island systems, altered climatic conditions, differences in the timing of food abundance, and island size and distance from the continent are all potential factors that would result in island populations displaying a different breeding ecology than continental populations (Blondel, 1985; Lambrechts & Dias, 1993; Wiggins et al., 1998). For example, Common Kestrel (*Falco tinnunclus*) mean egg laying date and clutch size varied across a latitudinal gradient and between island and continental populations; clutch size increasing along with latitude is a commonly documented phenomenon thought to be driven by increased photoperiods at more northerly latitudes during the breeding season (Carrillo & González-Dávila, 2009; Lack, 1947). Given the potential for variance in breeding ecology based on biogeography and increased extinction risk for island-restricted species, regional studies are necessary to ensure that conservation and management actions reflect the ecology of each population (Buechley et al., 2019).

Investigating the differences in life history parameters across populations not only provides critical region-specific ecological knowledge to inform local management of threatened species, but also provides data to investigate the relationship between intraspecific niche expansions in widely distributed species. The Niche Variation Hypothesis suggests that populations with wider niches are more variable than populations with narrower niches, and has been used to explain why bird populations on oceanic islands tend to display more morphological variance than their mainland counterparts (Bolnick et al., 2007; Van Valen, 1965). This niche widening in populations may result from increased niche width of all individuals within that population, or from increased distances between each individual's niche, which remains relatively narrow (Van Valen, 1965). This theory has often been investigated by looking at the morphology of a species as a proxy for niche expansion, even though variation in behaviors and resource use may not necessarily correlate to variation in morphology (Araújo et al., 2011; Bolnick et al., 2007). Thus, studies seeking to understand individual versus population niche expansion should look at actual measures of resource use, such as comparing diet or habitat use data (Araújo et al., 2011; Bolnick et al., 2007). For example, Montagu's Harriers (*Circus pygargus*) are broadly considered a diet generalist, but studies of individual diet composition and foraging behavior showed individual specialization of breeding birds (Terraube et al., 2014). As individual variation in resource use may affect population and community

ecology dynamics, this is an important aspect of a species' ecology to understand as it can impact conservation and management decisions (Araújo et al., 2011; Terraube & Arroyo, 2011).

Short-eared Owls (*Asio flammeus*) are one of the few raptors with a global distribution inhabiting every continent except for Australia and Antarctica (Wiggins et al., 2020). Ten subspecies occur globally, including three different subspecies found across South America, six endemic island subspecies found in the Greater Antilles, the Galapagos, the Falklands, and the Hawaiian Islands, and the nominate subspecies *A. f. flammeus* found across North America, Europe, and Asia (Wiggins et al., 2020). Despite this global distribution, the bulk of our understanding of Short-eared Owl ecology stems from research of *A. f. flammeus* in North America and Europe (Booms et al., 2014; Wiggins et al., 2020). One of the main research objectives for *A. f. flammeus* in North America is identifying critical habitat, especially within their breeding range, to inform conservation planning and management (Booms et al., 2014). This objective holds true for other Short-eared Owl populations, where their breeding ecology and critical habitat is even less well understood. As a globally distributed species with both continental and island populations, Short-eared Owls provide an interesting opportunity to investigate intraspecific variations in life-history traits driven by latitudinal and geographical variation, but regional studies are needed to draw global comparisons.

In the Hawaiian Islands, the Pueo (*A.f. sandwichensis*) is the only native raptor that breeds on all the main islands yet their population dynamics, habitat use, and even basic breeding parameters remain poorly understood (Hawai'i Department of Land and Natural Resources, 2005). On O'ahu they are thought to be in decline and are state-listed as endangered, and recent efforts have been made to petition the state Department of Land and National Resources to request the listing of Pueo as endangered at the federal level (Hawai'i State Legislature, 2021). Pueo are thought to be threatened by habitat loss, the effects of which are exacerbated by the already restricted land area of the island system, as well as introduced mammalian predators such as feral cats (*Felis domesticus*), feral dogs (*Canis lupus familiaris*) and Indian mongoose (*Herpestes auropunctatus*) (Bell et al., 2021; Hawai'i Department of Land and Natural Resources, 2005). Addressing these knowledge gaps in Pueo nest site characteristics, breeding phenology, and breeding parameters will allow for a better understanding of their population trends and conservation needs. In this study, I: (1) described the breeding parameters, phenology,

and nest site characteristics of Pueo; (2) investigated the habitat characteristics influencing Pueo nest site selection and nest success; and (3) investigated diet variation in breeding Pueo and whether different nests are feeding on different prey types. This information is crucial for informing best management practices such as altering the schedule of potentially disruptive land management activities or identifying areas with the highest probability of Pueo nesting and minimizing disturbance in potential nest sites.

METHODS

Data collection

Focal study sites

Focal studies of nesting ecology took place at two study sites on Oʻahu. Marine Corps Base Hawaiʻi - Kaneohe Bay is located on east/windward Oʻahu (21.43272, -157.75211) on the Mōkapu Peninsula and primarily consists of urban and developed land cover in addition to the 482 acre Nuʻupia Ponds Wildlife Management Area (hereafter, Nuʻupia WMA). The Nuʻupia WMA contains mostly brackish wetlands in addition to small patches of wooded kiawe (*Prosopis pallida*) and haole koa (*Leucaena leucocephala*) forest (Figure 2.1). Surveys for Pueo nests primarily occurred within the Nuʻupia WMA. The other site, Joint Base Pearl Harbor Hickam Lualualei VLF Transmitter Annex (hereafter, Lualualei Valley), is an approximately 1,700 acre field located on west/leeward Oʻahu (21.42463, -158.15368) and is dominated by patches of grasslands and wooded kiawe savanna (Figure 2.2). These two study sites were selected because preliminary surveys confirmed Pueo use and breeding activity at these sites in the past and because funding for Pueo research was provided by the U.S. Navy (Federal Grant Number W9126G-20-2-0017) and U.S. Marine Corps (Federal Grant Number W9126G-19-2-0063), with an expectation that core study activities would take place at the funded locations. All activities were conducted under appropriate federal, state, and institutional permits (Bird Banding Lab permit no. 24137 and 23395; Hawaiʻi Department of Forestry and Wildlife Scientific Collecting Permit no. WL18-10 and WL20-05; University of Hawaiʻi Institutional Animal Care and Use Committee protocol no. 18-2752).

Figure 2.1. Map of the Nu'upia Ponds Wildlife Management Area located within Marine Corps Base Hawai‘i - Kaneohe Bay (Nu‘upia Ponds WMA) on O‘ahu, Hawai‘i**.**

Figure 2.2. Map of the Joint Base Pearl Harbor Hickam Lualualei VLF Transmitter Annex (Lualualei Valley) on O‘ahu, Hawai‘i.

Nest discovery

Surveys were conducted at both focal study sites from March 2020 through June 2022. Surveys began with observers scanning from roads and lookout points to look for Pueo breeding behaviors such as courtship displays and calls, territorial displays and prey carrying (Wiggins et al., 2020). When breeding behaviors were observed in a particular area, it was revisited at least twice a week in the weeks following to confirm establishment of a nesting territory and whether a female had begun incubating. Within a month of observing breeding behaviors and identifying an area suspected of containing a nest, the exact location of the nest was ascertained by observing prey deliveries to the nest or by observing the incubating female leaving or returning to the nest. If observations from a distance were not enough to reveal the location of the nest, the approximate area was searched by observers spaced out approximately 1.5 meters apart walking transects through the area in order to flush the incubating female Pueo from the nest so that the exact location of the nest was revealed (Holt & Larson, 2018; Leasure & Holt, 1991). Once a nest was located and confirmed to be active (containing either eggs or chicks), observers retreated to a distance and observed to be sure the female returned to the nest and both parents resumed normal nesting behaviors. The exact GPS location of the nest was recorded at the time of nest discovery.

Breeding parameters

Nests were monitored approximately every other day from a distance of at least 200 meters away and then checked directly by observers on a weekly basis to determine clutch size, nesting success and productivity. Though the use of nest cameras to document breeding parameters has been used successfully in many avian breeding studies, nest camera use has been documented to increase predation risk and nest failure for Short-eared owls in North American study systems (Holt pers. comm). I chose not to use nest cameras for this study based on this information, along with the fact that Pueo are state-listed as endangered on O‘ahu, no prior research existed on their breeding ecology and response to nest disturbance, and that mammalian predators (i.e. feral cats, dogs, mongoose, and rats) were all present at both study sites, increasing predation risk from olfactory and visual cues. Nest checks during the egg incubation stage were used to inform estimates of first-egg lay date and first-egg hatching date. Nest checks after chicks hatched were used to further refine the lay date, hatch date, and first-fledge date estimates.

I defined “nest initiation” as the date of first-egg laying. The incubation period for Short-eared Owls ranges from 21-42 days, with most studies reporting an incubation period of 28 days (Wiggins et al., 2020). Thus, nest initiation dates were estimated by subtracting 28 days from the first-egg hatch date, which in turn was either directly observed during nest checks or estimated from nestling age if a nest was discovered after hatching. Nestling age was determined based on size, plumage characteristics, and other physical characteristics following a Short-eared owl aging guide (Wiggins et al., 2020). In some cases, I was able to collect biometrics (i.e. tarsus length, tarsus width, wing chord, and weight) of chicks and compared these measurements to Short-eared owl growth curves (Arroyo et al., 2000; Holt et al., 1992). I was not able to determine lay date from nests that were abandoned before eggs hatched; however, I estimated an earliest possible nest initiation date by backdating from the date of nest discovery.

Clutch size was defined as the maximum number of eggs laid. Nest success was defined as whether at least one young was raised to 14 days old, the approximate age of dispersal from the nest. While this is technically not fledgling age (approximately 28 days old), once the chicks disperse from the nest on foot they are extremely difficult to find and thus I quantified nest success as survival of a chick to the dispersal stage (Clark, 1975; Fondell & Ball, 2004; Holt, 1992); a similar definition of “fledgling” has been used in other studies quantifying Short-eared owl nest success (Fondell & Ball, 2004). Nests were monitored regularly until all chicks dispersed from the nest or the nest was abandoned, predated, or otherwise failed. Once chicks began dispersing, I searched the general area of the nest (up to 500 meters away from the nest) to relocate chicks, confirm the outcome of the nest, and document dispersal distance. Dispersed chick locations were also determined by observing parent Pueo delivering prey to chicks away from the nest or by listening for chick begging calls. Final nest fate was recorded as successful (at least one chick disperses), failed (with specific sources of nest failure such as predation or abandonment), or unknown. Probable causes of abandonment were noted for each abandoned nest, including but not limited to predator presence, anthropogenic disturbance, or extreme weather. The stage at which the nest failed (egg stage or chick stage) was also noted.

Biometric measurements

When possible, I took biometric measurements of nestlings at approximately 13-15 days old, including mass, wing, tarsus, tail, and culmen lengths. At this age, nestlings can

thermoregulate by themselves and were large enough to be banded with metal U.S. Geological Survey Bird Banding Lab (USGS BBL) aluminum butt-end bands and VID aluminum rivet bands, which allowed for future re-sightings of individuals and will assist in future studies investigating survival and dispersal.

Nest site selection

Pueo nest site selection characteristics were determined using a paired design in which site data were collected both for nests and for four randomly selected points within 100m of each nest site (Fondell & Ball, 2004; Keyes et al., 2016). All nest site characteristic data and random point data were collected as soon as possible after discovery of the nest. At the nest site and the four random points, I collected a mean high and low visual obstruction reading (VOR) (method modified Robel et al., 1970 and USDA Agricultural Research Service, n.d.), percent vegetation cover within a 0.5-meter radius of the point, tallest vegetation height, and the top three dominant vascular plant species within a 0.5-meter radius of the point, ranked 1-3 in order from most (1) to least (3) abundant (Fondell & Ball, 2004; Monroe et al., 2019). Distance to nearest human-made structure, road, and body of water was also recorded for each nest and random point using either a rangefinder or satellite imagery and in ArcGIS.

Diet

Pellet and prey remains were collected from both study sites during weekly nest checks and during searches of each nesting area for dispersed chicks. Observers also searched known perch locations of the breeding adults and collected pellets as we came across them incidentally around the site, even if they could not be associated with a particular nest or breeding Pueo. Each pellet or prey remain was dried in a fume hood and then stored individually. Once dried, pellets were dissected to extract parts, such as bones, feathers, and insect exoskeleton components, that could be used to identify prey items to lowest possible taxa.

State-wide data collection

To obtain a broad overview of Pueo breeding phenology and nesting habitats, I reached out to federal, state, non-profit, and private partners across the Hawaiian Islands and asked them to report any observations of Pueo breeding behaviors, nests, or chicks and juveniles that they encountered incidentally during their fieldwork. Along with this request for information was sent an informational document showing how to identify Pueo breeding behaviors, nests, and chicks;

this information was also made available on the project website, pueoproject.com. Data requested included the date of observation, location of observation (GPS points), type of observation (breeding behavior or nest with eggs or chicks), and as much detail about the behavior, nest site characteristics, and eggs or chick as possible, including photos. An email, online form, and physical datasheet were sent to help guide data collection (Appendix A). I followed up on each reported observation to confirm observations and obtain additional details as necessary. I also reviewed journal articles and project reports to look for historical records of Pueo breeding phenology and nesting habitats.

Data analysis

Pueo breeding parameters and nest site characteristics

All statistical analyses were conducted using program R (version 4.2.0). Breeding parameters (nest initiation date, clutch size, nesting success, and nest productivity) were combined across all breeding seasons, and the means, standard errors, and ranges of all parameters calculated. The mean, standard errors, and range of dispersal distance of the fledged chicks were also calculated. The means, standard errors, and ranges of all the quantitative nest site characteristics were also calculated, and the top three most abundant plant species across all nest sites summarized.

Effect of nest site characteristics on nest site selection

I used a conditional logistic exposure model to estimate the relative probability of use of a site for nesting. I built a fully parameterized model with terms for tallest vegetation height, mean high and low VOR, ratio of high to low VOR, and percent vegetation cover fitted as predictor variables and use of site (1 for Pueo nests, 0 for random points) as the response variable (package “lmer4”). Due to the small sample size of nests overall, I constrained models to one covariate at a time and only looked at vegetation characteristic covariates, excluding the distance to nearest human structure, road, and body of water covariates from the fully parameterized model. I then generated a model selection table that dredged the fully parameterized model to look for the combination of covariates in the best fit model based on AICc values (using an ΔAICc value cutoff of 2) and a Hosmer and Lemeshow goodness-of-fit test with R packages “MuMin” and “ResourceSelection”.

Effect of nest site characteristics on nesting success

I used a logistic exposure model, a form of logistic regression model that includes a custom logit link function to account for exposure days, to examine the Nest Survival (NS) and Daily Nest Survival Rate (DSR) of all Pueo nests (Schwarz & Rivers, 2018; Shaffer, 2004). Exposure days were calculated as the number of days between the date the nest was found to the date the nest failed or was successful in fledging at least one Pueo chick. To investigate the influence of nest site characteristics and nest timing on DSR, I created a fully parameterized model with covariate terms for tallest vegetation height, mean high and low VOR, ratio of high to low VOR, percent vegetation cover, and relative day of nesting season that the nest was initiated. Relative day of nesting season was calculated as the number of days between the beginning of the Pueo breeding season, which I set as November 1st based on the earliest date that pueo breeding behaviors such as courtship displays have been observed (Cotín et al., 2018), and each nest's initiation date (I.e. November 1st is relative day of nesting season 0, November 2nd is day 1, etc.). I then generated a model selection table that dredged the fully parameterized model to look for the combination of covariates in the best fit model based on AICc values (using an ΔAICc value cutoff of 2) and a Hosmer-Lemeshow goodness-of-fit test. Due to the small sample size of nests overall, I constrained models to one covariate at a time and only looked at vegetation characteristic covariates, excluding the distance to nearest human structure, road, and body of water covariates from the fully parameterized model.

Diet

All prey items were identified to lowest possible taxa by consulting reference collections and scientists at the Bernice Pauahi Bishop Museum. For rodents, the lowest possible taxonomic delineation was to species for House Mouse (*Mus musculus*) or genera for rats (*Rattus sp*.). Differentiation between the three rat species found in Hawai‘i - Norway Rat (*Rattus norvegicus*), Black Rat (*Rattus rattus*), and Pacific Rat (*Rattus exulans*) – requires comparing whole skulls from specimens, which are often not intact in owl pellets and prey remains (Mostello, 1996). However, differentiation between House Mice and *Rattus* sp. can be done by examining the incisor shape, molar occlusion pattern, and mandible size, which are all bones that are more frequently retained in owl pellets. Measurements of the bird bones most frequently retained in the pellets (tarsometatarsus, tibiotarsus, femur, humerus, ulna, radius, and coracoid) were taken from all available skeletal specimens of likely prey species from the Bishop museum reference

collection. These bird bone measurements were used to create a set of classification trees in R (package “rpart”) that could classify to taxonomic family (Appendix B). These classification trees were used alongside other identifiable parts, such as skull shape and feather characteristics to identify bird remains to lowest possible taxa. Insect remains were cleaned and separated out and identified to lowest possible taxa by Bishop Museum entomologists.

Diet comparison studies often utilize contingency tables or analysis of variance, but the data does not meet the assumptions of independence to be able to use these techniques (Bilder et al., 2000; Lemons et al., 2010; Loughin & Scherer, 1998). Thus, to compare diet composition among Pueo nests, I followed an approach that treats each sample (i.e. each pellet or prey remain) as a multinomial vector representing the presence or absence of each prey type within a pellet (i.e. a 1 for present and 0 for absent, and a vector in the form “0100” for which there are 4 potential prey types available). As there is often more than a single prey item within each pellet, establishing each sample as a multinomial vector thus accounts for dependence of the different prey items within one sample. Approaching the data in this way is similar to how data are analyzed in capture-mark-recapture studies that investigate the probability of recapturing an individual given different variables, and thus I can use the same analytical methods to determine if nest served as a predictor for the presence of different prey items (Lemons et al., 2010; Morin et al., 2019). I used package “RMark” to build a closed population capture-recapture model (Huggins, 1989). In building the models, I constrained p (initial encounter probability in a traditional capture-recapture model) to equal c (reencounter probability), since traditionally a different p and c value is used to account for behavioral responses of an animal to recapture, which is not relevant for my data structure or analysis. Due to a low sample size, the fully parameterized model only included nest ID and year as covariates. I also calculated the overdispersion parameter, $\hat{c}$, from the global model to control for correlation among the different prey items. Use of $\hat{c}$ allows for a conservative estimate of model performance. I incorporated this parameter into the model selection process, and thus quasi-AICc (QAICc) values are used to compare model fit.

State-wide incidental data summary

Reported breeding parameters were summarized in the same manner as breeding parameter data from focal study sites. To standardize reported information of Pueo nesting

habitats, I mapped each observation location over a 30-meter resolution land-cover map from the U.S. Geological Survey Carbon Assessment of Hawaii Land Cover Map and identified the General Land Cover class for each observation (Jacobi et al., 2017). To standardize observations with regards to breeding phenology, I looked at the photos and descriptions of Pueo chicks to age them and estimated the date of nest initiation for each observation by back-dating and assuming a 28-day egg incubation period.

RESULTS

Pueo breeding parameters

A total of 34 nesting observations were collected; 13 observations were from focal study sites and 21 incidental observations were from across the Hawaiian Islands (Figure 2.3). Due to the variety of sources from which data were compiled, the level of detail of each observation varied greatly, and sample sizes varied depending on the parameter reported. Maximum clutch size across all observations ranged between one and seven eggs ($\bar{x}$ = 3.63 ± 0.39 SE, n=19). The maximum number of chicks per nest across all observations ranged between one and five ($\bar{x}$ = 2.67 ± 0.44 SE, n=9). Many incidental chick observations were of fledglings that had dispersed from the nest and thus we could not reliably judge the maximum number of chicks observed from that nesting instance; thus, only incidental observations of chicks pre-fledging were included in this calculation as they provided a more reliable estimate of the actual number of chicks that hatched from a nest. Nests or fledglings were observed between November and July (Figure 2.4), across seven different vegetation cover types (Figure 2.5).

At the two focal study sites, a total of 13 nests were discovered from the 2020-2022 breeding seasons, all between mid-December and mid-June of the respective years (Table 2.1). The maximum clutch sizes observed ranged between one and seven eggs ($\bar{x}$ =3.5 ± 0.58 SE, n = 10). The maximum number of chicks observed ranged between one and five ($\bar{x}$ = 2.57 ± 0.61 SE, n=7). Six of the 13 nests (46%) had at least one nestling successfully disperse from the nest. Morphometrics for Pueo chicks from four different nests are reported in Appendix C. Pueo chicks were observed dispersing from the nest as early as 12 days old. I was able to document chick dispersal distances from four of the six successful nests; one chick was found twice on two different days, in two different locations. Dispersal distances range from 9 to 198 meters from the nest ($\bar{x}$ = 91.84 ± 35.67 SE, n=5). All dispersed chicks found were between approximately 12 and 24 days old. At the remaining two successful nests, I confirmed chick dispersal and thus nest success by hearing the begging calls of dispersed chick or witnessing prey deliveries by the parents to areas away from the nest but within the general nesting territory. However, I was unable to locate these chicks directly and obtain exact dispersal distances.

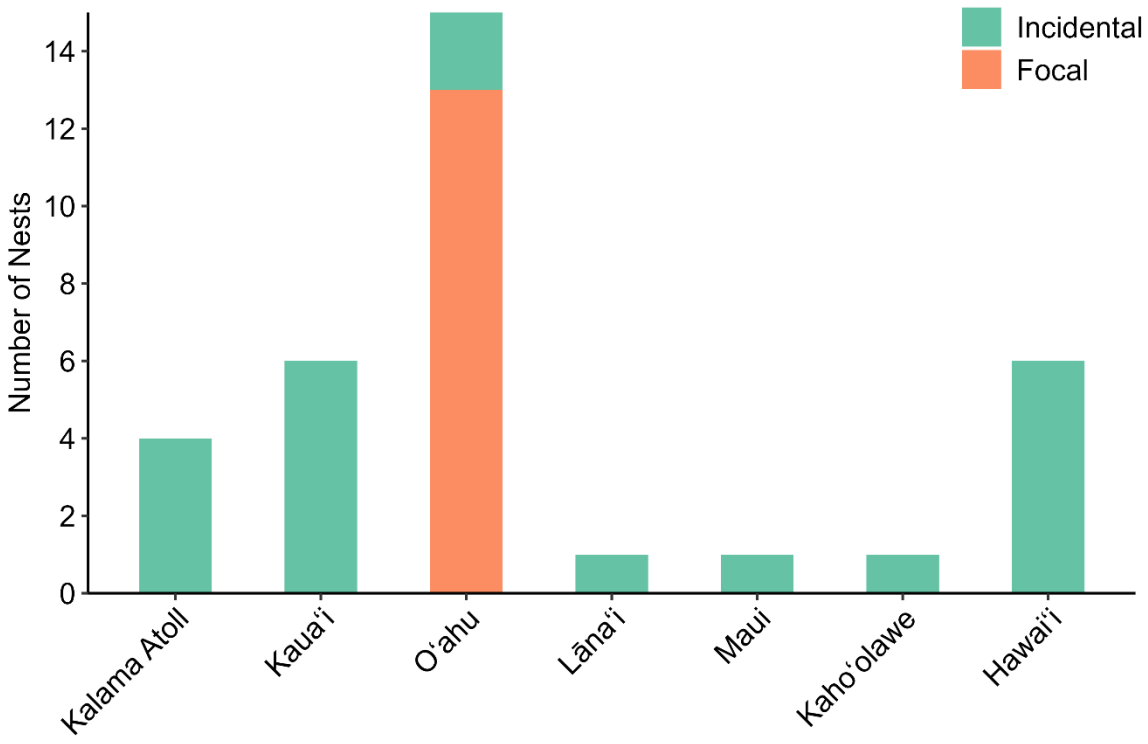

Figure 2.3. Number of Pueo nests found at both the focal study sites and incidentally, broken down by island.

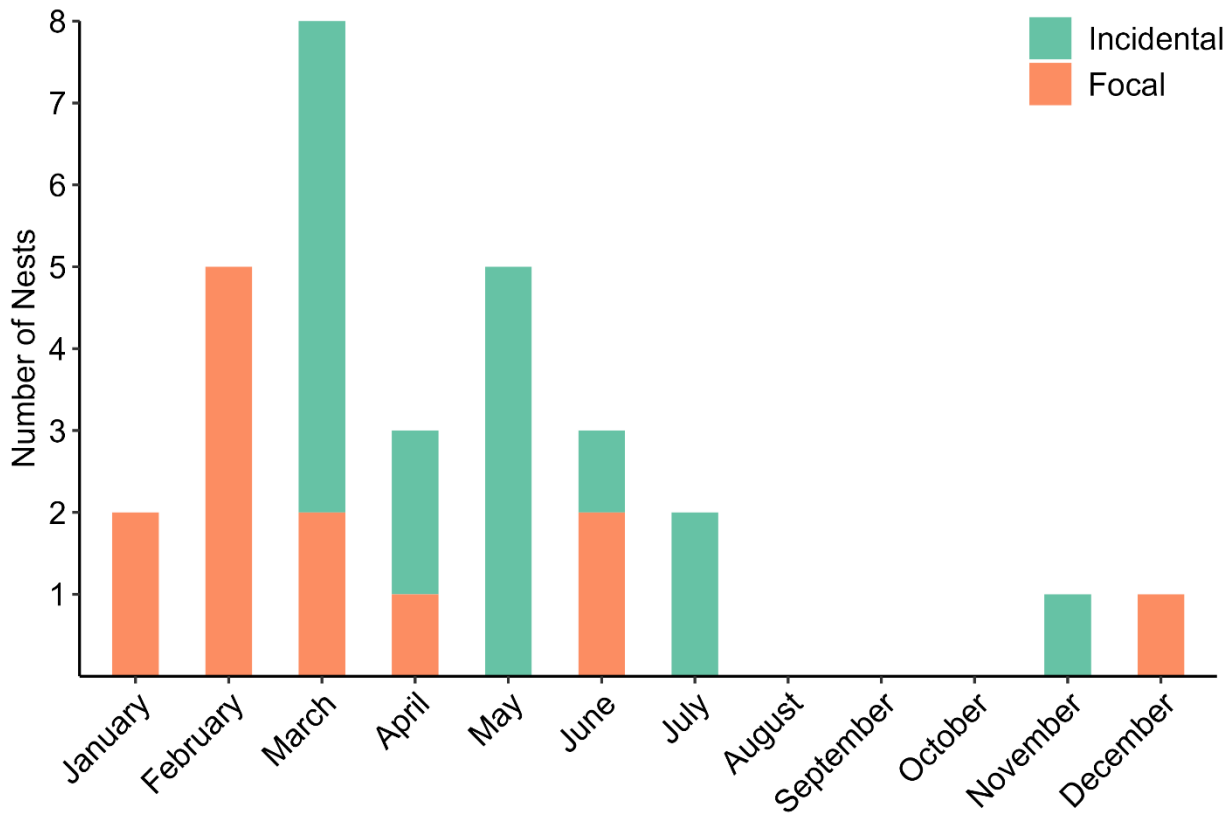

Figure 2.4. Number of Pueo nests found at both the focal study sites and incidentally, broken down by month of discovery.

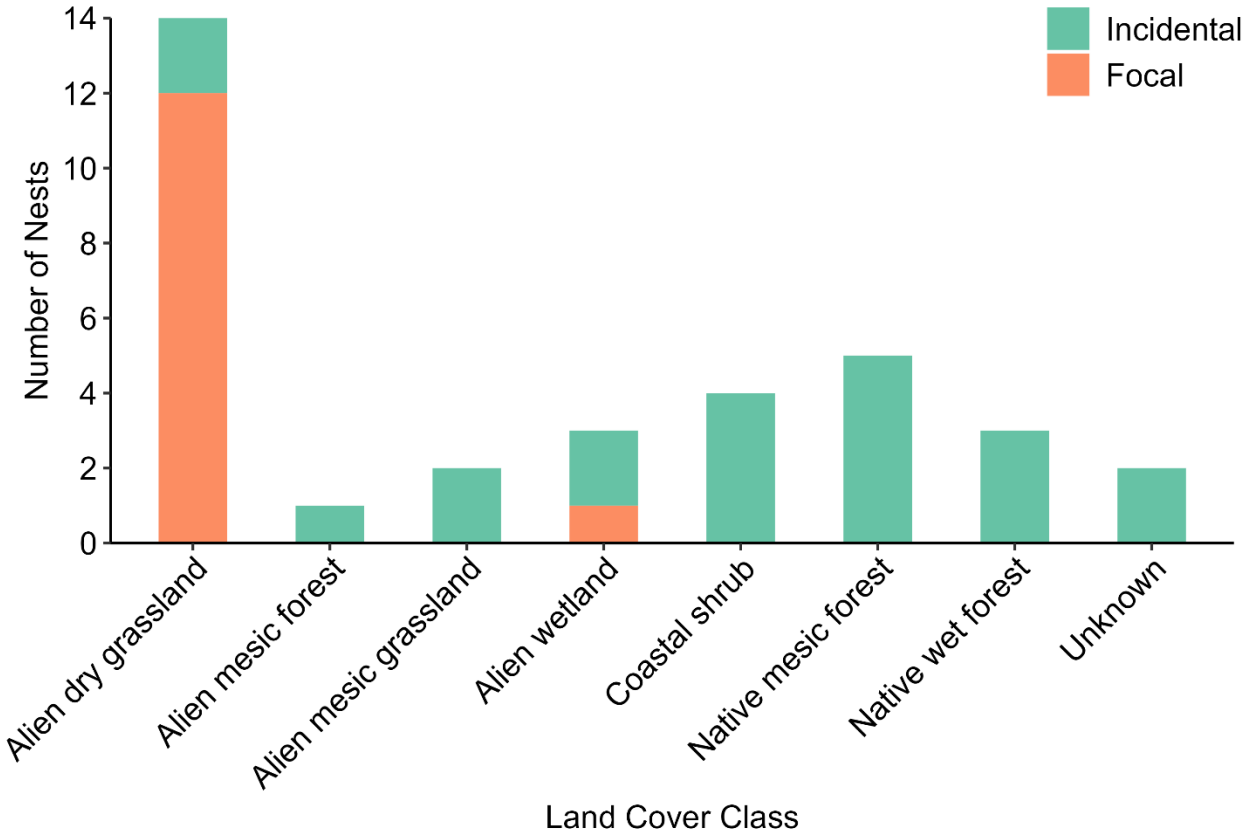

Figure 2.5. Number of Pueo nests found at both the focal study sites and incidentally, broken down by habitat type. Habitat types derived from the General Land Cover class from the U.S. Geological Survey Carbon Assessment of Hawaii Land Cover Map (Jacobi et al., 2017).

Table 2.1. Summary of Pueo nest breeding parameters, from focal study sites on O‘ahu (Nu‘upia WMA and Lualualei Valley).

Nest ID	Date discovered	Latitude	Longitude	Estimated initiation date[1]	Estimated hatch date[1]	Number of eggs[2]	Number of chicks[3]	Nest fate
01	12/18/2019	21.42625	-158.15402	2019-12-16	2020-01-11	2	0	Fail - unknown cause
02	1/7/2020	21.43134	-158.1525	2020-01-02	2020-01-31	5	0	Fail - predated
03	1/28/2020	21.42417	-158.16338	2020-01-24	2020-02-21	NA	1	Success
04	2/13/2020	21.42794	-158.15572	2020-02-09	2020-02-26	2	1	Fail - predated
05	2/14/2020	21.43187	-158.15607	2020-02-10	2020-03-09	4	0	Fail - unknown cause
06	2/18/2020	21.43541	-158.15607	2020-02-13	2020-03-13	NA	NA	Fail - unknown cause
07	3/25/2020	21.42673862	-158.1453365	2020-02-11	2020-03-10	NA	1	Success
08	6/3/2020	21.434984	-157.751928	2020-04-29	NA	2	0	Fail - unknown cause
09	2/5/2021	21.42573	-158.14495	2021-01-31	2021-03-06	7	3	Success
10	2/16/2021	21.42269	-158.14564	2021-01-16	2021-02-13	NA	5	Success
11	3/31/2021	21.42327	-158.14956	2021-03-01	2021-03-28	NA	3	Success
12	6/8/2021	21.42729	-158.14441	2021-05-27	NA	1	0	Fail - unknown cause
13	4/26/2022	21.43336	-158.15164	2022-04-20	2022-05-13	4	4	Success

[1]Based on status of nest at time of finding, using a 28-day incubation period, or from direct observation.

[2]Maximum number of eggs observed at the nest.

[3]Maximum number of chicks observed at the nest.

Nest site characteristics and site selection

I collected vegetation characteristic data from 11 nests found between March 2020 and June 2022. Two of the 13 nests included in the other analyses were discovered prior to the development of the nest characteristics protocol, and thus these data types were not collected for those nests. Tallest vegetation height ranged from 38-67 cm ($\bar{x}$ = 48.82 ± 3.15 cm SE, n=11). VOR ranged from 3.25-42 cm ($\bar{x}$ = 15.43 ± 3.467 cm SE, n=11). Percent cover ranged between 62-98 % ($\bar{x}$ = 83.82 ± 3.77 % SE, n=11).

For nest site selection, the best fit models as determined by AICc values and goodness-of-fit tests included mean high VOR and mean low VOR as predictor variables; Table 2.2 summarizes the AICc values of the top 3 models. The top models (Figures 2.6a and 2.6b) indicates that as the mean high VOR and mean low VOR at a given site increases, the probability of use of that site by a Pueo for nesting also increases. However, given the small sample size, there was high model uncertainty among these top models.

Nests were generally in small, bowl-shaped depressions in the ground surrounded by vegetation that was tall enough that incubating females were fully obscured by vegetation cover (on average 40 cm in height). The most common vegetation at nests in the grassland were buffelgrass (*Cenchrus ciliaris*), haole koa (*Leucaena leucocephala*) shrubs (less than 1 meter tall), and yellow bluestem (*Bothriochloa ischaemum*), while the nest in the wetland was surrounded by pickleweed (*Batis maritima*). The terrain of both the grassland and wetland sites was naturally quite uneven, and therefore it is unknown whether the Pueo were choosing pre-existing depressions in the ground or creating their own as the female incubated and brooded. While some nests were sparsely lined with some vegetation and a few Pueo feathers, most of the eggs sat directly on bare ground. The carrying of nest material or nest building was never observed.

Table 2.2. Model selection table for relative probability of use of a site for nesting by a Pueo in response to vegetation characteristics.

Model Predictor Variables	**AICc**	**ΔAICc**	**Model Weight (w_i)**	**Negative log Likelihood (-2(L))**
Tallest	52.7	0.00	0.37	-24.22
VOR high	53.1	0.42	0.30	-24.32
VOR low	54.2	1.49	0.18	-24.97

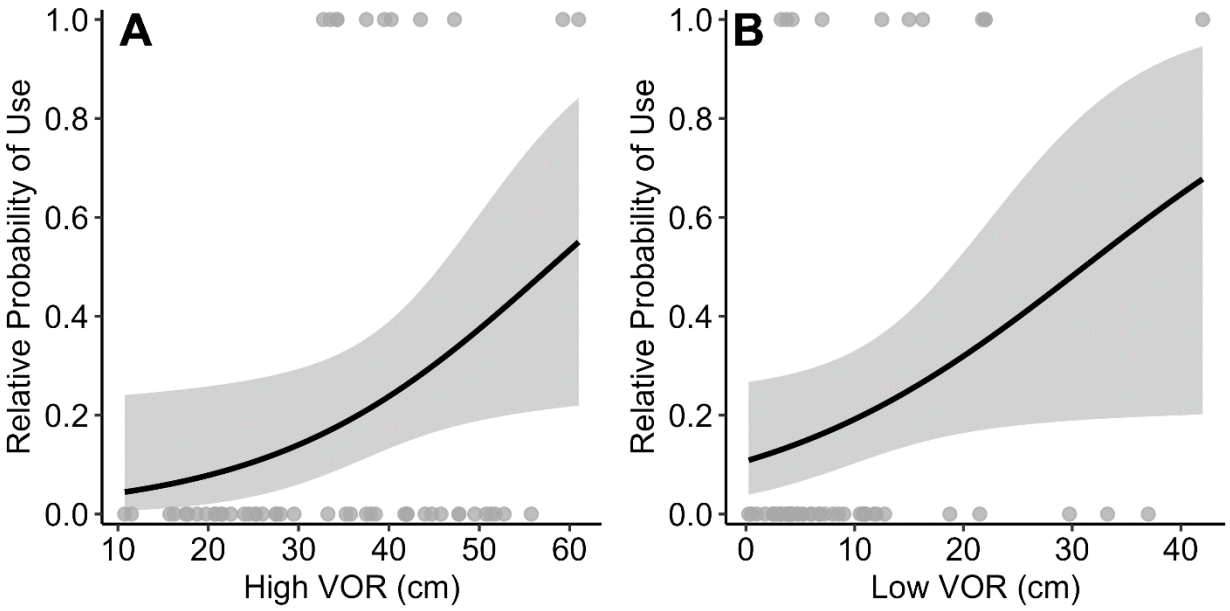

Figure 2.6. Plot of the relative likelihood of use of a site for Pueo nesting versus (A) mean High VOR (Visual Obstruction Reading) and (B) mean Low VOR. Gray dots are the VOR at each site. Solid line indicates the predicted likelihood of use, grey areas are the 95% confidence intervals.

Nest success

All 13 nests were included in calculating the estimate of Nest Survival (NS), but the two nests discovered prior to the development of the nest characteristics collection were excluded from the analysis investigating the relationship between predictive covariates and Daily Nest Survival Rate (DSR). DSR was 0.97 (± 0.01 SE, n=13), while NS (DSR^number of days to success) was 0.24 (± 0.12 SE, n=13). The null model, (i.e. constant nest survival) was the top model, with separate models including relative day of nesting season and percent cover as the second and third best model, respectively (Table 2.3). Given the high model uncertainty among the top models due to the small sample sizes, and that the second and third models had an ΔAICc value of less than one, I examined the effect of covariates in the second and third best models on DSR. Relative day of nesting season was negatively correlated with DSR, while percent cover was positively correlated with DSR (Figures 2.7a and 2.7b).

For the seven failed nests I was unable to definitively determine the causes of nest failure, but strongly suspect predation to be the cause of at least two nest failures. At one nest, feral dogs were seen within 150 meters of the nest on the last day that the nest was known to be active (i.e. female Pueo was seen incubating the nest). At the next nest check, no eggs were present in the nest, though there had been 5 eggs upon initial discovery of the nest, and the remains of an adult Pueo were found nearby. The remains looked consistent with tearing by a large animal, likely a feral dog. In another failed nest the eggs were damaged, likely by a mongoose or rat, and a fully intact dead Pueo nestling was found a couple meters outside the nest bowl. In one nest that succeeded, prior to egg laying but after the establishment of the nesting territory, I watched one Pueo chase and dive at a feral cat encroaching on its territory.

Table 2.3. Model selection table for the effect of nest site characteristics on Daily Nest Survival.

Model Predictor Variables	AICc	ΔAICc	Model Weight (w_i)	Negative log Likelihood (-2(L))
Null (Constant survival)	28.4	0.00	0.28	-11.12
Relative day of nesting season	29.0	0.60	0.21	-10.36
Percent cover	29.1	0.71	0.20	-10.42
VOR low	30.2	1.85	0.11	-10.99

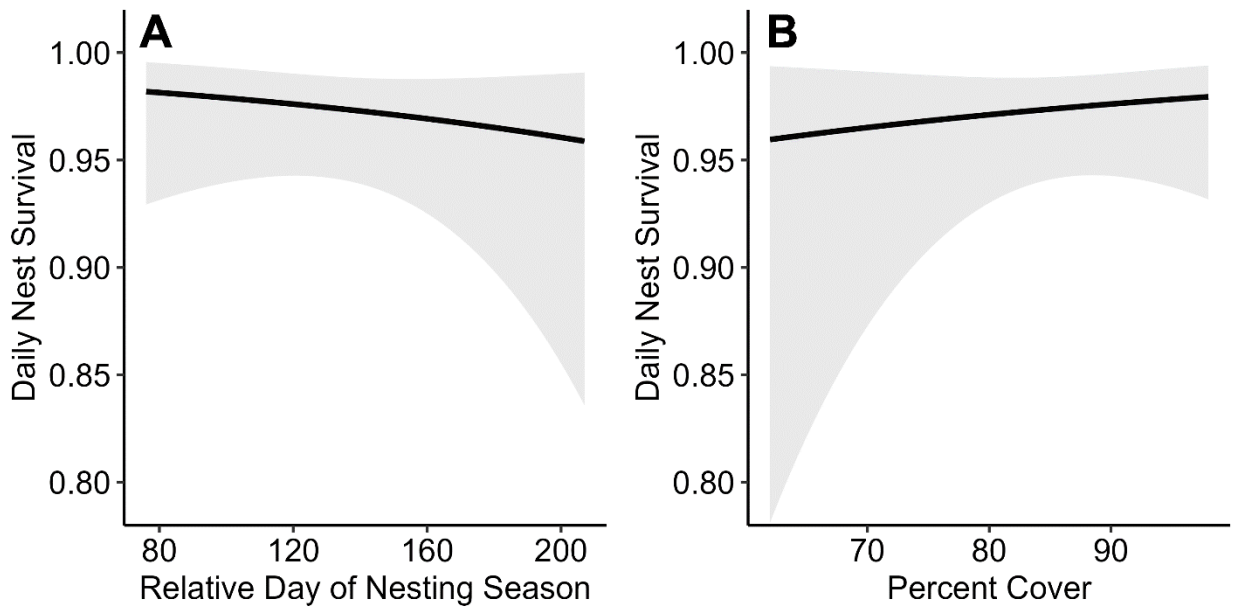

Figure 2.7. Plot of the estimated Daily Nest Survival Rate in relation to (A) Relative day of nesting season and (B) Percent cover of vegetation at the nest. Solid line indicates the predicted DSR, grey area is the 95% confidence interval.

Nesting Pueo diet

A total of 71 pellets and prey remains were collected from six different Pueo nests (Table 2.4). House Mice (*Mus musculus*) were the most frequently occurring prey type, occurring in 69.01% of the samples. Birds were the next most frequently occurring prey type, occurring in 38.03% of the samples, followed by *Rattus* species and insect species occurring in 14.1% and 11.3% of samples, respectively (Figure 2.8). Figure 2.9 summarizes the frequency of occurrence of different prey items by nest. Before accounting for overdispersion, my top model predicting the occurrence of different prey items included only Nest ID as a covariate, suggesting that there is a difference in diet composition of each nesting Pueo pair (Table 2.5). However, once accounting for overdispersion, the null model is the top model, ranking higher than any combination of Nest ID and year as covariates, lending little support to the hypothesis that Pueo diet may vary from nest to nest (Table 2.6).

Table 2.4. List of prey taxa found in nesting Pueo pellets and prey remains.

MAMMALS	
	Mus musculus
	Unidentified species of genus *Rattus*
BIRDS	
	Geopelia striata (Zebra Dove)
	Zosterops japonicus (Warbling White-eye)
	Estrilda astriid (Common Waxbill)
	Unidentified species of genus *Lonchura*
	Unidentified species of family Fringillidae
INSECTS	
	Unidentified species of family Carabidae
	Unidentified species of family Tenebridae
	Unidentified species of family Elateridae
	Unidentified species of family Curculonidae

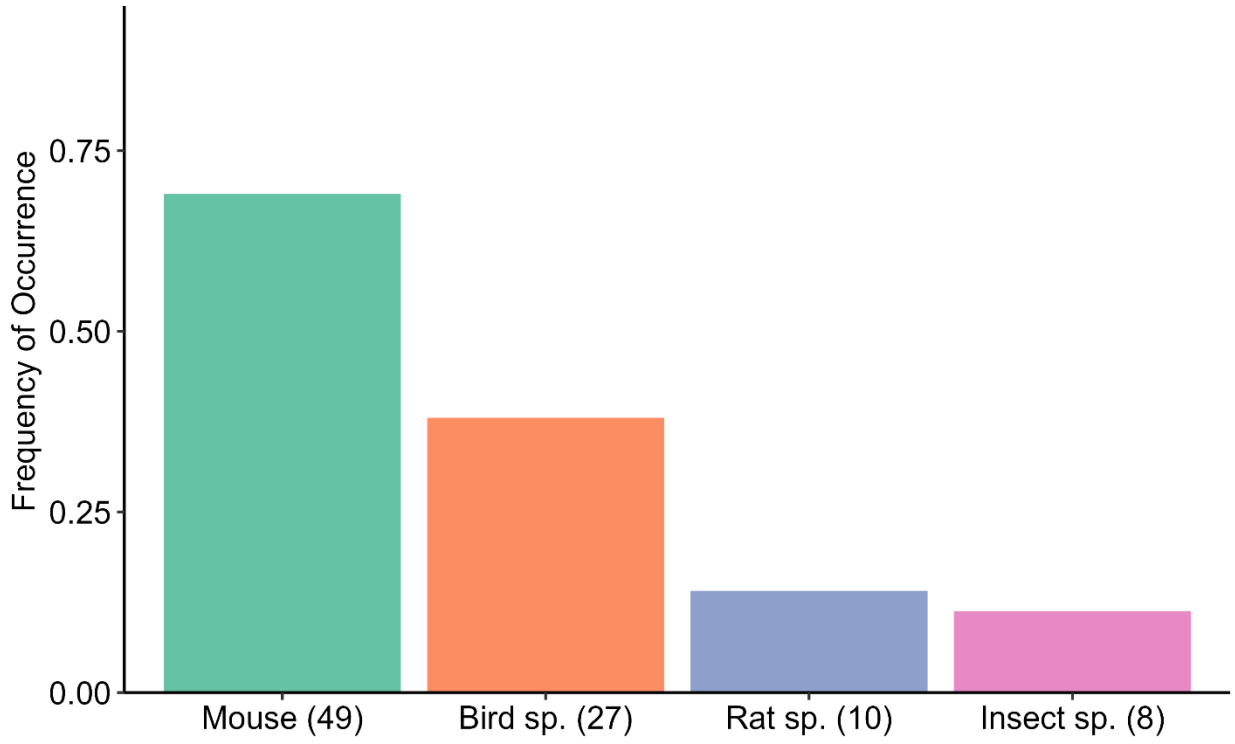

Figure 2.8. Frequency of occurrence of each prey type across all samples. Numbers in parentheses represent the number of occurrences of that prey type in pellets and prey remains.

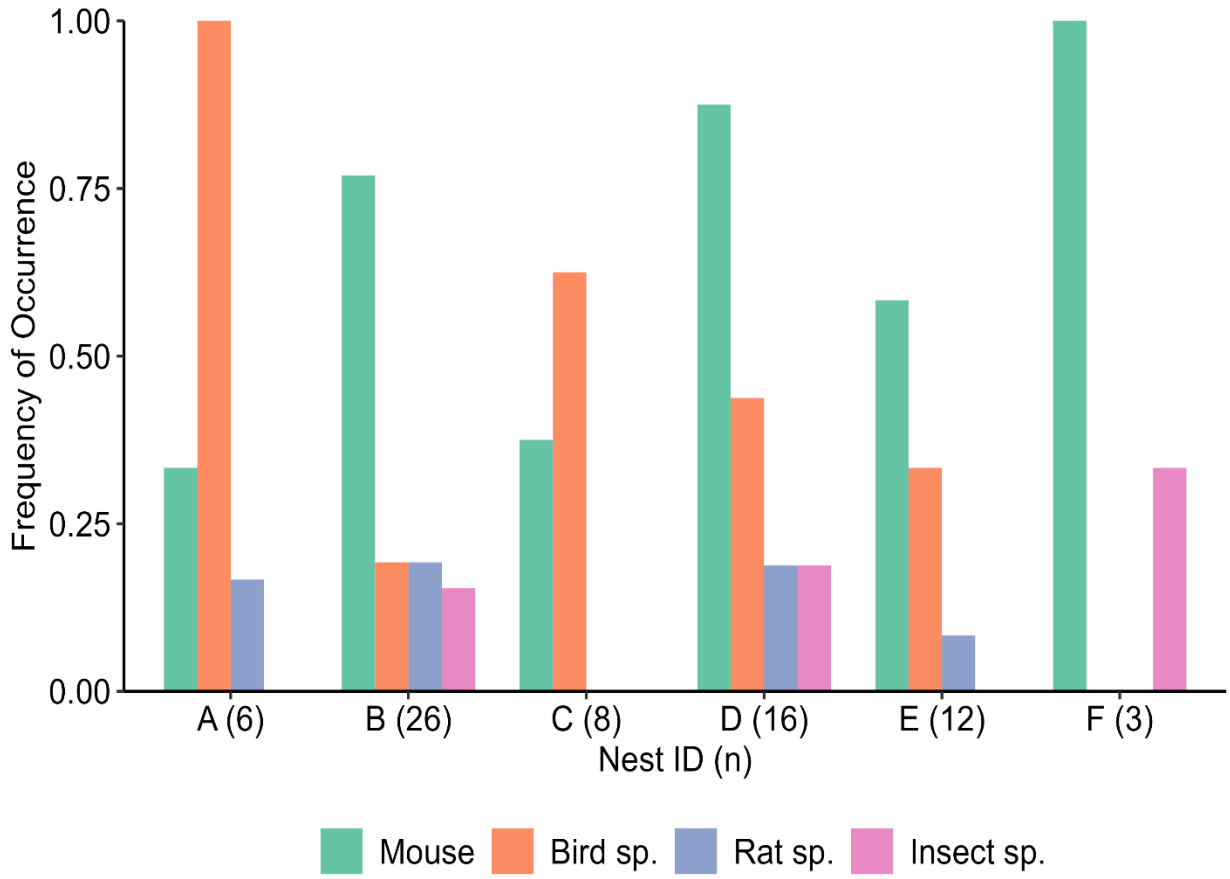

Figure 2.9. Frequency of occurrence of each prey type across all samples, broken down by individual nests. Numbers in parentheses represent the number of samples (pellets or prey remains) from each nest.

Table 2.5. Model selection table for models used to predict diet of nesting Pueo without incorporating overdispersion parameter.

Model Predictor Variables	AICc	ΔAICc	Model Weight (w_i)	Number of model parameters
Nest	339.10	0.00	0.75	6
Nest + Year	341.99	2.89	0.18	8
Year	344.19	5.09	0.06	3
Null model	347.99	8.89	0.01	1

Table 2.6. Model selection table for models used to predict diet of nesting Pueo, with overdispersion parameter. Ĉ equals 18.916.

Model Predictor Variables	**QAICc**	**ΔQAICc**	**Model Weight (w_i)**	**Number of model parameters**
Null model	20.30	0.00	0.85	1
Year	23.95	3.65	0.14	3
Nest	29.54	9.23	0.01	6
Nest + Year	33.65	13.35	0.001	8

State-wide incidental data summary

A total of 21 separate incidental breeding observations from across the Hawaiian Islands were collected. Incidental breeding observations were defined as a nest with eggs or chicks inside, or a recently dispersed chick found outside of its nest. Observations were reported from Hawaiʻi island, Maui, Lānaʻi, Oʻahu, Kauaʻi, and Kalama Atoll (also known as Johnston Atoll). Thirteen of the observations were reported as a response to requests for data during the 2020-2022 breeding seasons; these observations were reported by staff from Hawaiʻi Department of Forestry and Wildlife, U.S. Fish and Wildlife Service, U.S. Forest Service, Archipelago Research and Conservation, Pūlama Lānaʻi, and Kahoʻolawe Island Reserve Commission. The remaining eight observations were from prior project reports or the single publication on Pueo nests by Thomas Snetsinger (Snetsinger, 1995).

Table 2.7 summarizes the locations, breeding dates, habitat types, and nest contents or number of dispersed chicks observed per observation across all the incidental reports; Table 2.8 breaks the number of observations down by island and month. Pueo breeding was discovered between the months of March and November. Of the 17 observations that noted specific nest contents (i.e., eggs or chicks), 12 were discovered after at least one chick had hatched and five were discovered during the egg stage. Nine observations were of Pueo chicks that had already dispersed from the nest but were not yet fully fledged (between 14 and 28 days old). Of the 15 observations that could be mapped for comparison with the U.S. Geological Survey Carbon Assessment of Hawaii Land Cover Map for habitat standardization, three were found in native wet forest, five were found in native mesic forest, three in alien mesic grassland, one in alien mesic forest, and three in areas categorized as "very sparse vegetation to unvegetated" (Table 2.6). Based on habitat descriptions and photos associated with these observations, I determined that two nests were in a wetland and one in sparse nonnative mesic grassland. Reported clutch sizes ranged from two to seven eggs ($\bar{x}$ = 4.6 ± 0.8 SE, n = 5). Because most of the reports were one-time visits to a nest or a single observation of a Pueo chick or fledgling, nesting success and productivity could not be determined in most cases. However, eight of the observations were of fledged chicks who had already dispersed from their nests, indicating successful nesting.

On Kalama Atoll, all four observations were made by U.S. Fish and Wildlife staff between March 1st and 19th of 2020. Land cover class data for Kalama Atoll was not available

but all four observations were of nests found in small depressions on the ground within bushes of *Pluchea spp* and therefore considered coastal shrub. Pueo nests were found during routine surveys for seabird nests. In one of these nests, three dead downy Koa‘e‘ula (Red-tailed Tropicbird, *Phaethon rubricauda*) chicks and the remains of one adult ‘Ewa‘ewa (Sooty Tern, *Onychoprion fuscatus*) were found alongside three young (less than 10 days old) Pueo chicks and one Pueo egg. Upon revisiting the same nest a few days later, the observers found one of the Pueo chicks 3.5 meters away in a different *Pluchea spp.* bush next to another dead Red-tailed Tropicbird chick.

On Hawai‘i island, three observations from March through May of 1993 reported in Snetsinger (1995), two observations were reported to my team in May of 2021, and one observation was reported to my team in April of 2022. Snetsinger reported finding Pueo nests in the Mauna Kea area between March and May, while the new observations were all from or around the Hakalau Forest National Wildlife Refuge around the eastern slope of Mauna Kea. In both 2021 and 2022, fledgling Pueo were reported within areas fenced to exclude predators and protect Nēnē (Hawaiian Goose, *Branta sandvicensis*) nest sites. The predator exclusion fencing in that area protects nesting birds from mongoose, feral cats, feral dogs, and pigs, and live traps and A24 rodent traps were also present at the site in case of incursions into the fenced area. The April 2022 observation was of two Pueo fledglings found approximately 152 meters from each other and assumed to be from the same nest. The observer returned to the same area a few days later and found one dead Pueo fledgling, presumed to be one of the two fledglings seen prior. The observer said the carcass looked intact with no visible wounds and noted that it was found within the predator-proof fenced area, making predation an unlikely cause of death. The observer did note that it had been raining for the past few days and that inclement weather such as heavy rain in the area was common, suggesting that exposure was the likely cause of death for the Pueo fledgling. Snetsinger (1995) also observed a Pueo nest failure after a period of heavy rainfall, first finding the nest on May 5 1993 with four owlets and returning a week later to find three dead owlets near the nest.

On Kaua‘i, six observations were submitted by staff from Archipelago Research and Conservation (ARC) during their field work monitoring endangered seabirds in montane wet forests on Kaua‘i; one found in 2022 and the other 5 of unknown date. These six observations

included stage of nesting as well as general location of the observations, but the observer noted that Pueo are seen regularly at all of their main study sites near seabird colonies. In Maui Nui, three observations, one each from Lānaʻi, Maui, and Kahoʻolawe were reported in 2011, 2019, and 2021, respectively. The two incidental observations from Oʻahu were found within the Nuʻupia WMA in 2017 and 2018.

I also obtained Pueo patient records from 2012-2022 from the Hawaiʻi Wildlife Center (HWC), a state-wide non-profit that provides medical and rehabilitative care to native wildlife. Many Pueo were not aged in their records or did not have photos that would allow me to age the birds. Thus, only patients that were clearly indicated as juveniles on their records were included in my count of juvenile birds. Due to a lack of photos, patients could not be aged and therefore I could not estimate a nest initiation date, but a summary of the HWC data is in Appendix D. Given the uncertainty around these data, I did not include it in the broad summary of nesting phenology and habitat types above.

Table 2.7. Incidental reports of Pueo nests or chick observations across the Hawaiian Islands and nearby atolls. A request for observations was sent out to organizations and individuals working in natural resources and wildlife fields on a regular basis from 2020 to 2022. Historic observations were also found through literature review.

Island	*GPS Coordinates*	*General Location Description*	*Discovery Date*	*Estimated Initiation Date*[1]	*General Habitat Type*[2]	*Nest Contents*	*Nest / Chick Location Site Description*
Kahoʻolawe	20.573884, -156.572857	Pu'u Moaulaiki	5/26/2019	4/16/2019	Alien dry grassland	One fledgling	-
Kalama Atoll	16.729505, -169.534767	Johnston Atoll	3/6/2020	2/7/2020	Coastal shrub	One chick, 3 eggs	Directly on ground, within *Pluchea* bush
Kalama Atoll	16.729505, -169.534767	Johnston Atoll	3/1/2020	2/27/2020	Coastal shrub	Four eggs	Directly on ground, within *Pluchea* bush
Kalama Atoll	16.729505, -169.534767	Johnston Atoll	3/1/2020	1/24/2020	Coastal shrub	Three chicks, 1 egg	Directly on ground, within *Pluchea* bush
Kalama Atoll	16.729505, -169.534767	Johnston Atoll	3/19/2020	3/14/2020	Coastal shrub	Five eggs	Directly on ground, within *Pluchea* bush
Lanai	20.818405, -156.883064	-	6/8/2021	5/1/2021	Native wet forest	One fledgling	Found approximately one meter from base of Oʻhia tree, in Uhule understory
Hawai'i	19.686944, -155.359722	Hakalau Forest National Wildlife Refuge	7/14/2021	5/26/2021	Alien mesic grassland	One fledgling	Found in field with kikuyu grass and uluhe
Hawai'i	19.79187, -155.319529	Hakalau Forest National Wildlife Refuge	7/6/2021	5/15/2021	Native mesic forest	One fledgling	Found approximately 10 meters from the base of a Koa tree, in tall, green, kikuyu grass
Hawai'i	19.687778, -155.358333	Hakalau Forest National Wildlife Refuge	4/7/2022	2/8/2022	Alien mesic grassland	Two fledglings	Found in field with kikuyu grass and uluhe, near
Kaua'i	22.205564, -159.573353	Upper Manoa	3/2/2022	1/9/2022	Native wet forest	One fledgling and one egg	Small divot within Uluhe understory
Kaua'i	22.163618, -159.613631	Pihea	-	-	Native mesic forest	Nest	-
Kaua'i	22.190265, -159.578707	Upper Manoa	-	-	Native wet forest	Fledgling	-
Kaua'i	22.189046, -159.605427	Pohakea	-	-	Native mesic forest	Eggs	-
Kaua'i	22.063382, -159.354399	Sleeping Giant	-	-	Alien mesic forest	Nest	-
Hawai'i*	19.795769, -155.321464	Kanakaleonui, Mauna Kea	3/22/1993	-	Native mesic forest	7 Eggs	Found approximately 30 cm from a dead Māmane snag, in grass about 30 cm tall
Hawai'i*	19.795769, -155.321464	Kanakaleonui, Mauna Kea	4/3/1995	-	Native mesic forest	2 Chicks	Found perched in Pukiawe bush
Hawai'i*	19.837282, -155.587708	Pu'u La'au, Mauna Kea	5/5/1993	-	Alien dry grassland	4 Eggs	Found near base of a small Māmane tree
Oʻahu	-	Mōkapu Peninsula	5/30/2018	-	Alien wetland	Fledgling	-
Oʻahu	-	Mōkapu Peninsula	5/18/2017	-	Alien wetland	Chick	-
Maui	-	-	11/1/2011	-	Unknown	Nest	-
Kauaʻi	-	-	5/1/2017	-	Unkown	Nest	-

[1]If photos or detailed descriptions of the chicks or eggs were provided, an estimated initiation date (i.e. date of first egg laying) was calculated in order to standardize observation timing. [2]General habitat type was ascertained by mapping observations over the U.S. Geological Survey Carbon Assessment of Hawaii Land Cover Map and using their General Land Cover categories (Jacobi et al., 2017). *Indicates observations from Snetsinger 1995, "Observations of Pueo Nests on the Slopes of Mauna Kea".

Table 2.8. Number of breeding observations found across the Hawaiian Islands and nearby Atolls, separated by island and month. Numbers include both incidental observations (from data request and literature review) and observations from our main study areas on O‘ahu.

	Kaua'i	**O'ahu**	**Maui**	**Hawai'i**	**Lanai**	**Kaho'olawe**	**Kalama Atoll**
January	0	2	0	0	0	0	0
February	0	5	0	0	0	0	0
March	1	2	0	1	0	0	4
April	0	1	0	2	0	0	0
May	1	2	0	0	1	1	0
June	0	2	0	0	0	0	0
July	0	0	0	3	0	0	0
August	0	0	0	0	0	0	0
September	0	0	0	0	0	0	0
October	0	0	0	0	0	0	0
November	0	0	1	0	0	0	0
December	0	1	0	0	0	0	0
Total	**2**	**15**	**1**	**6**	**1**	**1**	**4**

DISCUSSION

This study is one of the first to document Pueo nests across the state of Hawaii and investigate the factors influencing Pueo breeding ecology, filling an important geographical gap in our understanding of the basic life history traits of a globally distributed raptor. By using a combination of systematic nest searching and incidental observations reported from partners across the region, I was able to obtain insights on specific vegetation characteristics influencing nest site selection and nesting success, as well as provide evidence that Pueo are selecting a wider variety of habitat types for breeding than their continental counterparts. Understanding the variety of habitats and the specific site characteristics that are important to Pueo reproduction and nestling survival is directly relevant to the conservation of this endemic raptor. When compared to results from Short-eared Owl breeding ecology studies in other regions, these results suggest that the global population of Short-eared Owls may be a generalist species, with island and tropical subspecies displaying variation among individuals than continental and higher latitude subspecies.

In grassland systems, Pueo are selecting nesting areas with taller (40 to 50 cm) and denser vegetation compared to unselected sites, which is expected based on results from similar systems on North American Short-eared Owls (Fondell & Ball, 2004; Keyes et al., 2016). North American Short-eared Owls are also thought to have an upper limit in terms of tallest vegetation heights at nesting sites; Herkert et al. (1999) found that Short-eared Owl nests were nesting primarily in managed grasslands that had been mowed in the year prior and thus only had a maximum vegetation height of 50 cm, compared to Northern Harriers (*Circus hudsonius*), another ground nesting raptor, which nested primarily in undisturbed areas with taller vegetation. Other studies have indicated that some level of habitat management and disturbance is beneficial for Short-eared Owl nesting, as grasslands that are periodically mowed, hayed, or grazed results in a mid-range vegetation height that they seem to prefer (Dechant et al., 1998). In Hawaii, The Lualualei Valley site is regularly mowed due to fire risk concerns; this management action may provide more suitable nesting habitat for Pueo, but also presents an additional threat for Pueo nests to be disturbed or destroyed using heavy machinery.

While the null model assuming constant nest survival was the top model selected, likely due to a low sample size of nests, the other top models (ΔAICc < 1) suggest some environmental

factors may be significant in determining Pueo nest success. The second-best model selected included relative day of nesting season as the only covariate, with nests initiated earlier in the nesting season having a higher Daily Survival Rate. This is similar to seasonal nest success patterns observed in the Hawaiian Stilt (Harmon et al., 2021), and is likely an effect of higher precipitation during that time period (i.e. November through March) on O‘ahu, thus resulting in both rapid plant growth and higher prey abundance (Giambelluca et al., 2013). The third-best model selected included percent vegetation cover, with nests with higher percent vegetation cover having a higher Daily Survival Rate; these results are in line with a study from North America that found greater Short-eared Owl nest success in fields with taller and denser vegetation (Fondell & Ball, 2004). Additionally, my study did not look at survival after dispersal from the nest, which would provide a more complete understanding of juvenile survival and population trends overall. Rivest (1998) examined post-fledging dispersal of Short-eared Owls in Idaho with radio-tagged individuals and found a high mortality rate (88.2%) in the period between dispersal from the nest and first flight. Given the low survival rates found in my study and Rivest 1998, future studies should look at both pre- and post-dispersal survival of chicks to fully understand factors that influence juvenile survival and population dynamics.

Pueo diet composition did not vary significantly among nests. Pellets and prey remains associated with nests were only found at the Lualualei grassland site. Mostello and Conant (2018) also analyzed Pueo pellets collected from the Lualualei Valley site between 1993 and 1995 and found that birds and mice were the most frequently occurring prey items, occurring 70% and approximately 45% of the time, respectively. I observed slightly different proportions, with mice occurring more frequently than birds despite including prey remains, which were entirely avian prey, in my analyses while Mostello and Conant only looked at pellets. The differences in these frequencies may not be statistically significant, and both mice and small passerines can be subject to irruptive population dynamics depending on environmental conditions, so I cannot draw conclusions regarding changes in Pueo diet from this area between 1993 and 2020. However, it is interesting to note that birds have remained a significant contributor to Pueo diet at this site. Furthermore, Mounce (2008) and Tweed (2006) documented Pueo eating native passerines such as Kiwikiu (*Pseudonestor xanthophrys*), ‘Apapane (*Himatione sanguinea*), and Puaiohi (*Myadestes palmeri*), and one of our incidental nest observations noted Koa‘e‘ula and ‘Ewa‘ewa remains in Pueo nests. That Pueo predate on other

native and threatened bird species poses a potential conservation challenge, but further research is necessary to determine the magnitude of effect of Pueo predation on other native bird species, given their archipelago-wide distribution.

This study contributes to global indications that Short-eared Owl diets vary geographically. Thus, though globally the species appears to be a foraging generalist, there are strong regional dietary preferences, suggesting potential specialization at this level. In the Galapagos, seabirds in the genera *Oceanodroma*, *Phaeton*, *Sula*, and *Puffinus* are thought to be major elements in the Short-eared Owl diet, and in North America, coastal populations of Short-eared owls are thought to take a greater proportion of avian prey than inland populations (Grant et al., 1975; Holt, 1994). In contrast, multiple studies from inland North America and Europe found that small mammals, especially *Microtis* voles, make up at least 80% of the breeding season diet (Evrard et al., 1991; Glue, 1977; Holt, 1992; Korpimaki & Norrdahl, 1991; Roberts & Bowman, 1986). Thus, my study more closely follows expected patterns for island and coastal species, despite substantial rodent contributions to diet.

Table 2.9 summarizes the breeding parameters, phenology, and nesting habitat found in this study compared to what is known about the breeding parameters, phenology, and nesting habitat of other Short-eared Owl subspecies. Though there are far fewer studies from regions in latitudes closer to the equator (i.e. tropical regions between 23.5˚ North and 23.5˚ South, there seems to be greater variation in breeding phenology and nesting habitat in Short-eared Owls in tropical regions and in island systems compared to Short-eared Owls in continental systems. A previous study suggested that island populations may have later breeding seasons compared to their continental counterparts (Lambrechts & Dias, 1993; Wiggins et al., 1998). I did not find evidence of a later breeding season but instead a prolonged breeding season, perhaps driven more by different seasonal patterns in tropical climates resulting in broader periods of net productivity and prey availability (Wagner, 1957). Similar to this study, Greater Antillean Short-eared Owls (*A.f.domingensis and A.f.portoicensis*) were observed nesting as early as November and as late as June, with activity peaking in February (Garrido, 1984; Guerrero, 2005; Rodríguez Castañeda, 1998; Thorstrom & Gallardo, 2017). Similarly, Galapagos Short-eared Owls (*A.f. galapagoensis*) also have an expanded breeding season, with active nests found between September and May (de Groot, 1983).

I did not find a reduced clutch or brood size relative to continental Short-eared Owls. In contrast, Galapagos Short-eared Owls had smaller clutch sizes (2-5 eggs), fewer number of fledglings, and slower development of chicks (de Groot, 1983). Both the Galapagos and Hawaiian Islands have a similar suite of invasive mammalian predators, but Galapagos Short-eared Owls are thought to have diverged from *A.f. flammeus* between 890,000 and 1.7 million years ago, a much longer evolutionary period compared to that of Pueo which were thought to establish in the Hawaiian Islands between 1000 and 1200 A.D. ((Pyle, n.d.; Schulwitz et al., 2018). Given their longer existence in an island system without mammalian predators, Galapagos Short-eared Owls may have lost defenses to mammalian predators, allowing them to evolve smaller clutch sizes and a longer chick developmental period, while Pueo never lost their defenses to mammalian predators due to their relatively shorter evolutionary history.

Within the Hawaiian Islands, nests were found across a wide range of habitat types and elevation ranges. Although my focal study sites were composed of grasslands and wetlands, similar to those of studies from North America and Europe, I also received reports of nests and chicks in high elevation wet and mesic forests of Hawai‘i. Pueo are known to reside in these habitats and a previous study suggested that Pueo utilize forested areas for roosting more often than their continental counterparts (Hawai’i Department of Land and Natural Resources, 2005; Wilhite, 2021). Though the small sample size and nature of incidental observations collated in this study preclude population-wide conclusions about Pueo nest site selection across different habitat types, my study suggests that vegetation structure may be more important than the broader habitat type in identifying potential Pueo nesting sites. All Pueo nests or young were found in spots with relatively dense ground plant cover, whether it be of non-native grasses such as kikuyu grass (*Pennisetum clandestinum*) and bufflegrass (*Cenchrus ciliaris*) in grasslands, ‘uluhe (False staghorn ferns, *Dicranopteris linearis*) understory in native wet forests, or *Pluchea* bushes in coastal vegetation. Successful Pueo nesting in these areas further supports the fact that there are a variety of habitat types that are critical to their life history. This diversity in habitat use, especially for nesting, must be accounted for when determining what constitutes critical habitat for Pueo. Roberts and Bowman (1986) also suggested a broad spectrum of breeding ecology strategies based on their five-year study of breeding and diet of Short-eared Owls in heather moor in Wales; they noted that Short-eared Owls in heather moor had a narrower breeding season, smaller and more consistent clutch sizes, and a different diet than Short-eared

Owls in grasslands in Great Britain. Future research in the Hawaiian Islands should focus on nest searching and monitoring across all potential Pueo breeding habitats to examine if clutch size, brood size, diet, and nesting success differ based on vegetation type, as differences in breeding parameters could have important consequences for conservation and management actions.

My nesting habitat results, along with prior studies of Pueo movement and habitat use with GPS-VHF tracked individuals, suggest decreased habitat specialization and expanded habitat use of Pueo compared to continental Short-eared Owl (Garcia-Heras et al., 2022; Wilhite, 2021). Antillean and Galapagos Short-eared Owl nests have also been documented closer to forested and wooded areas at the bases of trees or in bushes, tentatively suggesting that the variation seen in these subspecies (including Pueo) are driven by island biogeography (Garrido, 1984; Guerrero, 2005; Rodríguez Castañeda, 1998; Thorstrom & Gallardo, 2017). Niche expansion with regards to diversified habitat use in island systems may result from the simultaneous decrease in interspecific competition and increase in intraspecific competition relative to the continental system (Blondel, 1985; Sayol et al., 2018; Van Valen, 1965). These simultaneous pressures on the population can result in increases in among-individual niche variation along with population niche breadth (Bolnick et al., 2003). Movement and habitat use data from GPS-VHF tagged Pueo suggest that they can travel relatively large distances, such as exploratory movements across and between different islands (Garcia-Heras et al., 2022). While I documented nesting at the Lualualei Valley site in consecutive years, adults were not marked, and I could not confirm if the same individuals were returning to the site to breed. Future research focused on tracking breeding birds over multiple years could shed light on whether individual Pueo are moving between among nesting areas in different habitat types each breeding season and thus displaying individual niche width widening (Bolnick et al., 2007).

The expanded breeding habitat use and diet of Pueo is especially interesting when considering that globally, Short-eared Owls are generally thought to be foraging and habitat specialists. The movement patterns and breeding habitat use of *A .f. flammeus* are strongly tied to fluctuating small mammal populations in grassland systems, and population-wide management recommendations stem heavily from this predator-prey dynamic (Booms et al., 2014). These Short-eared Owls display low breeding site fidelity, which is thought to stem from small rodent population irruptions and breeding wherever preferred prey is abundant (Johnson et al., 2017;

Korpimaki & Norrdahl, 1991). However, though the ability of a species to specialize is often thought to be relatively static, short-term changes in habitat degradation, population density, and source-sink dynamics caused by rapid environmental change can result in a species quickly becoming less specialized (Barnagaud et al., 2011). This relationship between prey population dynamics and Short-eared Owl breeding habitat use may be weaker in tropical and island regions such as the Hawaiian Islands, where various biogeographical dynamics have allowed for the species to become less specialized in their diet and habitat use and therefore less reliant on nomadic movements to obtain necessary resources. Indeed, studies of Short-eared Owl site colonization and extinction rates in both North America and the Hawaiian Islands have provided evidence that Pueo are indeed less nomadic than those on the continent (Miller et al., 2022; Wilhite, 2021).

Overall, I provide insight into factors affecting the nest site selection and nesting success of Pueo, while also providing evidence of diverse resource use across the Hawaiian Islands. Pueo selected sites for nesting that had greater vegetation density than the surrounding areas and had greater nest survival for nests initiated earlier in their breeding season and at nests with greater percent vegetation cover. Across the Hawaiian Islands, Pueo utilized a variety of habitats ranging from native wet forests to alien mesic grasslands for breeding and utilized a variety of different prey types including insects and birds throughout their breeding period. Though it is difficult to draw population-wide conclusions due my small sample size and incidental state-wide data collection methodology, these results illuminate the fact that habitat conservation and management plans for Short-eared Owls in one region may not be applicable across their global populations, nor even across a single state with as much habitat diversity as Hawaiʻi. Thus, regional studies are crucial in forming relevant and effective regional management plans.

Table 2.9. Summary of current knowledge of the breeding parameters of the nominate subspecies *Asio flammeus flammeus* and four of the island endemic subspecies. Notes on the sample sizes for each subspecies provided in the footnotes.

Subspecies	Location	Latitude	Breeding season	Number of eggs	Number of chicks	Nest habitat types	References
A.f.flammeus	North America (Canada and the contiguous United States.) and Europe	65 - 26° N	February - May	4-10 eggs	2-5 chicks	Natural grasslands, agricultural fields, and marshes	Urner 1925, Clark 1975, Hammerstrom 1961, Mikkola 1983, Saunders 1913, Arroyo et al. 2000, Holt et al. 1992
A.f. domingensis & *A.f. portoricensis*[1]	Greater Antilles	23 - 17° N	November – June	3-4 eggs	2 chicks	Natural grasslands, agricultural fields (pineapple fields), bases of Agave sp. trees	Garrido, 1984; Guerrero, 2005; Rodríguez Castañeda 1998, Thorstrom & Gallardo, 2017
A.f. galapagoensis[2]	Galapagos	0.9538° S	September – May	2-5 eggs	2 chicks	Natural grasslands, transition forests, and vegetated lava fields	de Groot, 1983
A.f. Sandwichensis	Hawaiian Archipelago[3]	28 - 16° N	November – June	1-7 eggs	1-5 chicks	Natural grasslands, wetlands, high-elevation wet and mesic forests	This study

[1]*A.f. domingensis* & *A.f. portoricensis*: Garrido 1984 and Guerrero 2005 each reported metrics from 1 nest (total n=2). Rodríguez Castañeda 1998 and Thorstrom & Gallardo, 2017 report nesting habitat types and breeding season dates but no specific numbers for eggs or chicks.

[2]*A.f. galapagoensis:* De Groot 1983 reports number of eggs and chicks from 7 nests, and breeding season dates comes from a total of 22 nest observations.

[3] Includes nearby atolls

CHAPTER 3

RECCOMENDATIONS FOR THE MANAGEMENT OF BREEDING PUEO IN HAWAIʻI

INTRODUCTION

This chapter serves to synthesize the results of the prior chapter into management recommendations specific to Pueo. First, I present recommendations for state guidelines regarding spatial and temporal Pueo nest buffers. Second, I present specific recommendations for land and natural resource managers who may have Pueo breeding in their lands. These recommendations are informed by the many hours of observation and targeted nest searching conducted at the two Oʻahu focal study sites, but these recommendations are general enough that they should apply across all islands and habitat types.

STATE-LEVEL RECOMMENDATIONS

Overview

Direct and indirect effects of human disturbance are known to negatively impact breeding raptors, and establishment of spatial and temporal buffer zones are an effective way to protect raptor nests from disturbance (Richardson & Miller, 1997; White & Thurow, 1985). Buffer zones are defined as a minimum area or time frame around a nest/nesting event where human activity should be avoided in order to prevent negative effects to the nest (Richardson & Miller, 1997; White & Thurow, 1985). Currently, there is no official guideline set by Hawai‘i Division of Land and Natural Resources (hereafter, DLNR) or Hawai‘i Division of Forestry and Wildlife (hereafter, DOFAW) for buffers around Pueo nests, despite their endangered species status on the island of O‘ahu (Hawai’i Department of Land and Natural Resources, 2015). Different projects across the state have been recommended various Pueo nest buffer distances, ranging from 20 meters to 100 meters (Raine et al., 2018, DOFAW pers. comm.). Temporal buffers are nonexistent as no research existed on the timing of Pueo nest establishment and chick development (Hawai’i Department of Land and Natural Resources, 2005). Based on the findings of this study, I advise that the state adopt and enforce s set guideline of a 200-meter minimum spatial buffer and a three-month minimum temporal buffer for Pueo nests.

Spatial buffer

A buffer of at least 200 meters should be maintained around the Pueo nest from the time that the nest is discovered until chicks are capable of flight. I found that the average Pueo chick dispersal distance was 98 meters, with chicks being found up to 200 meters away from their nest. These dispersal distances are comparable to observations of chick dispersal distances in North America and Europe (Arroyo & Bretagnolle, 1999; Clark, 1975). Chicks begin dispersing at around 12 days old and are not capable of flight until they are at minimum 28 days old. During this dispersal period, chicks are still dependent on their parents to feed them and cannot fly. The inability of chicks to flush when disturbed is especially concerning; adult Pueo will flush when approached by humans or when habitat is disturbed (i.e. grass mowing, heavy machinery use) and thus escape the area and alert observers of their presence, while chicks cannot. Pueo nests are also sensitive to disturbance at the incubation stage, and repeated disturbance in the area surrounding the nest may cause the Pueo to abandon their nest.

Temporal buffer

If a Pueo nest with eggs or chicks is discovered, a two-month temporal buffer, starting from the estimated nest initiation date, should be observed. If Pueo breeding behaviors are observed over repeat surveys of an area, then a conservative approach would be to observe a three-month temporal buffer of the area. I found that the time that the first egg is laid to the time that the first chick fledges takes approximately 47 to 56 days; this timing is comparable to the observations of the timing of Pueo nests in North America and Europe (Wiggins et al., 2020). I also observed that breeding behaviors (i.e. courtship displays, vocalizations, etc.) associated with each nest were observed in the nesting area up to three weeks before the first egg was laid. In order to be effective, temporal buffers should encompass the entire span of nesting activities, beginning with the presence of adult birds in the area displaying breeding behaviors until nesting is complete (Fyfe & Olendorff, 1976; Richardson & Miller, 1997). The total span of nesting activities for Pueo amounts to approximately 77 days or approximately 2.5 months. However, Pueo breeding behaviors are often difficult to observe without repeat surveys of an area, and all the incidental observations of Pueo breeding collated in this study were of nests that already had eggs or chicks.

LAND MANAGER-LEVEL RECOMMENDATIONS

Overview

Site-specific Pueo management actions should be follow official Hawai‘i DLNR and DOFAW guidelines, but may vary depending on the specific region (i.e. habitat type), physical characteristics of each site, and the potentially disturbing activities that may occur at the site. The following recommendations are general enough to be tailored to site-specific situations. Management recommendations are listed below in brief, with further contextualization and detail in the text that follows.

I. Minimize habitat alterations and disturbance during Pueo breeding season. Before any potentially disturbing activity, especially ground-based disturbance, conduct surveys during crepuscular hours and walk line transects through the area to detect any active Pueo nests.
II. If a Pueo nest is discovered, minimize time spent at the nest and establish a minimum buffer distance of 200 meters from the nest until chicks are capable of flight.
III. Reduce anthropogenic threats: use non-toxic methods of pest control and lower traffic speed limits.
IV. Remove and exclude non-native mammals such as mongoose, cats, dogs, and ungulates from the nesting area.

Minimize habitat alterations and disturbance during Pueo breeding season

Actions such as vegetation mowing, clearing, construction, or harvesting in agricultural areas alters important Pueo nesting habitat and directly threatens Pueo adults and nests through crushing by heavy machinery and trampling by personnel walking through the area. Prolonged, intensive human activity (i.e. mowing grass, constructing structures) can also cause Pueo to abandon nests. Importantly, grassland nests are often in tall and dense vegetation that is difficult to see, even when standing as close as a meter to the nest. If habitat altering actions must be conducted during the Pueo breeding season, the target areas should be surveyed for Pueo nests prior to the start of the activity.

Initial surveys should check for Pueo activity in the general area, which includes point counts and targeted searches for other signs of Pueo activity such as looking for pellets. Because

adults may be sitting on nests and are not visible, surveys should take place during the time when Pueo are most active (i.e. when they make a prey delivery to the nest or take an incubation break where they may perch elsewhere for a small period of time), which occurs between dawn and sunrise and between sunset and dusk. Observing either of these behaviors can confirm nesting in the area without having to access the nest directly and create additional disturbance towards the Pueo. Surveys should take place from a favorable vantage point and last for at least 90 minutes (Larson & Holt, 2016). Surveys should begin at least a week before the habitat altering activity takes place; conduct as many surveys as possible within that time frame in order to maximize the probability of detecting Pueo breeding behaviors.

If Pueo display defensive behaviors towards an observer, the observer should try to leave the area immediately to minimize disturbance. In a few instances, adult Pueo would emerge from areas other than the nest, such as a nearby perch, and begin displaying defensive behaviors such as swooping, beak snapping, and other vocalizations in response to observers entering a nesting area (Wiggins et al., 2020). Defensive behaviors towards observers strongly suggests the presence of a nest nearby and thus can also be used to confirm breeding activity in the area. These behaviors were also observed when checking known nests or searching for dispersed chicks in a nesting area.

If breeding behaviors are observed, a conservative approach would be to avoid any activities in the area until Pueo are no longer observed using the area or until 2 months from the first day that breeding behaviors are observed. If the habitat altering activity cannot be delayed, an exact nest location will be necessary to obtain and a buffer established around the nest that activities cannot be conducted in until the nest is no longer active. Transect searches should be used to flush the incubating Pueo off the nest and thus discern the exact location of the nest. This method is described in depth in Chapter 2 (See Chapter 2 Methods: Nest Discovery), but essentially entails multiple observers spaced approximately 1 meter apart walking through an area of interest to search for a nest. During nest searching I found that incubating Pueo varied greatly in their flight initiation distance when approached. Some Pueo flushed when observers were roughly 10 meters away while others did not flush until observers were less than a meter away. Thus, thoroughly searching through the vegetation and doing multiple sweeps may be

necessary to flush the Pueo off its nest (Larson & Holt, 2016). The section below ("If a Pueo nest is discovered…") details the next steps to take after discovery of a Pueo nest.

This study documented Pueo nests in grasslands yet failed to detect Pueo nests in agricultural areas. Nonetheless, studies of Short-eared Owls elsewhere have described breeding in croplands, cattle grazed fields, and other intensively managed grassland-type systems (Arroyo & Bretagnolle, 1999; Clark, 1975; Fondell & Ball, 2004; Herkert et al., 1999; Sviridova et al., 2020). Therefore, particular care should be taken to survey for Pueo and search for nests in both agricultural areas and managed grasslands.

If a Pueo nest is discovered, minimize time spent at the nest and establish a minimum buffer distance of 200 meters from the nest until chicks are capable of flight

Upon discovery of a nest, observers should take note of the location and quickly leave to minimize disturbance and allow the parent Pueo to return to the nest as soon as possible. To avoid attraction of predators to discovered nests, observers should check if vegetation surrounding the nest was moved or trampled and re-cover the vegetation so that no obvious gap or opening to the nest remains. I observed that nests were more likely to be abandoned during the early egg laying and incubation stages compared to once chicks had hatched and were older. (i.e. at least 5 days old). If a nest is discovered at the incubation stage, extra care should be taken to leave the area as soon as possible.

I found that Pueo chicks dispersed up to approximately 200 meters from the nest, beginning at about 12 days old, which is comparable to observations of chick dispersal in North America and Europe (Arroyo & Bretagnolle, 1999; Clark, 1975). At this dispersal stage, chicks are still dependent on their parents to feed them and cannot fly. Thus, a buffer of at least 200 meters should be maintained around the nest until chicks are capable of flight. I found that the time that the first egg is laid to the time that the first chick fledges takes approximately 47 to 56 days, so a temporal buffer of approximately 2 months from the estimated nest initiation date should be observed before resuming ground-disturbance activities in the nest area.

Reduce anthropogenic threats: eliminate usage of rodenticides and lower speed limits

Eliminating use of toxicants, such as replacing anticoagulant rodenticides with non-toxic Goodnature A24 rodent traps, in Pueo breeding areas will be crucial for nest survival. Across all stages of their life cycle Pueo are vulnerable to secondary poisoning from pesticides such as rat

poison (Nakayama et al., 2019; Siers et al., 2019). Siers (2019) found that 47% of Hawaiian raptor carcasses analyzed contained secondary-generation anticoagulant rodenticides. I found that both insects and rodents, common targets of toxicants, were prey items for breeding Pueo, with rodents representing a significant proportion of Pueo diet.

Additionally, speed limits should be reduced on high traffic roads in areas where Pueo are nesting when possible and erecting signage that alerts drivers to be aware of Pueo in and around the road. At my focal study sites, I regularly observed both adult and recently fledged juvenile Pueo hunting on and alongside roads; likely because the reduced vegetation cover along roads may create optimal hunting conditions. I found one dead adult Pueo off the side of the road, presumably killed by a vehicle collision. Vehicle collisions also pose a threat to Pueo chicks as multiple nests were found approximately 100 meters from roads. Although I did not observe any instances of this occurring, dispersing chicks could be hit by passing vehicles.

Remove and exclude non-native mammals such as mongoose, cats, dogs, and ungulates from the nesting area

Thirty percent of the nests we monitored failed due to predation – one likely due to feral dog predation on the adult and chicks, and another due to egg predation likely from a mongoose or rat. Other mammals such as feral cats and wild boars were often observed at my study sites in the vicinity of Pueo nesting areas, and in one instance I observed a Pueo chasing a cat away from its nest. Predator traps were set once Pueo nests were discovered, but given that the longer a nest is established the more likely it is to be discovered, it is unknown how many nests may have been initiated but abandoned or otherwise failed early on due to the presence of a predator. If Pueo appear to be repeatedly breeding at a given site, ongoing predator removal should be considered in order to minimize predation probability. Some incidental observations of Pueo nesting on Hawaiʻi Island and Kauaʻi were located in areas that had predator-exclusion fencing installed for the purposes of protecting other endangered ground-nesting birds (i.e. Nēnē and seabirds), further supporting that removing mammalian predators from an area increases Pueo nest survival.

CHAPTER 4

SUMMARY

This thesis is the first attempt to study Pueo breeding ecology using both targeted nest searching and monitoring and collation of state-wide incidental observations. My results provide insight into the breeding parameters, nest site selection, and factors influencing nesting success that are directly relevant to the management of Pueo in Hawaiʻi while also broadening our understanding of Short-eared Owl ecology globally by filling a biogeographical knowledge gap.

I found evidence of selection of taller and denser patches of vegetation for Pueo nesting, but that these same metrics did not necessarily correlate to greater nest survival. These results are similar to results of Short-eared owl nest site selection in similar grassland and wetland systems in North America and Europe, but more research is needed to see if these relationships between habitat characteristics and nest site selection and success hold true in other habitat types in Hawaiʻi. Similar to other tropical and island Short-eared Owl populations, I found evidence of expanded breeding season and a greater diversity in habitat use compared to continental and higher latitude Short-eared Owls. While this study provides preliminary evidence that Pueo have more diverse breeding habitat use and diet than continental Short-eared Owl subspecies, more research focused on long-term tracking of individual breeding birds is necessary to determine if Pueo are a case of individual niche width widening or population-wide niche breadth increase.

Long-term studies of Short-eared Owl population dynamics, breeding, and conservation needs in continental systems have relied on community science projects such as the Breeding Bird Survey (BBS), Christmas Bird Count (CBC), and the Western Asio flammeus Landscape Study (WAfLS) in North America, Proyecto Asio in South America, and multi-national surveys of conservation and wildlife professionals in Europe (Fernández-Bellon et al., 2021; Gahbauer et al., 2021). These projects generally rely on short site visits to monitor for Short-eared Owl occupancy and provide some insight into general breeding habitat use and movement ecology of breeding populations, but any further understanding of specific breeding parameters or the effects of different habitat characteristics on breeding success require targeted nest searching and monitoring. I recommend that Hawaiʻi adopts a similar strategy of using community science or other forms of collaborative data collection to obtain broad scale data of Pueo population dynamics and breeding, which can eventually serve as a baseline for more detailed

monitoring and further investigation into factors influencing Pueo breeding ecology. While this study provides some insight into how habitat characteristics and phenology affect nest site selection and nest survival, my targeted nest monitoring was limited to only two sites from one island and yielded a small sample size. Further research in Hawai‘i to increase this sample and cover a greater variety of habitat types and islands will allow us to draw stronger conclusions about factors influencing Pueo breeding state-wide.

APPENDIX A

STATE-WIDE INCIDENTAL PUEO BREEDING OBSERVATION DATA COLLECTION FORMS

Pueo Project Breeding/Nest Observation Data Sheet

Observer Name: **Date:** **Time:**

Latitude: **Longitude:**
(please use decimal degrees for locations)

General habitat type (circle):

- **Grassland**
- **Savanna**
- **Forest**
- **Urban/developed**
- **Agricultural**
- **Wetland/Marsh**
- **Beach/Coast**

Please email completed form and photos to Olivia Wang at owang@hawaii.edu

ADULT PUEO BEHAVIOR	**Number of pueo**	**Circle breeding behaviors observed**	**Behavior notes**
		• Courtship display / wing clap • Nest incubation • Prey delivery to nest • Other (describe in notes)	

NEST CONTENTS/CHICKS	**Number of eggs**	**Egg description** (shape: spherical (golf-ball like) or more oblong (chicken egg)	**Number of chicks**	**Chick description** (color: white or tan? feather texture: downy and soft or larger, pin-like feathers also present?)	**General notes**	**PHOTOS:** 1. Photo of the eggs in nest (do NOT touch eggs) 2. Photo of each individual chick (do NOT touch chicks)

NEST SITE (0.5 radius area from the center of the nest)	**Height of tallest vegetation** (cm)	**Most abundant plant species** (rank 1-3; 1 being the most abundant)	**Distance to nearest tree** (m)	**General Habitat Description**	**PHOTOS:** 1. One photo of an aerial view of the nest from 1m high 2. One photo from each of the four cardinal directions from 1m above the ground, while standing 1m away

Figure A.1. Paper version of the datasheet that will be sent to federal, state, non-profit, and private partners.

The online version is accessible at https://airtable.com/shriqVYZY3z7eDBBr

APPENDIX B

CLASSIFICATION TREES FOR DETERMINING SPECIES OF AVIAN PREY

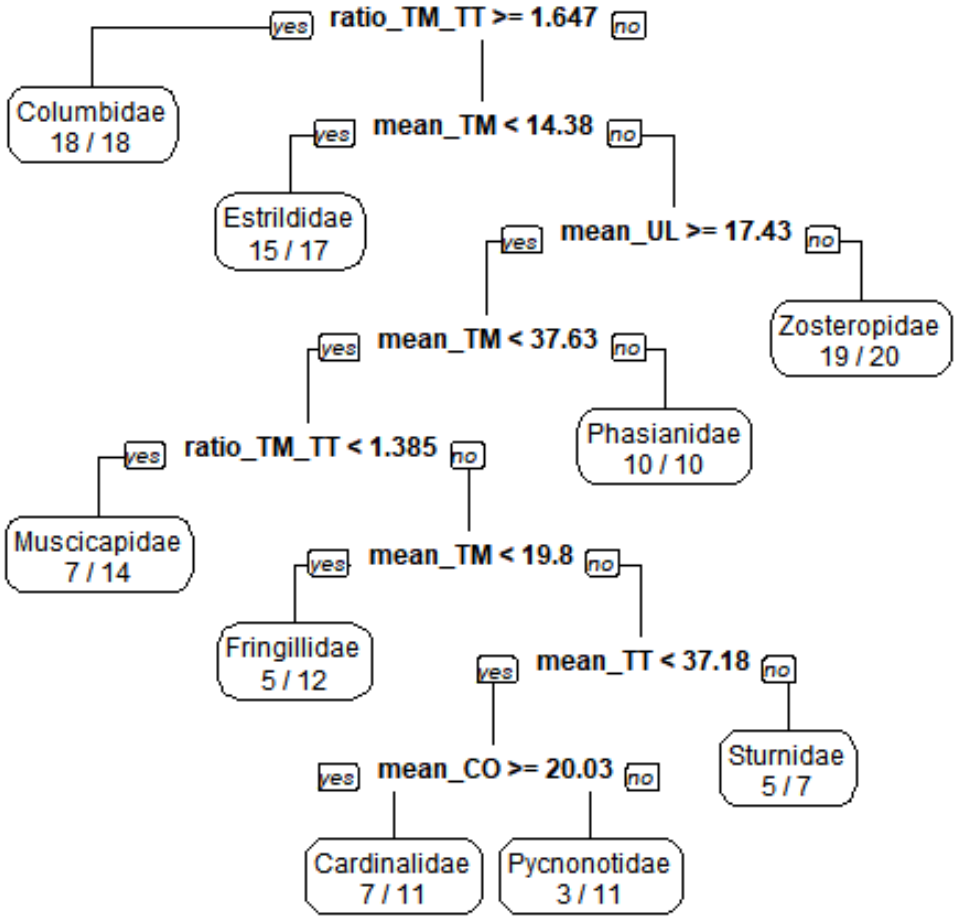

Figure B.1. Classification tree categorizing likely avian prey families based on select bone measurements. Numbers underneath the avian family name at each node are the number of correct classifications / the number of total observations within the node.

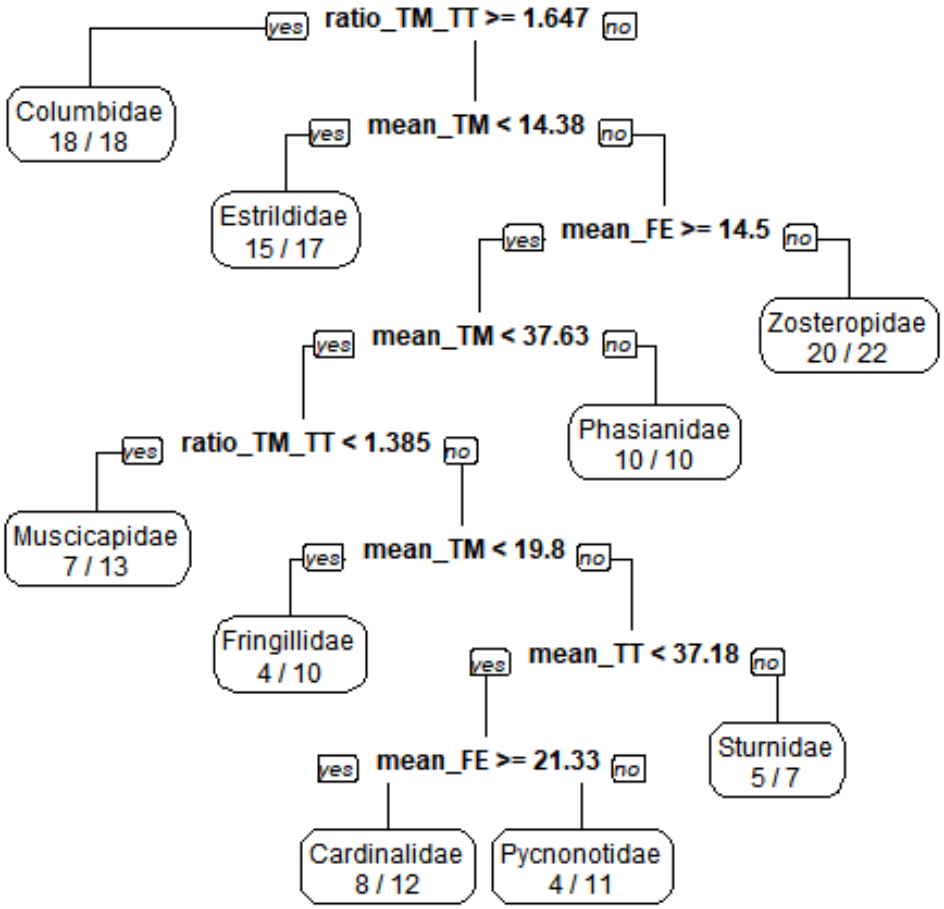

Figure B.2. Classification tree categorizing likely avian prey families based only on leg bone measurements. Numbers underneath the avian family name at each node are the number of correct classifications / the number of total observations within the node.

APPENDIX C

PUEO NESTLING MORMPHOMETRICS AND PHOTOS

Table C.1. Pueo nestling morphometrics. Age estimates were based on both morphometrics by comparing with other studies of Short-eared Owl nestling morphometrics (Arroyo et al. 2000, Holt et al. 1992) and based on the age of nest through repeated nest checks.

Nest ID	Chick ID	Estimated Age (days)	Weight (g)	Metatarsus Length (mm)	Culmen Length (mm)	Unflattened Wing Chord (mm)	Tail Length (mm)
03	03_01	15	362	47.5	26.7	NA	NA
07	07_01	15	307	46	26.6	148	NA
09	09_01	12	245	37.1	NA	85	15
09	09_02	11	245	36.5	NA	79	<10
09	09_03	10	214	30.82	NA	68	<10
10	10_01	16	308	40.98	14.7	105	20
10	10_02	15	253	36.07	13.45	78	<10
10	10_03	13	178	30.53	12.34	45	0
10	10_04	11	173	29.05	11.89	52	0

Photos for some chicks documenting plumage and primary feather development can be found at https://github.com/oliviawang115/Pueo_Breeding_Ecology_Photos?raw=true

APPENDIX D

HAWAIʻI WILDLIFE CENTER JUVENILE PUEO PATIENT DATA

Table D.1. Juvenile Pueo patient records from the Hawaiʻi Wildlife Center. Island and general location where the Pueo was found are reported along with intake date and the status of the patient.

Island	Discovery Location	Intake Date	Status
Oʻahu	NA	2014-10-21	Released
Hawaiʻi	Parker Ranch, Old Saddle Rd	2014-08-26	Released
Maui	Kihei	2018-07-05	Released
Hawaiʻi	Waimea HS	2019-05-28	Died
Hawaiʻi	Hakalau Forest NWR	2021-7-06	Released*
Lanaʻi	Manele Rd	2020-07-28	Released
Hawaiʻi	Hawi	2019-06-04	Died

*Discovery of this juvenile Pueo was also reported to our online data collection form and is included in the state-wide incidental observation summary.

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