FACTORS INFLUENCING THE DISTRIBUTION OF THE HAWAIIAN SHORT-EARED OWL (PUEO) ON THE ISLAND OF MAUI, HAWAI‘I

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ABSTRACT

Multiple factors influence the selection of foraging habitat in raptors. To conserve energy, many raptor species tend to hunt in areas with reduced cover for ease of prey detection and capture, but prey type and availability varies across the landscape and also influences distribution. The pueo, or Hawaiian short-eared owl (*Asio flammeus sandwichensis*), occurs across the Hawaiian Islands in diverse habitats, including forests, grasslands, wetlands, and shrublands, and consumes a variety of prey items including rodents, birds, and invertebrates. In my thesis research I evaluated which factors influence pueo occupancy on the island of Maui. I expected that the pueo would hunt in areas that were the most accessible (short vegetation and low ground cover) compared to areas with dense vegetation, and that the biomass of prey items most commonly found in pellets (mice and zebra doves) would play a greater role in predicting pueo presence than all potential prey items combined. Using a random stratified design to sample across environmental gradients, I conducted point count surveys for birds and bats, mark-recapture surveys for rodents, and sweep net surveys for insects (Order Orthoptera). Pueo were detected across a range of vegetation characteristics but were most often seen in mid to high elevation, using both open and forested areas. The detectability of pueo was influenced by vegetation height. The top single-season occupancy models indicated that bird biomass, relative total prey biomass, and ground cover were slightly negatively correlated with the estimated likelihood of pueo occupancy, while elevation, relative insect (Order Orthoptera) biomass, and vegetation height were slightly positively correlated with the estimated likelihood of pueo occupancy. Given the weak correlations observed in this study, factors other than vegetation complexity and prey biomass are also likely influencing occupancy. However, the number of detections of pueo in the study were low (n=11) and may have decreased my ability to detect stronger correlations. Future studies should investigate seasonal differences, home range size, and available nesting habitat, in relation to occupancy. As individual pueo may exhibit preferences for particular prey types and vegetation characteristics, further research tracking individual pueo for specific behaviors is needed to elucidate variation within and among island populations.

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CHAPTER 1

Introduction

The patterns and processes underlying the structure of natural communities and associations between predators, prey, and their habitat are foundational to ecology and conservation biology (Morrison et al., 2006; Ritchie & Johnson, 2009). Prey availability and accessibility are predicted to drive the distribution of predators, but for generalist species that rely on multiple species of prey, the relationship between prey distribution and predator response may be more complex (Smout et al., 2010). Prey population dynamics are strongly influenced by environmental fluctuations both temporally and spatially (Regan et al., 2018; Schmidt et al., 2018). In contrast, a generalist predator can opportunistically prey switch throughout the year, but other factors may hinder hunting success (Donázar et al., 2016).

As top-level predators, raptors often exist at low densities, requiring large foraging areas and healthy prey populations (Newton, 1979; Korpimaki, 1984; Williams, 2012). Therefore, population demography is strongly influenced by inter- and intraspecific interactions, such as competition for food resources and nest site establishment (Katzner et al., 2003; Thirgood et al., 2003; Hakkarainen et al., 2004; Martínez et al., 2008). Given global declines in many species of raptors, it is crucial to further examine factors limiting population growth, such as prey abundance and vegetation characteristics selected for hunting (Wiggins et al., 2006; Miller et al., 2017).

Some top-level predators exhibit generalist hunting behavior utilizing diverse habitats and prey switching more readily than narrow-niched species that primarily hunt a single species in a specific vegetation type (Smith, 2012). On isolated islands with reduced competition and reduced susceptibility to predation, predators may expand their niche, broadening foraging habitats and prey types due to relative profitability (Thiollay, 1998; Thirgood et al., 2003; Whittaker & Fernández-Palacios, 2007). Therefore, it can be predicted that individuals with less competition and a wider realized trophic niche should establish foraging territories with higher diversity of ecosystems and prey (Lopez, 2015).

Some models of predator-prey relationships assume a predator will hunt more frequently in areas with high prey density to reduce time and energy spent on the hunt (Poole, 1974; Pyke et al., 1977; Krebs et al., 1983). This relationship acknowledges the process of searching for and capturing prey, which requires high energy expenditure (Norberg, 1977; Donázar et al., 2016). Horizontal flapping in birds necessitates metabolic rates that can be ten times as high as that during rest; hovering involves energy expenditures that can be fifteen times higher than a resting metabolic rate (Tucker, 1971). Capture success for multiple raptor species has been estimated at ten percent, highlighting the necessity to hunt a large portion of each day, and thus habitats and hunting techniques that require less effort are utilized to minimize energy expenditure (Bechard, 1982; Toland, 1987; Preston, 1990; Thirgood et al., 2002; Tseng et al., 2017).

Prey density, however, is not the only predictor of raptor foraging behavior—vegetation characteristics also strongly influence the effort required to detect and capture prey (Bechard, 1983). Another important consideration in raptor foraging ecology is that each prey assemblage across the landscape varies in energy spent versus gained by an individual raptor. An insect may be most easily captured by a raptor but contains a low amount of biomass per item captured. In contrast, a small rodent, such as a mouse, requires a mid-level of effort but contains more biomass per item captured. Birds require the most energy to capture if on the wing, but a large bird contains more biomass than a small mouse (Toland, 1987). Further, the effort required to obtain each of these prey items differs depending upon the height and complexity of the vegetation (Toland, 1987; Thirgood et al., 2002). Layers of three-dimensional structure provide extensive habitat for prey items but may make it more difficult to access those prey. Because of this, raptors may select foraging habitat with lower prey biomass to expend less energy during discovery and capture (Bechard, 1982; Preston, 1990; Thirgood et al., 2002; Tseng et al., 2017). Therefore, energetic tradeoffs exist across different vegetation characteristics and prey types.

A medium-sized raptor, the short-eared owl (*Asio flammeus*) is a globally distributed species that typically occupies open vegetation types, but has also been observed using forest systems (Wiggins et al., 2006). Distribution, foraging strategies, and breeding ecology are highly variable across the species' range, likely driven by prey availability and distribution (Newton, 2006; Calladine et al., 2010). In locations with stable prey populations, short-eared owl population sizes appear stable as well (Roberts & Bowman, 1986). In contrast, populations of short-eared owls breeding in grasslands of North America are highly nomadic, reflecting the reproductive variability of their prey (Pitelka et al., 1955; Holzinger et al., 1973; Mikkola, 1983; Johnson et al., 2013). Foraging strategies vary considerably among geographic locations as well. Some coastal and island short-eared owl populations consume higher proportions of birds, mostly passerine species, compared with continental short-eared owls, which generally prefer rodents (Holt, 1993; Mostello & Conant, 2018). Short-eared owls have even been observed shifting between diurnal and nocturnal hunting strategies dependent upon prey availability and on the presence of potential predators or competitors (Reynolds & Gorman, 1999; Calladine & Morrison, 2013; Tseng et al., 2017). These versatile life history strategies highlight the importance of local prey abundance and vegetation characteristics in shaping regional population dynamics of short-eared owls (Roberts & Bowman, 1986; Holt, 1993).

The Hawaiian short-eared owl (*Asio flammeus sandwichensis*, hereafter pueo) is the only native raptor widely distributed across the Hawaiian archipelago (Hawaiʻi Department of Land and Natural Resources, 2005). As a result, competition and predation risk among raptors is minimal on most of the Hawaiian Islands, in contrast to continental systems. The invasive nocturnal barn owl (*Tyto alba*) now occurs across the islands and is a potential competitor and predator of the pueo (Tomich, 1962; Mostello, 1996). Other raptors include the Hawaiian hawk (*Buteo solitarius* or ʻio), which now only occurs on Hawaiʻi Island, and vagrant raptor species, such as the peregrine falcon (*Falco peregrinus*) that arrive infrequently during the winter months (Tomich, 1962; Scott et al., 1986; Mostello, 1996; Wiggins et al., 2006; Tseng et al., 2017; Mostello & Conant, 2018). Other potential competitors or predators are rats (*Rattus* spp.), feral cats (*Felis catus*), and the small Indian mongoose (*Herpestes javanicus*) that are present on Hawaiʻi Island (commonly referred to as the Big Island), Maui, Molokaʻi, and Oʻahu (Tomich, 1962; Scott et al., 1986; Mostello, 1996; Wiggins et al., 2006; Tseng et al., 2017; Mostello & Conant, 2018). Given limited interspecific competition and predation, the niche space for pueo is likely larger than the niche space of continental short-eared owls and driven largely by environmental variables and prey availability (Tomich, 1962; Bechard, 1982; Preston, 1990; Thirgood et al., 2003; Priestley et al., 2008; Smith, 2012).

Pueo consume the prey biomass equivalent of about 10 percent of their own body mass daily (Graber, 1962; Clark, 1975; Mostello & Conant, 2018), and may select from a variety of rodents, birds, and insects to meet metabolic and nutritional requirements (Mostello & Conant, 2018). A short-eared owl typically egests one or two pellets of indigestible matter per day (Clark, 1975). A diet analysis of pueo across four of the main Hawaiian Islands (Hawaiʻi Island, Oʻahu, Lanaʻi, and Kauaʻi) determined that 73 percent of pueo pellets contained mice (*Mus musculus*) and less than 20 percent of pueo pellets contained rats (*Rattus* spp.) (Mostello, 1996; Mostello & Conant, 2018). However, birds were also important prey items for pueo, in contrast with continental short-eared owls that consume primarily rodents (Wiggins et al., 2006). Seventeen percent of pueo pellets contained zebra doves (*Geopelia striata*) and 15 percent of pueo pellets contained other birds—passerines and game birds (Mostello, 1996; Mostello & Conant, 2018). Insects, primarily of the order Orthoptera, also appeared to be important prey items as they were found in 46 percent of pueo pellets (Mostello, 1996; Mostello & Conant, 2018). Bats have not been observed in pueo pellets, but have been found in short-eared owl pellets elsewhere, and are likely consumed by owls in Hawaiʻi (Holt, 1993a; Wiggins et al., 2006).

Each of these potential prey types – rodents, birds, bats and insects (Orthoptera) – vary in composition and density among vegetation types; hence, evaluating the ecological niche of potential prey species may provide insight into the foraging behavior and distribution of pueo (Hawaiʻi Department of Land and Natural Resources, 2005; Regan et al., 2018; Schmidt et al., 2018). Three rat species, the black rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*) and Polynesian rat (*Rattus exulans*), are present across the Hawaiian Islands with broad fundamental niches dependent on the presence of competition and predation (Shiels, 2010; Harper & Bunbury, 2015). The *R. rattus* is considered to be mainly arboreal in Hawaiʻi, most dense in forest or shrubland (Shiels, 2010), while *R. exulans* and *R. norvegicus* occur more frequently on the ground surface in a variety of habitats from developed to forest systems (Harper & Bunbury, 2015). The house mouse (*Mus musculus*) also occurs more frequently on the ground surface and is considered to be most dense in grasslands (Shiels, 2010; Harper & Bunbury, 2015; Shiels et al., 2017; Tseng et al., 2017). Both taxa are also active both day and night (Shiels, 2010; Harper & Bunbury, 2015; Shiels et al., 2017). All rodents (*Rattus* sp. and *Mus musculus*) exhibit an omnivorous diet of native and nonnative plants, birds, and invertebrates, which drive their distribution and abundance (Scott et al., 1986; Hadfield et al., 1993; Hadfield & Saufler, 2009; Meyer III & Shiels, 2009; Shiels, 2010; Harper & Bunbury, 2015; Shiels et al., 2017). Another common prey item of pueo are insects, primarily of the Order Orthoptera, that occur across a variety of vegetation types, and vary in activity periods and dietary preferences from predatory to herbivory (Hawaiʻi Department of Land and Natural Resources, 2005; Tripplehorn & Johnson, 2005), and thus are driven by factors including weather and available resources. Bird species that are potential prey of pueo range in diet preferences from specific to general, and native to non-native species, with diets composed of seeds, nectar, fruit, and/or insects (Scott et al., 1986). Prey bird species also exhibit differences in habitat preferences, varying in distribution across the landscape and thus in the energy needed to capture them (Scott et al., 1986). The only bat species present across the Hawaiian Islands is the Hawaiian hoary bat (*Lasiurus cinereus semotus*) which uses both native and non-native habitat for foraging and roosting across a wide range of vegetation types and elevations (Hawaiʻi Department of Land and Natural Resources, 2005).

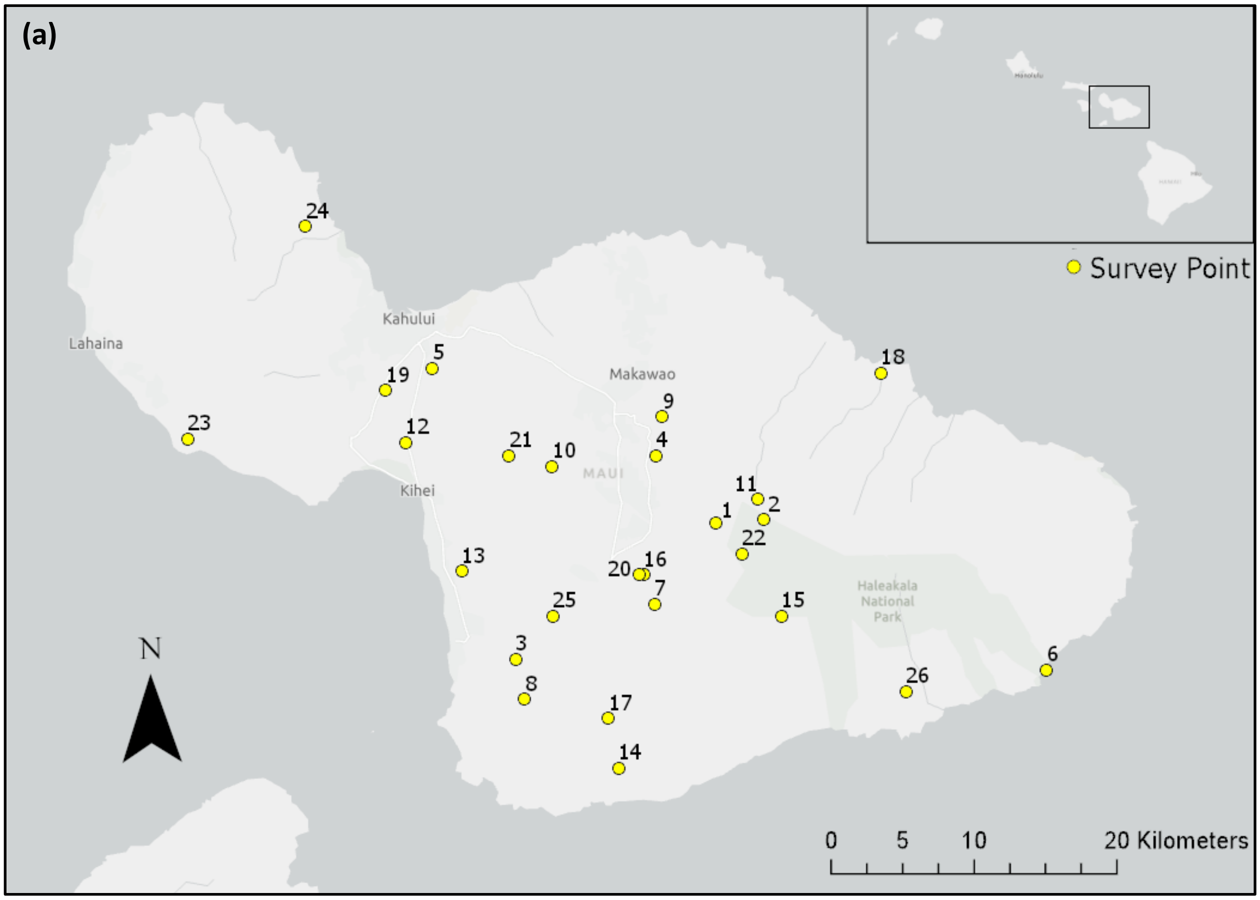
This is the first study to examine both native and non-native potential prey species across three taxonomic groups and multiple vegetation types in relation to the occurrence of a top-level predator—the pueo—in Hawaiʻi. In this study, I examined the distribution of potential prey items across the island of Maui, and utilized the predicted distribution of prey biomass along with vegetation characteristics to identify factors driving pueo occupancy (Fig. 1). I expected that the pueo would hunt in areas that were the most accessible (short vegetation and low ground cover) because of the lower energy required for hunting compared to areas with dense vegetation. I also expected that specific prey items (mice and zebra doves) would play a greater role in predicting pueo presence than all potential prey items combined, because they likely occur in shorter vegetation and provide more biomass than other prey types, such as insects.

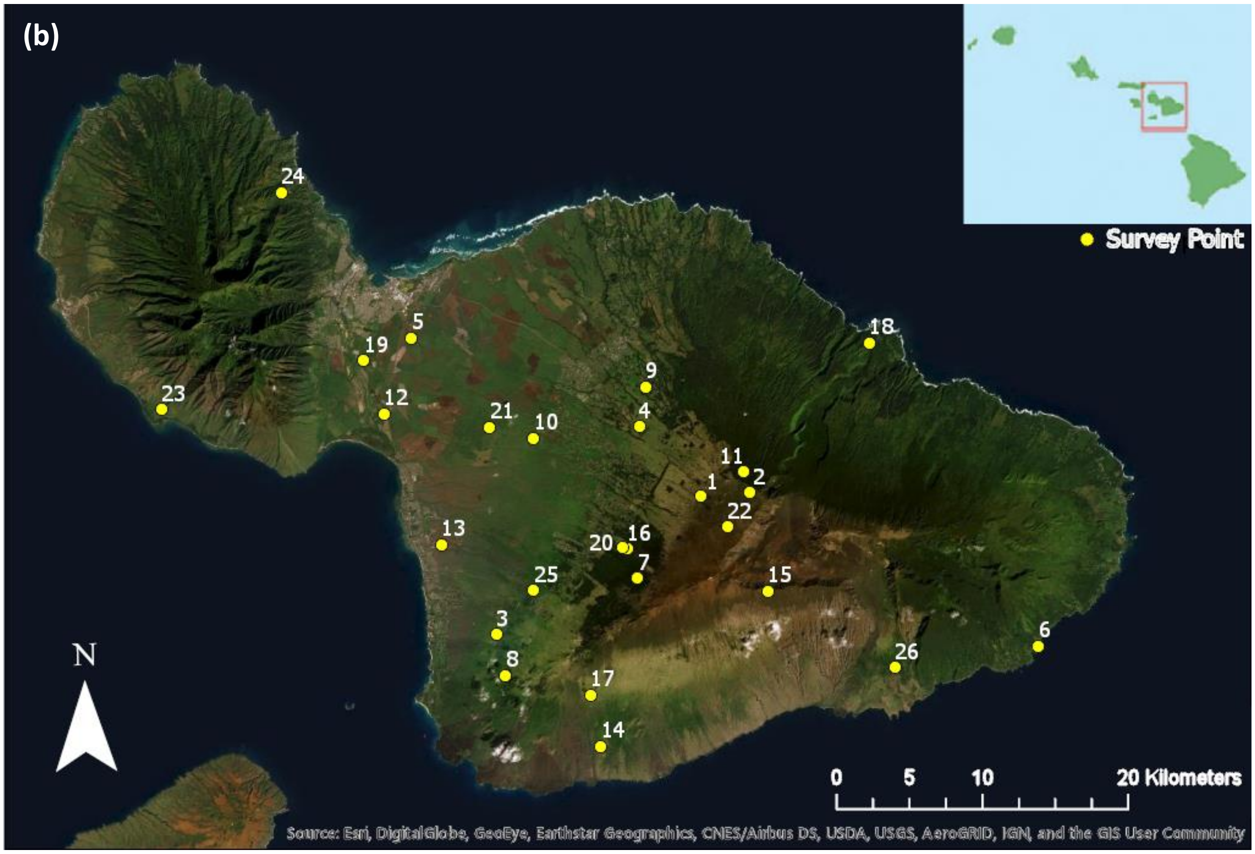
Fig. 1. Biomass pyramid of common prey items (birds, rodents, insects (Orthoptera)) consumed by pueo on the second tier (blue background) and vegetation types on the bottom tier (green background; left to right: cropland, forest, shrubland, and grassland) used by pueo on Maui.

Methods

Study Area Description. The island of Maui consists of 1,883 square km (188,300 ha) of land and is the second largest island in the Hawaiian Island archipelago (Fig. 2) (Sinton, 1987). The island was created by a series of volcanic events that formed two shield volcanoes, the West and East Maui Mountain Ranges (Sinton, 1987). The older (1.2 to 1.6 million years old), more rugged volcano, is the West Maui Range, and currently stands at 1,764 m above sea level (Sinton, 1987). The younger, more gradually sloping East Maui Range (Mt. Haleakalā) formed 0.4 to 0.86 million years ago and rises to 3,055 m (Sinton, 1987). The two shield volcanoes are joined by a valley-like isthmus that was formed by sandy erosional deposits (Sinton, 1987), that now contain towns and agricultural operations, including the port area of Wailuku and major airport in Kahului. Long-term mean annual rainfall varies across Maui from 250 mm to over 10,000 mm (Giambelluca et al., 2013). The north-eastern face of Mt. Haleakalā receives the greatest amount of rainfall due to the predominant northeasterly trade winds, while the least amount of rain falls at the lower elevation, southwestern regions of both mountain ranges. A characteristic of mountain systems is that the temperature decreases as the elevation increases. The average annual temperature on the summit of Mt Haleakalā is 7.2^{o}C, which is 16.7^{o}C cooler than the average temperature of 23.9^{o}C at sea level. Average annual rainfall increases up to the inversion layer, about 1,800-2,400 m (summit= 3,055 m), and above the inversion layer rainfall decreases, forming arid and relatively dry sub-alpine and alpine zones (Nullet, 2003). Major land cover types on Maui include cropland (1.2%), shrubland (8.7%), grassland (12.9%), forest (28.9%), and developed (36.4%) (see Appendix A) (ArcGIS Pro, version 2.5.1, Esri). Cropland habitat at the time of surveys was in the process of transitioning from fallow sugarcane to diverse croplands, and experienced a frequent and severe fire season in 2019 that left some areas unusually dry and barren (pers. obs.; pers. comm. with ag. producers).

Site Selection. Access to approximately 70 percent of the island was granted by cooperating landowners and managers. Potential survey sites were located by rasterizing the island of Maui into 500 by 500-m units using R packages ‘raster’ (Hijmans et al., 2017) and ‘rgdal’ (Bivand et al., 2018) in the statistical programming software R (version 3.5.2) (R Core Team, 2020; RStudio Team, 2020). To ensure sampling across an elevational gradient and multiple vegetation types, potential survey areas were divided equally into three altitudinal bands (0-1000 m, 1000-2000 m and >2000 m). An equal number (*n*=15 per band) of survey sites was randomly drawn from these three altitudinal bands. Survey sites were evenly sampled across all dominant vegetation types and adjusted within a 500 m radius if accessibility was limited due to terrain.





Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Fig. 2. Twenty-six survey points were accessed out of the forty-five points selected using a random stratified design and numbered in order of completion. Surveys started in May, 2019 and finished in December, 2019. (a) Light gray canvas map (b) Imagery map created in ArcGIS Pro (version 2.5.1, Esri**)**.

Surveys. At each site, surveys took place over three days and two nights. The dominant vegetation type within 200 m surrounding the survey point was determined using the ‘Buffer’ tool in ArcGIS Pro (version 2.5.1, Esri**)**. Site characteristics (ground cover, canopy cover, and mean height of dominant vegetation) were collected upon arrival at the survey point from three randomly selected one-meter square quadrats (Miller et al., 2017). A clinometer or measuring tape was used to estimate vegetation height and a densiometer was used to estimate canopy cover (James & Lockerd, 1986). Using a field thermometer, mean temperature per survey was determined by the temperature at the start and end of each audio/visual avian survey. Mean annual rainfall at each survey point was extracted from the online Rainfall Atlas of Hawai‘i database (Giambelluca et al., 2013). At each survey point, three different wildlife survey methods were utilized to evaluate the abundance of birds, bats, rodents, and insects (Orthoptera). Pueo pellets were collected opportunistically.

Bird and bat point count distance surveys. Bird and bat audiovisual surveys started one hour prior to sunset and ended thirty minutes after sunset (Cotin & Price, 2018). During the duration of each 90-minute survey, all aerial vertebrate species (bat, bird) seen or heard up to 200 m from the survey point were recorded. At the end of every audiovisual survey period, two distinct short-eared owl vocalizations from the *Merlin Bird* application were broadcast from a small Bose speaker twice, thirty seconds apart. The speaker was positioned between one and two m above the ground with the volume set for human ears to hear at a maximum distance of 100 m (Boscolo et al., 2006).

Rodent surveys. Capture, mark, and recapture were utilized to target rodents on the landscape, the house mouse (*Mus musculus*) and three rat species (*Rattus exulans, Rattus norvegicus, Rattus rattus*), using 50 Sherman traps (standard model LFA-TDG, 7.5 x 9 x 23 cm), baited with rolled oats, and set five meters apart in a 2 x 25 grid formation to estimate population density of a given vegetation type (area= $625\,m^2$) (Hoffman et al., 2010; Shiels, 2010). Traps were set prior to sunset and checked the following morning. All traps were re-baited after the first night of trapping and removed after two nights for a total of 100 trap nights per survey point. Two nights of trapping (100 trap nights) have been determined sufficient for providing an accurate index of rodent abundance (Krebs, 1966; Thirgood, 2003). Trapped rodents were anesthetized, biomass was recorded, and rodents were marked on both ears and tail with a black marker. After reviving from anesthesia, the rodents were released back into the environment.

Insect (Orthoptera) sweep net surveys. A combination of high (~20 cm), fast (0.9 s), low (~5 cm), and slow (1.3 s) sweeps were performed using a medium-size net (0.4 m in diameter and 0.6 m in depth) to sample a 10 x 50-m area (area= $500\,m^2$) at each survey point for ten minutes approximately an hour prior to sunset (Larson et al., 1999). Captured individuals were photographed, their length (head to abdomen) was recorded, then released back into the environment (Eklöf et al., 2017; Orinda et al., 2017).

Determination of biomass. The biomass of bird and bat species detected during surveys was determined by searching the Birds of North America and the Encyclopedia of Life online databases (The Cornell Lab of Ornithology's guide to birds of North America; 2001; Encyclopedia of Life). For analysis, bird species were grouped into two size classes (Table 1): "Small" (0-30 g, e.g. house finch, *Carpodacus mexicanus*) and "Large" (30-350 g, e.g. zebra dove, *Geopelia striata*, or grey francolin, *Francolinus podcicerianus*). Pueo are not known to consume prey items greater than their own body mass, so the maximum biomass of a potential prey species predated by a pueo was considered anything lower than the mean body mass of a pueo (350 g) (Wiggins et al., 2006; Mostello, 1996; Mostello & Conant, 2018).

Table 1. Prey Bird Species Size Class:

Size class	Species examples	Biomass ($\overline{x}$ ± S) (g) [a]
Small, <30 g	African silverbill (*Lonchura cantans*), chestnut munia (*Lonchura atricapilla*), common waxbill (*Estrilda astrild*), Hawai‘i ‘amakihi (*Chlorodrepanis virens*), house sparrow (*Passer domesticus*), Java sparrow (*Padda oryzivora*), red-billed leiothrix (*Leiothrix lutea*), warbling white-eye (*Zosterops japonicus*)	17.4 ± 8
Large, 30-350 g	Chukar (*Alectoris chukar*), common myna (*Acridotheres tristis*), Eurasian skylark (*Alauda avarensis*), gamebirds (e.g. junglefowl (*Gallus gallus*), grey francolin (*Francolinus podcicerianus*), northern cardinal	108.9 ± 102

	(*Cardinalis cardinalis*), rosy-faced lovebird (*Agapornis roseicollis*), seabirds (e.g. *Puffinus pacificus*), spotted dove (*Streptopelia chinensis*), zebra dove (*Geopelia striata*)

[a]The small biomass class value is based on the eight most common species seen in the group. The large biomass class is based on the eight most common species seen in the group.

The biomass of rodents was derived by weighing individuals. The biomass of insects (order Orthoptera) was derived by measuring the length and classifying individuals (Table 2) (Eklöf et al., 2017; Orinda et al., 2017; Encyclopedia of Life). Borror and DeLong's invertebrate dichotomous key was utilized for species identification (Tripplehorn & Johnson, 2005; Eklöf et al., 2017; Orinda et al., 2017; Encyclopedia of Life).

Table 2. Insect (Orthoptera) Size Class:

Size class	Length of body [a]	Mean biomass [a]
Small	<1 cm	0.1 grams
Medium	1-3 cm	0.4 grams
Large	3-5 cm	0.7 grams
Very Large	>5 cm	1.0 grams

[a]Length (head-abdomen) to biomass relationship determined from literature review (Tripplehorn & Johnson, 2005; Eklöf et al., 2017; Orinda et al., 2017).

Authorizations. All activities were conducted following Institutional Animal Care and Use Committee permit: #3094, Institutional Review Board permit: #2019-00064, Hawai‘i Department of Land and Natural Resources (DLNR)- Division of Forestry and Wildlife permit: MDF-060319A, DLNR- Natural Area Reserve and Native Invertebrate Research permit: l1333, and Haleakalā National Park federal research permit: HALE-2019-SCI-0001.

Data Analysis

Prey bird distance models. Multi-covariate detection functions and density surface models were produced for the "small" and "large" prey bird size classes to predict species abundance using the 'dsm' and 'Distance' packages and 'predict.glm' function in the statistical programming software R (Miller et al., 2019; R Core Team, 2020; RStudio Team, 2020). Biomass was derived from the predicted abundance outputs from the top distance sampling models for the "small" and "large" bird size classes.

Rodent and insect (Order Orthoptera) generalized linear models. Generalized linear regression models were created in R to predict mouse, rat, and insect (Orthoptera) relative abundance and relative biomass (R Core Team, 2020; RStudio Team, 2020). All models were evaluated for appropriateness by examining diagnostic plots. Models explaining the most deviance based on the ANOVA F-test results in R were retained for inference (Burnham & Anderson, 2002; R Core Team, 2020; RStudio Team, 2020). The coefficient of determination (r^2) for each model was derived using the 'modEvA' package and 'RsqGLM' function in R (Barbosa et al., 2015; R Core Team, 2020; RStudio Team, 2020).

Pueo occupancy. Occupancy models were constructed with vegetation characteristics and predicted index of prey biomasses using the package 'unmarked' in R (Fisk & Chandler, 2011; R Studio Team, 2016; R Core Team, 2018). Predicted bird densities were extracted using the 'predict.glm' function in R and an index of densities were extracted from rodent and insect (Orthoptera) GLM's (R Core Team, 2020; RStudio Team, 2020). Graphs were created using the 'ggplot2' package in R and derived using the mean value from each vegetation type (Wickham, 2016; R Core Team, 2020; RStudio Team, 2020).

Multiple single-season occupancy models were run using the package ‘unmarked’ to examine which covariates influence pueo detectability and occupancy (Fisk & Chandler, 2011; R Core Team, 2020; RStudio Team, 2020). Candidate models were ranked by AIC using the package ‘AICcmodavg’ and the top model was retained for inference (Fiske & Chandler, 2011; Kery & Royle, 2016; Mazerolle, 2019). Occupancy models jointly model the ecological process of *species occurrence* (psi) and the *observation process* (p) of species detection but estimate these as separate processes (MacKenzie et al., 2017). Detection covariates are utilized to account for the imperfect observation process of species detection data to predict true occupancy states more accurately (MacKenzie et al., 2017). Detection covariates included vegetation characteristics (e.g. canopy cover, ground cover, vegetation height). Occupancy covariates included vegetation characteristics (e.g. canopy cover, ground cover, vegetation height), elevation, mean annual rainfall, and the predicted prey biomass (bird, rodent, and insect (Orthoptera)) data. The ‘cor.test’ function in R was utilized to identify potentially autocorrelated covariates (R Core Team, 2020; RStudio Team, 2020). As a result, temperature was removed from downstream analyses due to autocorrelation with elevation (Pearson’s $r = -0.95$, $p<0.001$). I explored the suite of detection variables and retained the model with the lowest Akaike’s information criterion (AIC; Akaike, 1974) for inference (MacKenzie et al., 2017). Bootstrapping and a Pearson’s Chi-squared goodness-of-fit test was utilized for model evaluation (Royle & Dorazio, 2008; Fiske & Chandler, 2011; MacKenzie et al., 2017; R Core Team, 2020; RStudio Team, 2020).

Results

Sites. Twenty-six sites were accessed out of the 45 potential sites that were randomly identified. Sites covered a range of elevation, ground cover, vegetation height, and canopy cover. Cropland (n=7) was characterized by low elevation, variable ground cover, variable vegetation height, and low canopy cover. Forest (n=8) was characterized by variable elevation, medium to high ground cover, tall vegetation height, and high canopy cover. Grassland (n=7) was characterized by mid elevation, medium ground cover, low vegetation height, and low canopy cover. Shrubland (n=4) was characterized by high elevation, medium ground cover, low to medium vegetation height, and low canopy cover. Sites were often a mosaic of multiple vegetation types and characteristics, but the major land cover type and characteristics were recorded where the survey methods took place.

Prey bird detection probability models. The “small” prey bird size class produced the best fit model using a hazard-rate key function with mean vegetation height as a covariate (AIC=1890). The Cramer-von Mises (unweighted) test of goodness of fit (T) indicated the “small” prey bird model fit the data well (T= 0.24 and p=0.21) and was a valid model for inference. The “large” class produced the best fit model using a hazard-rate key function with vegetation height as a covariate (AIC=2012). The Cramer-von Mises (unweighted) goodness of fit test (T) results for the “large” prey bird model fit the data well (T= 0.26 and p=0.17) and indicated it was a valid model for inference. The diagnostic plots of the “small” and “large” prey bird detection functions fit well with the pattern of their respective models (Appendix C). Distance sampling models were used to create density surface models of “small” and “large” prey birds across Maui using a quasipoisson response (Fig. 3-4). Bats were not included in the analysis due to too few detections (n=3).

Prey bird abundance (14 ± 5 individuals per 1,000 m^2) and biomass (931 ± 461 g per 1,000 m^2) was highest in low elevation, low to medium vegetation height, and open cropland areas, and consisted of primarily non-native species. Most of the "large" birds observed in lower elevation areas were spotted doves (*Streptopelia chinensis*). They were observed foraging in croplands during the day then flew towards human development and nearby wetlands to roost at night. Occurrence was also higher near water sources, such as cattle troughs or active croplands with irrigation. Prey bird abundance (4 ± 0 individuals per 1,000 m^2) and biomass (148 ± 9 g per 1,000 m^2) was lowest in high elevation, shrubby areas which contained both native and non-native species, but native species (including bats) were typically observed above 1,200 m elevation. (Appendix D).

Relative rodent abundance and biomass models. The model of best fit for relative mouse abundance was a quasipoisson generalized linear model with canopy cover ($p=0.17$), vegetation height ($p=0.33$), elevation ($p=0.27$), and mean annual rainfall ($p=0.24$) as covariates ($r^2=0.32$). The model of best fit for relative mouse biomass was a quasipoisson generalized linear model with ground cover ($p=0.61$), canopy cover ($p=0.21$), vegetation height ($p=0.41$), elevation ($p=0.43$), and mean annual rainfall ($p=0.43$) as covariates ($r^2=0.2$). The model of best fit for relative rat abundance was a quasipoisson generalized linear model with canopy cover ($p<0.05$), vegetation height ($p=0.27$), elevation ($p=0.85$), and mean annual rainfall ($p=0.2$) as covariates ($r^2=0.87$). There was a positive relationship between relative rat abundance and canopy cover ($p<0.05$). The model of best fit for relative rat biomass was a quasipoisson generalized linear model with ground cover ($p=0.7$), canopy cover ($p=0.05$), vegetation height ($p=0.19$), elevation ($p=0.64$), and mean annual rainfall ($p=0.13$) as covariates ($r^2=0.97$). There was a positive relationship between relative rat biomass and canopy cover ($p=0.05$).

Forested areas with high canopy cover contained the highest relative rodent abundance (6 ± 8 individuals per 1,000 m^2) and biomass (380 ± 646 g per 1,000 m^2). High elevation, shrubby areas contained the lowest relative rodent abundance (3 ± 1 individuals per 1,000 m^2) and low elevation cropland areas contained the lowest rodent biomass (43 ± 25 g per 1,000 m^2). Mouse occurrence was moderate to high across all vegetation characteristics especially in short vegetation with low canopy cover (5 ± 3 individuals per 1,000 m^2), while rats occurred most frequently in areas with high canopy cover and medium to tall vegetation height (2 ± 2 individuals per 1,000 m^2). Across sites the average biomass of a single mouse was 11 ± 2 g and the average biomass of a single rat was 85 ± 17 g. (Appendix E).

Relative insect (Orthoptera) abundance and biomass models. The model of best fit for relative insect (Orthoptera) abundance was a quasipoisson generalized linear model with ground cover ($p=0.41$), canopy cover ($p=0.17$), vegetation height ($p=0.21$), elevation ($p=0.30$), and mean annual rainfall ($p<0.001$) as covariates ($r^2=0.87$). There was a positive relationship between insect (Orthoptera) relative abundance and mean annual rainfall ($p<0.01$). The model of best fit for relative insect (Orthoptera) biomass was fit with a quasipoisson generalized linear model and was positively correlated with mean annual rainfall ($p<0.001$; $r^2=0.84$).

Areas with high canopy cover, high ground cover, and tall vegetation height contained the highest relative insect (Orthoptera) abundance (46 ± 57 individuals per 1,000 m^2) and biomass (13.4 ± 14.8 g per 1,000 m^2). Low elevation, cropland areas contained the lowest relative insect (Orthoptera) abundance (13 ± 3 individual per 1,000 m^2) and relative biomass (3.1 ± 0.2 g per 1,000 m^2). Species that were observed were primarily non-native generalists and included the common conehead (*Neoconocephalus* spp.), field cricket (*Gryllus* spp.), house cricket (*Acheta domesticus*) katydid (*Microcentrum rhombifolium*), red-legged grasshopper

(*Melanoplus femurrubrum)*, spur-throated grasshopper (*Melanoplus ponderosus*), and two-striped grasshopper (*Melanoplus bivittatus*). (Appendix F).

Total prey abundance and biomass. High elevation areas with medium vegetation height had the lowest total prey abundance (22 ± 5 individuals per 1,000 m^2) and lowest total prey biomass (235 ± 21 g per 1,000 m^2). Forested areas with high canopy cover, high ground cover, and tall vegetation had the highest total prey abundance (57 ± 60 individuals per 1,000 m^2) and low elevation, medium ground cover, short to medium vegetation height, cropland contained the highest total prey biomass (976 ± 456 g per 1,000 m^2). (Fig. 5-6).

Owl presence and pueo occupancy models. Across all sites there were 16 owl detections total during the owl survey period (1 hour prior to sunset to half-hour after sunset), including 11 pueo, 2 barn owl, and 3 unknown owls (barn owl or pueo). The barn owl and unknown owl observations occurred in mid-elevation open areas with low vegetation height and cover. Pueo were observed across a range of vegetation characteristics using both open and forested areas but were most frequently observed at mid to high elevations, in areas with short to medium vegetation height, medium ground cover, and low to medium canopy cover. Pueo responded to audio playback vocalizations at 50 percent of the sites where a pueo was visually detected. At one site a pueo was audibly detected when it responded to audio playback vocalizations at the end of the survey where no pueo were visually detected. (Appendix G).

Vegetation height explained the most variance for pueo detectability and was therefore used in all models to account for detectability. Models with all possible combinations of occupancy level covariates that made biological sense were tested. The top five models were all within 5 Δ AIC so were considered for interpretation. The first model indicated a weakly negative relationship between the estimated likelihood of pueo occupancy and total prey bird biomass ($p=0.07$; Fig. 7a). The second model indicated a weakly negative relationship between the estimated likelihood of pueo occupancy and relative total prey biomass ($p=0.08$; Fig. 7b). The third model included large bird biomass ($p=0.29$) and relative rat biomass ($p=0.5$) variables, but explanatory variables showed no significant effects thus, no effects graph was generated or consideration of covariates was given when interpreting outputs. The fourth model indicated a positive relationship between the estimated likelihood of pueo occupancy and elevation ($p<0.05$; Fig. 7c). The fifth model indicated a weakly positive relationship between vegetation height ($p=0.15$), relative insect (Orthoptera) biomass ($p=0.09$), and the estimated likelihood of pueo occupancy. However, note that occupancy models approximate non-linear relationships because presence data are modeled on the logit scale (Table 3; Fig. 7).

Pueo pellets. During the field season, I opportunistically found two pueo pellets in a high elevation, shrubby area at Haleakalā National Park. The first pellet contained house mouse bones and the second pellet found nearby contained juvenile rat bones. (Fig. 8).

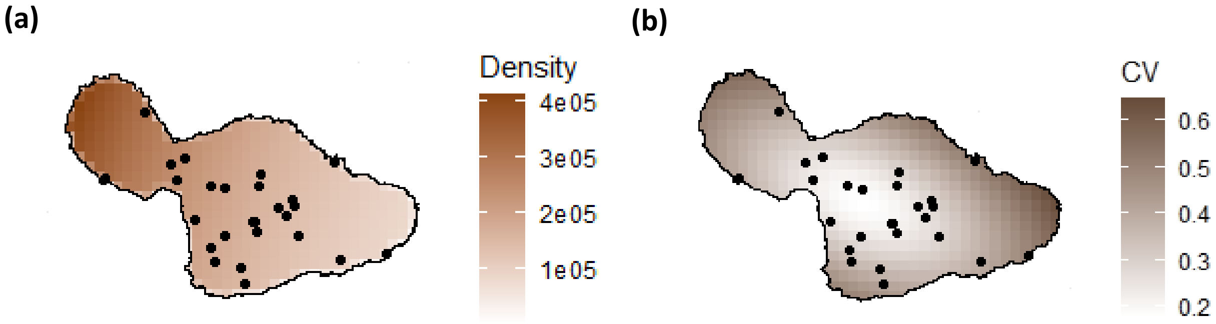


Fig. 3. (a) Map of the density of “small” prey bird size class (n/5 km²) with vegetation height as a covariate using a quasipoisson response (AIC=1890). (b) Map of the coefficient of variation (CV). The CV is a measure of relative variability. It is the ratio of the standard deviation to the mean and is expressed as a percentage. A lower CV score or lighter colored area, indicates higher accuracy than the darker or higher number CV. Black dots represent the sampled points.

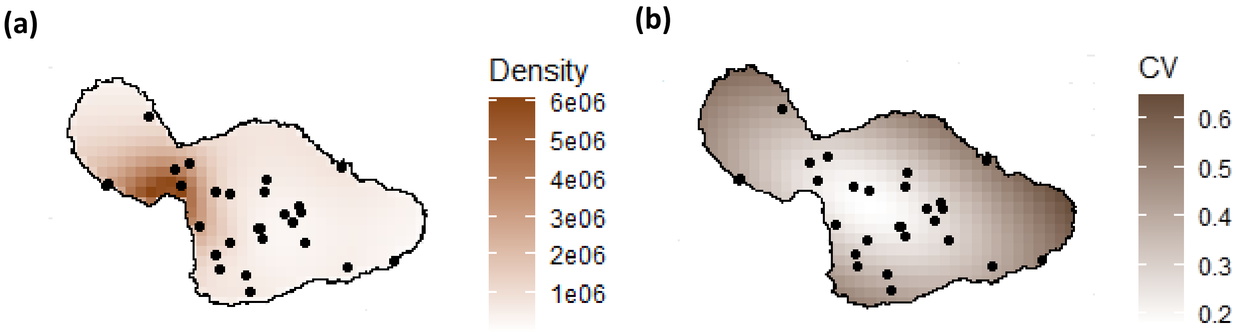


Fig. 4. (a) Map of the density of “large” prey bird size class (n/5 km²) with vegetation height as a covariate using a quasipoisson response (AIC=2012). (b) Map of the coefficient of variation (CV). The CV is a measure of relative variability. It is the ratio of the standard deviation to the mean and is expressed as a percentage. A lower CV score or lighter colored area, indicates higher accuracy than the darker or higher number CV. Black dots represent the sampled points.

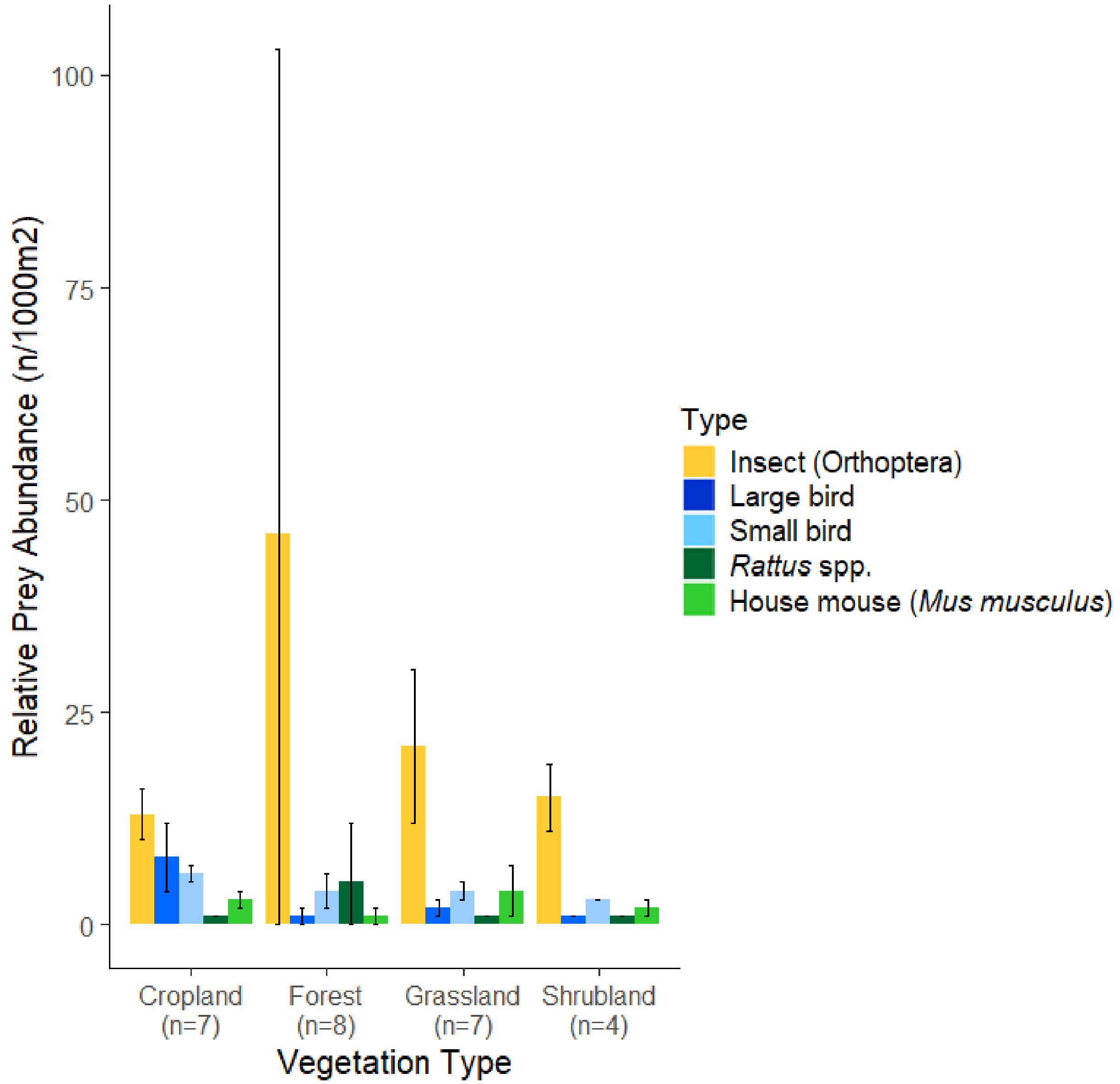


Fig. 5. Mean relative total prey abundance per 1,000 m^2 across four dominant vegetation types on Maui, Hawai‘i.

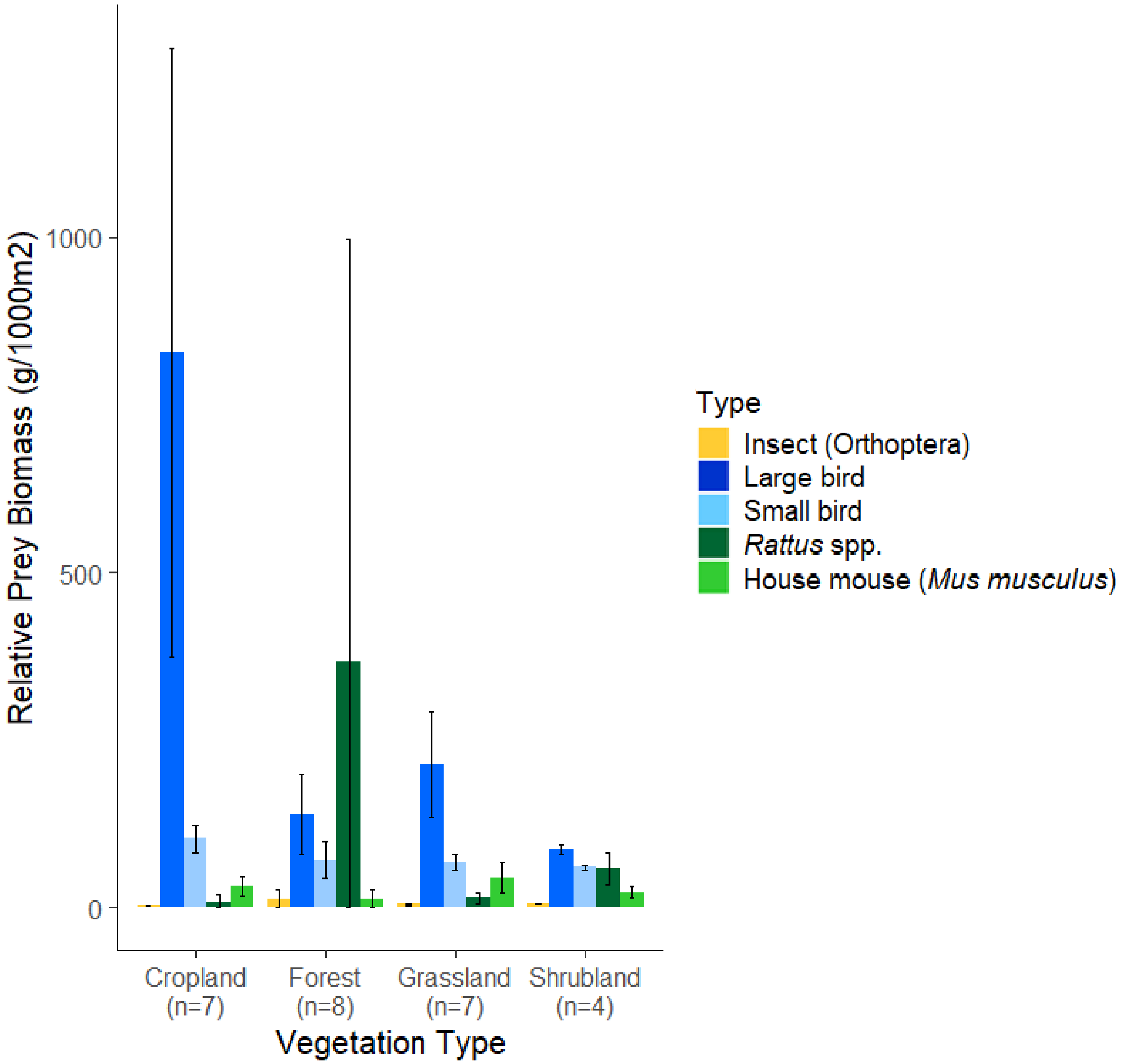


Fig. 6. Mean relative total prey biomass per 1,000 m^2 across four dominant vegetation types on Maui, Hawai‘i.

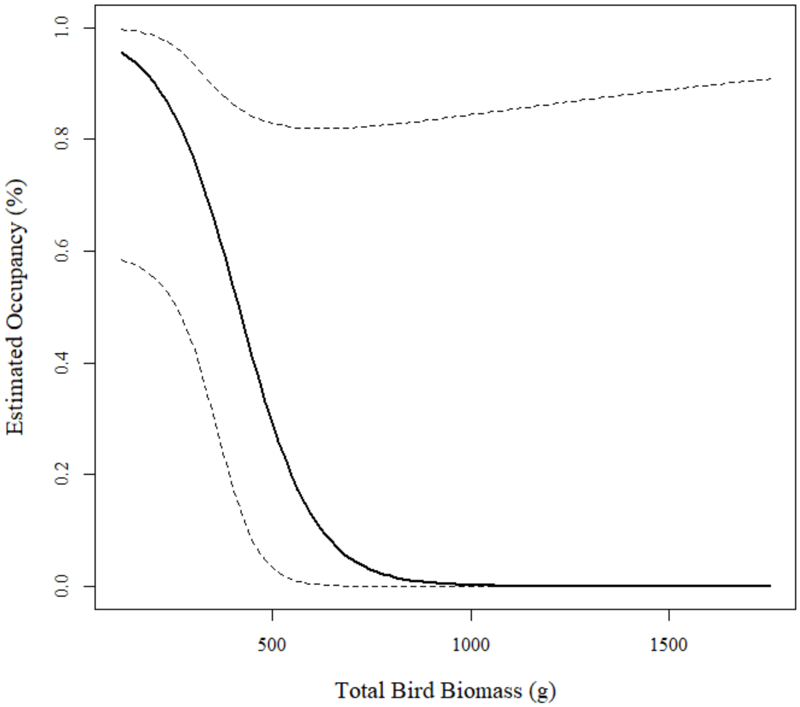
Table 3. Top-ranked models of pueo occupancy (psi) and detection (p) probability with standard error using predicted prey biomass (bird, rodent, and insect (Orthoptera)), vegetation characteristics (e.g. canopy cover, ground cover, vegetation height), elevation, and mean annual rainfall.

Model	AIC	AIC wt.	K	(psi) Covariate(s) (C.I. 0.025 ± 0.975)	(psi) Covariate(s) p-value	(p) Covariate(s) (C.I. 0.025 ± 0.975)	(p) Covariate(s) p-value	LL
(psi)(total bird) (p)(veg. height)	21.7	0.34	4	Total bird: 0.016 (-8.66 ± 0.36)	Total bird: 0.07	Veg. height: 1.2e-136 (-1294 ± 669)	Veg. height: 0.53	-5.88
(psi)(total prey) (p)(veg. height)	21.9	0.29	4	Total prey: 0.005 (-11.0 ± 0.60)	Total prey: 0.08	Veg. height: 1.01e-119 (-978 ± 431)	Veg. height: 0.45	-6.01
(psi)(large bird + rat) (p)(veg. height)	23.9	0.11	5	Large bird: 0.07 (-7.3 ± 2.2) Rat: 1.0 (-78.2 ± 159.8)	Large bird: 0.29 Rat: 0.50	Veg. height: 2.56e-132 (-1206 ± 600)	Veg. height: 0.51	-5.44
(psi)(elevation) (p)(veg. height)	24.6	0.08	4	Elevation: 0.97 (0.22 ± 6.67)	Elevation: 0.04*	Veg. height: 1.82e-12 (-262 ± 208)	Veg. height: 0.82	-7.35
(psi)(insect (Orthoptera) + veg. height) (p)(veg. height)	24.7	0.07	5	Insect: 1.0 (-3.5 ± 53.6) Veg height: 1.0 (-14.1 ± 95.1)	Insect: 0.09 Veg. height: 0.15	Veg. height: 4.57e-124 (-986 ± 419)	Veg. height: 0.43	-5.86
(psi)(insect (Orthoptera) + ground cover) (p)(veg. height)	26.9	0.02	5	Insect: 1.0 (-0.11 ± 45.3) Ground cover: 0.28 (-2.9 ± 1.02)	Insect: 0.05* Ground cover: 0.35	Veg. height: 1.89e-131 (-1132 ± 529)	Veg. height: 0.48	-6.94

(psi)(mouse + elevation) (p)(veg. height)	27.3	0.02	5	Mouse: 0.39 (-1.87 ± 1.0) Elevation: 0.98 (0.09 ± 7.4)	Mouse: 0.55 Elevation: 0.04*	Veg. height: 6.58e-13 (-259 ± 203)	Veg. height: 0.81	-7.16
(psi)(small bird + elevation) (p)(veg. height)	27.5	0.02	5	Small bird: 0.4 (-2.31 ± 1.53) Elevation: 0.96 (-0.43 ± 6.62)	Small bird: 0.69 Elevation: 0.09	Veg. height: 6.64e-13 (-262 ± 206)	Veg. height: 0.81	-7.26
(psi)(rodent + insect (Orthoptera)) (p)(veg. height)	27.6	0.02	5	Rodent: 4.2e-8 (-81.0 ± 47.0) Insect: 1.0 (-1.7± 47.0)	Rodent: 0.60 Insect: 0.07	Veg. height: 5.6e-128 (-1091 ± 505)	Veg. height: 0.47	-7.30
(psi)(rodent) (p)(veg. height)	29.5	0.01	4	Rodent: 1 (-10.1 ± 67.3)	Rodent: 0.15	Veg. height: 5.02e-121 (-968 ± 413)	Veg. height: 0.43	-9.79
(psi)(veg. height + elevation + rainfall) (p)(veg. height)	30.0	0.01	6	Veg. height: 0.99 (-21.3 ± 53.1) Elevation: 0.99 (-1.4 ± 13.2) Rainfall: 0.12 (-6.8 ± 2.9)	Veg. height: 0.40 Elevation: 0.12 Rainfall: 0.43	Veg. height: 3.0e-12 (-156 ± 103)	Veg. height: 0.69	-6.81

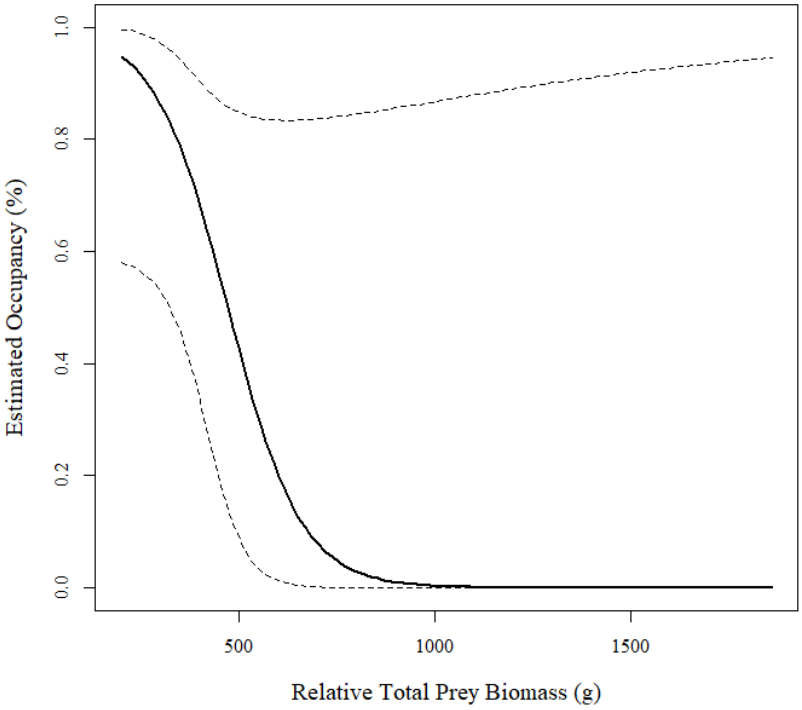
psi=site level covariates/occupancy, p=observation level covariates/detectability
*significant ($p<0.05$)

(a)



Estimated Occupancy (%)
0.0
0.2
0.4
0.6
0.8
1.0
500
1000
1500
Total Bird Biomass (g)

(b)



Estimated Occupancy (%)
0.0
0.2
0.4
0.6
0.8
1.0
500
1000
1500
Relative Total Prey Biomass (g)

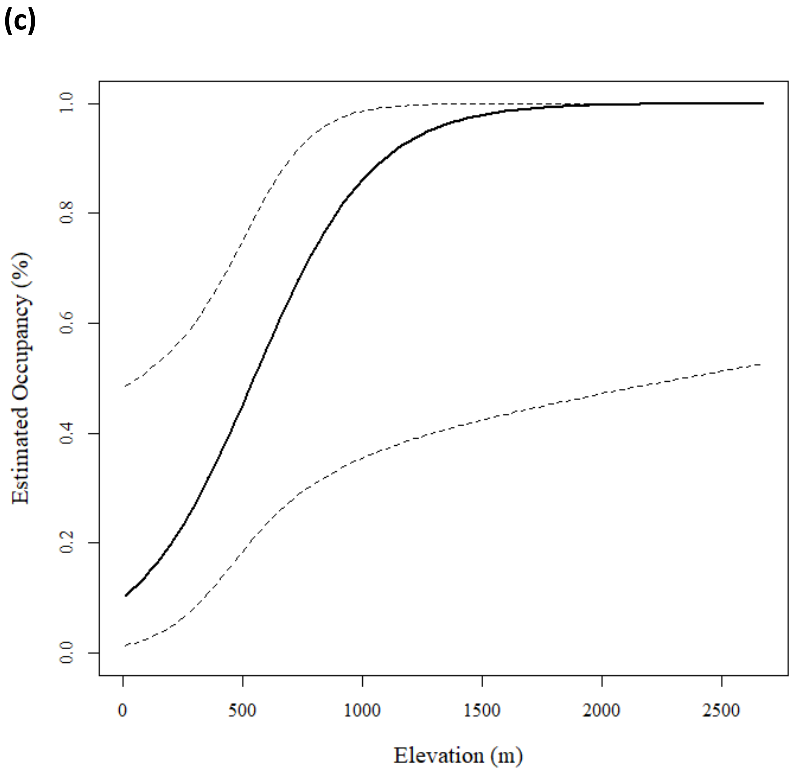


Fig. 7. Effect plots of the top three pueo occupancy models: (a) There is a weakly negative relationship between the estimated likelihood of pueo occupancy and total prey bird biomass (p=0.07, AIC wt.=0.34). (b) There is a weakly negative relationship between the estimated likelihood of pueo occupancy and relative total prey biomass (p=0.08, AIC wt.=0.29). (c) There is a positive relationship between the estimated likelihood of pueo occupancy and elevation (p<0.05, AIC wt.=0.08).

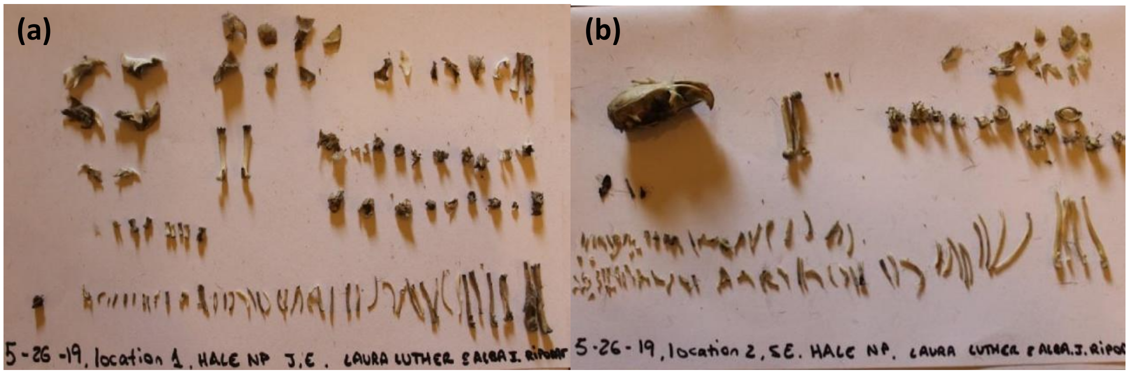


Fig. 8. (a) A pueo pellet found at Haleakalā National Park that contained mouse bones. (b) A pueo pellet found at Haleakalā National Park that contained a juvenile rat skull and bones.

Discussion

In this study, I examined both native and non-native potential prey species across three taxonomic groups and a range of vegetation characteristics in relation to pueo occupancy on Maui, Hawaiʻi. I expected that the pueo would hunt in areas that were the most accessible (short vegetation and low ground cover) compared to areas with dense vegetation, and that the biomass of prey items most commonly found in pellets (mice and zebra doves) would play a greater role in predicting pueo presence than all potential prey items combined. Pueo were detected across a range of vegetation characteristics but were most often seen in mid to high elevation, using both open and forested areas. The detectability of pueo was weakly positively influenced by vegetation height, suggesting that assumptions regarding a preference of pueo for open vegetation types may be skewed based on the ability of observers to detect pueo in these ecosystems or due to bias from species level information originating largely from select areas throughout the global distribution of short-eared owls. Single-season occupancy models indicated that bird biomass and relative total prey biomass were weakly correlated with the estimated likelihood of pueo occupancy, in other words, that pueo are more likely to occur in areas with lower prey biomass, while elevation was positively correlated with pueo occupancy, indicating they are more likely to occur at mid and upper elevations. Vegetation height and relative insect (Orthoptera) biomass also had a weakly positive relationship with the estimated likelihood of pueo occupancy. The occupancy models do not clearly identify whether vegetation structure (height/cover) or prey biomass are driving distribution but rather, suggest a combination of factors, and potentially others that were not accounted for in this study such as competition or predation risk, influence pueo distribution.

The sites in which pueo were most often observed contained low to moderate biomass of all the prey types for which I surveyed. The models were not driven solely by *Microtus* spp. biomass, as in the continental United States (Wiggins et al, 2006), but were weakly correlated with insect (Orthoptera) biomass. The two models with the highest AIC weight (combined 65 percent) indicated a weakly negative relationship between bird biomass and relative total prey biomass. Birds have been found in pueo and continental short-eared owl pellets (Holt, 1993; Mostello, 1996; Mostello & Conant, 2018) but require the most energy to hunt and therefore, may not be the optimal prey choice (Toland, 1987). Bird biomass and relative total prey biomass were also highest in low elevation areas where pueo were only detected once. Pueo could be using these areas at a different time of year from when this study was done (May-December) or at a different time of day from the survey window (one hour prior to sunset to one hour after).

Similar to previous studies, rat density was highest in tall vegetation and high canopy cover, and mouse density was highest in short vegetation and low canopy cover (Shiels, 2010; Harper & Bunbury, 2015; Shiels et al., 2017; Tseng et al., 2017). It may be more profitable for pueo to switch between different prey types in Hawaiʻi, given that rodent abundance was not as high overall in this study as in other rodent abundance studies globally (Mostello, 1996; Shiels, 2010). Furthermore, an average pueo pellet emitted per day is composed of prey items that are estimated to total 30-40 grams (Clark, 1975). At an average biomass of 11 g per mouse, this indicates that roughly three mice must be consumed daily to meet energetic demands. Thus, prey switching and hunting in diverse habitats may be necessary to meet metabolic and nutritional needs, considering the diverse and available prey biomass across the landscape. For example, the zebra dove (*Geopelia striata*), a common prey bird found in pueo pellets, is a slow-moving ground feeder with a mean biomass of 55 g, making it an energetically profitable species to capture (Mostello, 1996; Mostello & Conant, 2018). Juvenile birds were also observed in pueo pellets, reinforcing the notion that pueo are opportunistic and predate on energetically profitable prey (Mostello, 1996; Thirgood et al., 2003; Mostello & Conant, 2018). Further, pueo that feed on diverse prey items minimize the potential ingestion of rodenticide, potentially increasing the likelihood of survival and reproductive success. This study did not examine the distribution of reptiles, such as lizards, but future studies should include these potential prey items, as pueo have been observed ingesting these prey items (pers. obs.).

Prey distribution likely varies across vegetation types based on season and rainfall and may drive temporal variation in pueo habitat use. The top predictive models for both the rodents and insects (Orthoptera) contained mean annual rainfall as a covariate (significant for insects), consistent with expectations that prey occurrence is driven by moisture availability (Schmidt et al., 2018). Correspondence with technicians who were rodent trapping for the State of Hawaiʻi Vector Control Department reported similar results from trapping taking place concurrent to this study, with few, if any, rodents caught during the summer months at low elevations (Travis Barut, pers. comm.), which was likely due to low rainfall and high temperatures. Pueo, rarely seen on Kahoʻolawe (an island seven miles southwest of Maui), have been noted in abundance during cyclic rodent irruptions in the spring after a rainy winter season (Kahoʻolawe Island Reserve Commission Seabird Restoration Business Plan, 2015). These findings are consistent with other studies that correlate the timing of vegetation growth as stimulation for prey population growth (Banko et al., 2015; Schmidt et al., 2018).

Mid- to high elevation locations had a positive relationship with the estimated likelihood of pueo occupancy and were comprised of a range of vegetation characteristics ranging from short vegetation, low ground cover, and low canopy cover—potentially offering low-effort hunting opportunities—to tall vegetation, high ground cover, and high canopy cover that contained high amounts of prey biomass and may be profitable at times when other areas are scarce in prey. A mosaic landscape of open and forested areas likely provides an energetically profitable combination of prey biomass, accessibility, and perching opportunities (Banko et al., 2015; Shiels et al., 2017). Other characteristics of mid- to high elevation areas on Maui include cooler temperatures, increased connectivity, and little housing or development.

Because vegetation height had the greatest influence on pueo detectability, it is likely that pueo are under-detected in forests; alternatively, previous surveys may have under-sampled these locations, considering the North American and Eurasian short-eared owl preference for open landscapes (Wiggins et al., 2006). Also, increased vegetation height had a weakly positive relationship with the estimated likelihood of pueo occupancy. Forested survey sites were highly variable ranging from native rainforest with dense vegetation structure, to dry forest with open ground cover, to a mixture of non-native eucalyptus (*Eucalyptus* spp.), pine (*Pinus* spp.), and black-wattle (*Acacia mearnsii*) stands with varied understories, each requiring different energy expenditure for hunting. One of the occupancy models with low AIC weight (i.e. explained relatively little variation in the data compared to other models) predicted a weakly negative relationship between ground cover and the estimated likelihood of pueo occupancy, which is consistent with other raptor foraging studies that determined low ground cover was preferred for hunting due to increased prey accessibility (Bechard, 1982; Preston, 1990).

A potential explanation for a positive correlation between elevation and the estimated likelihood of pueo occupancy is temperature. Temperature was inversely correlated with elevation (Pearson’s $r = -0.95$, $p<0.001$, which is the reason it was not included in the occupancy models). Owls as a group (Order Strigiformes, of which pueo are members) have much lower metabolic rates and are less heat tolerant than other bird taxa (Weathers et al., 2001). The average temperature reading at low elevation cropland areas during audiovisual surveys was 26 ± 1^{o}C, whereas high elevation shrubland was 13 ± 4^{o}C. A preference for cooler temperatures for thermoregulation is a possible reason pueo occupancy was positively related to elevation. Further, pueo may utilize lower elevations at night when temperatures are lower (Weathers et al., 2001; Calladine & Morrison, 2013; Tseng et al., 2017).

Pueo distribution may be influenced by barn owls or other competitors or predators, as barn owls were observed hunting at sunset and night-time in mid- to lower elevation vegetation types, whereas pueo were observed hunting at daylight until sunset and utilizing higher elevation sites, suggesting that these two species overlap at sunset but primarily occupy two different temporal hunting periods and potentially two different elevational bands on Maui. There have also been reports of barn owls depredating pueo fledglings at the nest (Jake Muise with Maui Nui Venison, pers. comm.). Diet differs significantly among the four potentially competing terrestrial predators in Hawaiʻi: the feral cat, small Indian mongoose, barn owl, and pueo (Mostello, 1996; Mostello & Conant, 2018). The two owl species and cats prey primarily on rodents, but the diets of these three species vary by location (Mostello, 1996; Mostello & Conant, 2018). Dietary overlap is highest between the pueo and the barn owl (Mostello, 1996; Mostello & Conant, 2018), though pueo diet is not thought to have changed since the introduction of the barn owl (Mostello, 1996; Mostello & Conant, 2018). On Hawaiʻi Island (commonly referred to as the Big Island), Maui, Molokaʻi, and Oʻahu, where mongoose are present, both barn owls and pueo consume more insects (Mostello, 1996; Mostello & Conant, 2018). Although there is dietary overlap, competition between the four predators seems unlikely due to variation in distribution, abundance of prey, and the opportunistic nature of foraging by generalists (Mostello, 1996;

Mostello & Conant, 2018). However, during times of resource scarcity, competition may increase (Work & Hale, 1996; Mostello & Conant, 2018).

Since higher elevation areas of Maui contain a reduced number of predators and competition due to the increased distance from development and proximity to predator control activities in conservation zones, nesting success may be higher, resulting in increased pueo occupancy. However, as this study did not examine nesting success, further study is needed to explore this potential explanation.

Conservation Implications

It is important to recognize the value of preserving large expanses of unfragmented habitat used by pueo for hunting and nesting in the upcountry sections of Maui at large historic ranches, natural area reserves, and at Haleakalā National Park. A strategy to promote pueo hunting habitat is to maintain mowing regimes or the rotational grazing of domestic ungulates to retain short vegetation height in locations dominated by invasive grasses. Constructing raptor nests boxes does not benefit pueo and would promote the already prevalent barn owl that potentially competes with pueo. Since pueo nest on the ground and have elaborate courtship displays, it is important to observe and note this behavior that may indicate a nest is nearby. Observing a pueo repeatedly carrying prey (food provisioning) to the same area is an indication that a nest is nearby and a buffer zone of 30-50 meters around the potential nest site is recommended to reduce disturbance. It is also important to keep in mind that pueo fledglings are mobile and walk away from the nest before they can fly, so there is a possibility of encountering young that may seem to be in a random location. It is important to leave them where they are found because a parent is likely aware of the location and feeding them.

Roads are an energetically profitable place for raptors to hunt as there is no protective cover for prey (Bechard, 1982; Preston, 1990), but this has come at a cost as vehicular collisions are a major cause of raptor mortality (Wiggins et al., 2006; Donázar et al., 2016; Miller et al., 2017). An important conservation strategy is to identify sections of roads that are heavily utilized by owls, especially during fledgling season (April-June), and to set lower speeds in those regions with speed bumps and proper signage. Other modifications to reduce collisions with cars and manmade structures would include installation of raptor deterrents on fencing and telephone wire in high-traffic areas frequented by pueo.

Raptors can also be negatively impacted by secondary poisoning from consuming pests that have ingested rodenticide or other pesticides (Work & Hale, 1996; Donázar et al., 2016; Vyas et al., 2017; Mostello & Conant, 2018). After a prey species consumes poison, it may live up to a week and exhibit slower behavior, leading to an energetically profitable capture with potentially negative side effects for the raptor (Vyas et al., 2017). However, predator control of rodents, mongoose, and feral cats by trapping and removal may also benefit the pueo by reducing competition and predation of eggs and young. Utilizing one-way or A-24 traps instead of poison to reduce rodents provides an easy meal to pueo, who have been known to frequent A-24 rat traps to feed on carcasses, and reduces bioaccumulation of pesticides in their system (Franklin, 2013).

The largest cover type on Maui is development (36%) with more land area at lower elevations. Factors influencing nesting success, such as predator abundance, may provide a partial explanation for distribution of pueo in non-developed areas. Potential predators of the ground-nesting pueo, such as cats and mongooses, may occur in higher abundance closer to human dwellings due to increased food resources compared to higher elevation and rural areas

(Gaertner et al., 2017). Agencies such as Haleakalā National Park, Maui Forest Bird Recovery Project, and Maui Nui Seabird Recovery Project perform predator control activities to reduce rodent, mongoose, and feral cat populations in higher elevation areas where native and endangered species occur, which may also benefit pueo nesting activity. Targeted predator control efforts for mongoose and feral cats in lower elevation vegetation types, such as in croplands, would improve nesting success for pueo in these areas.

Agriculture producers can play an important role in conserving natural habitats and wildlife through use of beneficial practices (Lindell et al., 2018; McClure et al., 2018). Many farms and ranches in the continental United States play a vital role in wildlife conservation (Maas et al., 2013; Lindell et al., 2018; Heath & Long, 2019; Olimpi et al., 2020). Producers contribute to wildlife conservation partly because it can be profitable for them to do so ("natural" pest control) and partly because they believe it is the ethical thing to do (Maas et al., 2013; Lindell et al., 2018; McClure et al., 2018; Heath & Long, 2019; Olimpi et al., 2020; pers. comm. with ag. producers). Many also value the aesthetics of natural systems and seeing native wildlife thriving on their land (Lindell et al., 2018). Adopting a coexistence model of managing land in Hawaiʻi offers a multitude of services—economically, visually, and culturally (Maas et al., 2013; Lindell et al., 2018; McClure et al., 2018; Heath & Long, 2019; Olimpi et al., 2020).

For pueo in cropland and grassland areas, an agroecosystem management approach could be highly beneficial. In cropland, prey species were localized near water sources and active cultivation; by recognizing water resource locations, efforts can be focused on reducing potential pests in that area. The presence of an owl reduces the activity of pest species; thus, maintaining perch sites such as posts, trees, and hedgerows, or uncultivated areas for a pueo to nest, will aid in promoting their use across vegetation types. With the conversion of fallow sugarcane to active cropland, pests and their predators are likely to increase, which may provide an opportunity for agriculture operators to further benefit from pueo (Koopman & Pitt, 2007). Pueo consume a large number of non-native species that can become rampant pests. By minimizing the use of poison and encouraging habitat for owls, while also keeping larger invasive species (mongoose, cats) under control, land managers allow pueo to continue to provide a service to native ecological systems by reducing populations of invasive birds, rodents, and insects (Orthoptera).

Outreach to the general public and agricultural producers regarding conservation implications is necessary to improve the understanding of pueo identification, life history, and behavior, in addition to the many benefits of having pueo present across the landscape. Outreach can also increase engagement in best management practices and modifications to provide ideal habitat for pueo.

Conclusions

Vegetation height, ground cover, and canopy cover influence prey accessibility, while different prey types vary in energy exerted versus gained by a raptor. Prior to this study, I suspected the Hawaiian short-eared owl (*Asio flammeus sandwhichensis* or pueo) exhibited opportunistic foraging strategies and occurred across more vegetation types than the continental short-eared owl (*Asio flammeus*) given reduced competition and predation risk. Given energetic differences across the landscape, I also suspected that pueo would hunt more frequently in shorter and more accessible areas for prey items that provided medium to high biomass, e.g. mice (*Mus musculus*) and zebra doves (*Geopelia striata*). During the survey window of one hour prior to sunset to a half-hour after sunset, I observed pueo across a variety of areas but most frequently in mid- to high elevation areas where bird and relative total prey biomass was low. Vegetation height influenced the detectability of pueo; thus, individuals may be using forested areas more frequently than originally thought. Given Hawai‘i’s diverse environmental gradients, pueo may occupy high and low elevation areas to hunt at different times of the day and at different times of the year depending on prey availability, influenced by rainfall and micro-habitat. There may also be differences in vegetation characteristics and prey selection based on individual home ranges of pueo, as determined by intraspecific competition among pueo, or interspecific competition with barn owls. Further research investigating tracking of individual pueo, impacts of pueo predators, and seasonal variation in prey abundance, is needed to elucidate variation within and among island populations of this species.

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APPENDICES

Appendix A. Major land cover types by area and percentage occurrence on the island of Maui (Hawai‘i State Office of Planning, 2018).

Major Land Cover Type (alphabetical order)	Area (km^2)	Percentage of Major Land Cover Type on Maui
Cropland	22.07	1.2%
Developed	685.74	36.4%
Forest	545.73	28.9%
Grassland	243.44	12.9%
Not Vegetated	219.82	11.7%
Shrubland	163.48	8.7%
Other	2.72	0.2%
Total	1883	100%

Appendix B. Detailed vegetation characteristics at each survey point. The dominant vegetation type where the survey occurred is listed first in each row.

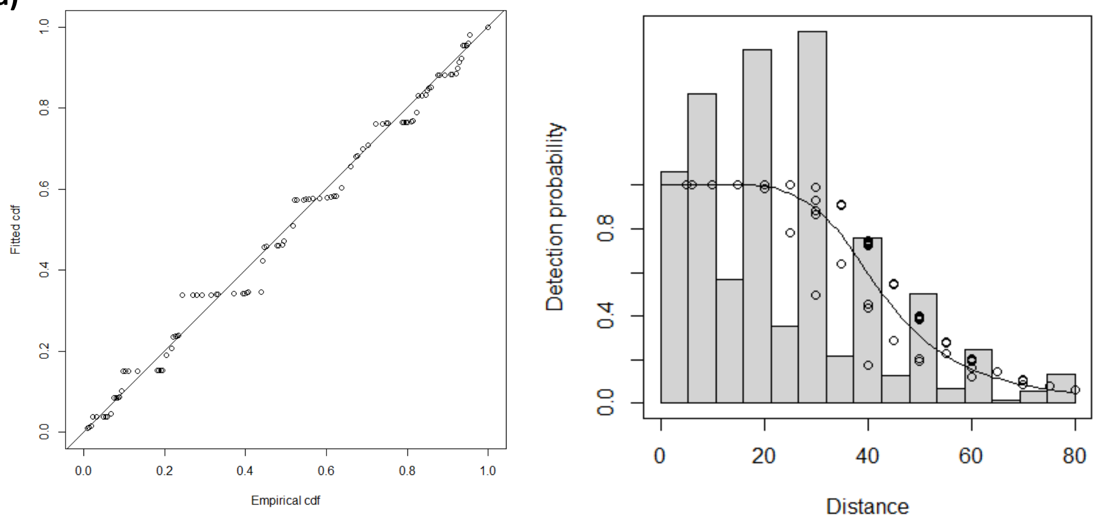
ID	Mean elevation (m)	Percent vegetation type within 200m (%)[a]	Mean ground cover (%)	Mean canopy cover (%)	Mean veg. height (m)	Mean annual rainfall (mm)[b]	Mean temp (°C)
1*	1,829	Shrubland (37.5%) Grassland (37.5%) Forest (25%)	80	0	0.3	1,008	18.3
2*	2,195	Shrubland (100%)	60	0	0.4	1,385	14.4
3*	503	Grassland (66.7%) Not vegetated (33.3%)	85	0	0.6	634	20.6
4*	945	Grassland (75%) Forest (25%)	95	0	0.2	1,371	18.9
5	31	Cropland (80%) Developed (20%)	80	0	0.4	410	25.6
6	27	Forest (50%) Grassland (25%) Developed (25%)	95	85	2.9	2,044	24.4
7	1,981	Forest (100%)	95	90	9	918	14.4
8	668	Grassland (33.3%) Not vegetated (33.3%) Shrubland (16.7%) Forest (16.7%)	95	0	0.1	734	18.9
9	747	Forest (40%) Grassland (40%) Developed (20%)	90	60	5	2,005	20.6
10	335	Cropland (80%) Developed (20%)	70	0	0.2	468	25.6
11	1981	Forest (100%)	80	75	20	1,843	12.2
12	11	Cropland (100%)	50	5	0.4	307	27.2
13	78	Cropland (20%) Grassland (20%) Forest (20%) Not vegetated (40%)	75	0	0.3	321	26.7
14*	359	Grassland (100%)	35	10	0.1	526	23.3
15*	2,673	Shrubland (83.3%) Not vegetated (16.7%)	50	0	0.5	1,178	11.7
16*	1,433	Forest (83.3%) Not vegetated (16.7%)	80	0	0.4	808	18.9
17*	986	Grassland (75%) Not vegetated (25%)	75	5	0.3	719	19.4
18	73	Forest (80%) Not vegetated (20%)	95	65	6	3,551	23.9
19	52	Cropland (75%) Developed (25%)	10	15	0.7	410	27.2

20*	1,343	Forest (50%), Shrubland (25%), Not vegetated (25%)	73	0	0.5	798	18.3
21*	182	Cropland (66.6%) Forest (16.7%) Developed (16.7%)	75	0	0.5	377	25.6
22*	2,569	Shrubland (75%) Developed (25%)	40	0	0.6	1,013	10.0
23	44	Cropland (66.6%) Developed (16.7%) Shrubland (16.7%)	70	0	0.5	352	25.0
24	396	Forest (83.3%) Grassland (16.7%)	100	65	8.3	1,352	25.6
25	690	Grassland (40%) Forest (20%) Shrubland (20%) Not vegetated (20%)	65	0	0.2	678	24.4
26	341	Grassland (83.3%) Not vegetated (16.7%)	70	0	0.7	1,250	22.8

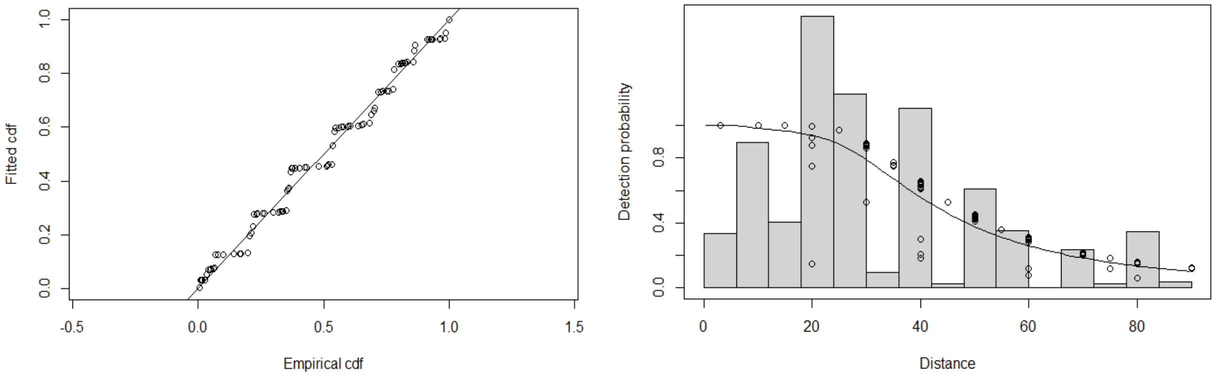
[a]DLNR Landcover layer [b]Online Rainfall Atlas of Hawai‘i *pueo detection

Appendix C. Prey bird model plots and goodness of fit tests. (a) The diagnostic plots of the “small” prey bird detection function fit well with the pattern of its respective model (T=0.24, p=0.21). (b) The diagnostic plot of the “large” prey bird detection function also fit well with the pattern of its respective model (T=0.26, p=0.17). Indicating these were both valid models for inference.

(a)



(b)



Appendix D. Observed native and non-native prey birds by size class and vegetation type.

Vegetation type (No. of surveys)	Native “small” bird	Native “large” bird	Non-native “small” bird	Non-native “large” bird
Cropland (n=7)	None	Kōlea or Pacific golden-plover (*Pluvialis fulva*), unidentified seabirds flying overhead towards Kihei coastline.	African silverbill (Euodice cantans), Chestnut munia (*Lonchura atricapilla*), Common waxbill (Estrilda astrild), House finch (*Carpodacus mexicanus*), House sparrow (*Passer domesticus*), Java sparrow (*Padda oryzivora*), Scaly-breasted munia (*Lonchura punctulate*), Warbling white-eye (*Zosterops japonicus*)	Common myna (*Acridotheres tristis*), Gray francolin (*Francolinus podcicerianus*), Mourning dove (*Zenaida macroura*), Northern cardinal (*Cardinalis* cardinalis), Red-crested cardinal (*Paroaria coronate*), Rock pigeon (*Columba livia*), Rosy-faced lovebirds (Agapornis roseicollis), Spotted dove (*Streptopelia chinensis*), Zebra dove (*Geopelia striata*)
Forest (n=8)	Hawaiʻi ʻamakihi (*Chlorodrepanis virens*), ʻApapane (Himatione sanguinea), ʻIʻiwi (*Vestiaria coccinea*)	None	Red-billed lieiothrix (*Leiothrix lutea*), Warbling white-eye (*Zosterops japonicus*)	Melodious laughing thrush or Hwamei (*Garrulax canorus*), Common myna (*Acridotheres tristis*)

Grassland (n=7)	None	Kōlea or Pacific golden-plover (*Pluvialis fulva*),	African silverbill (*Euodice cantans*), Chestnut munia (*Lonchura atricapilla)*, Common waxbill (Estrilda astrild), Eurasian skylark (*Alauda avarensis*), House finch (*Carpodacus mexicanus*), Japanese bush warbler (*Cettia diphone*), Warbling white-eye (*Zosterops japonicus*)	Common myna (*Acridotheres tristis*), Mourning dove (*Zenaida macroura*), Northern cardinal (*Cardinalis* cardinalis), Northern mockingbird (*Mimus polyglottos*), Zebra dove (*Geopelia striata*)
Shrubland (n=4)	Hawai‘i ‘amakihi (*Chlorodrepanis virens*), ‘Apapane (Himatione sanguinea), ‘I‘iwi (*Vestiaria coccinea*)	None	Eurasian skylark (*Alauda avarensis*)	Chukar (*Alectoris chukar*) Northern mockingbird (*Mimus polyglottos*)

Appendix E. Rodent mark and capture data per survey site (area=625m^2).

ID	Major vegetation type	Marked first night (n/ 50 traps)	Captured second night (n/ 50 traps)	Minimum number of rodents alive (n/100 trap nights)	Minimum available rodent biomass (g/ 625m^2) (marked + captured)
1	Shrubland	1 mouse (10 g)	2 mice (11, 12.5 g)	3	33.5
2	Shrubland	1 rat (108 g)	0	1	108
3	Grassland	2 mice (10 g, 11 g)	2 mice (10.5 g, 11 g)	4	42.5
4	Grassland	0	0	0	0
5	Cropland	4 mice (11 g, 13 g, 15 g, 10 g)	3 mice (12.5 g, 13 g, 12 g)	7	86.5
6	Forest	5 rats (86 g, 90 g, 110 g, 70 g, 92 g)	9 rats (80 g, 90 g, 71 g, 90 g, 86 g, 88 g, 79 g, 85 g, 94 g)	14	1,211
7	Forest	0	0	0	0
8	Grassland	0	0	0	0
9	Forest	0	0	0	0
10	Cropland	0	0	0	0
11	Forest	1 rat (40 g)	0	1	40
12	Cropland	0	0	0	0
13	Cropland	0	0	0	0
14	Grassland	0	0	0	0
15	Shrubland	1 mouse (12 g)	0	1	12

16	Forest	0	0	0	0
17	Grassland	1 mouse (13 g)	1 mouse (11 g)	2	24
18	Forest	3 rats (70 g, 100 g, 65 g)	3 rats (90 g, 120 g, 85 g)	6	530
19	Cropland	0	0	0	0
20	Forest	3 mice (13 g, 13 g, 11 g)	4 mice (10 g, 10 g, 12 g, 16 g)	7	85
21	Cropland	0	0	0	0
22	Shrubland	1 mouse (13 g), 1 rat (85 g)	0	2	98
23	Cropland	0	0	0	0
24	Forest	1 mouse (10 g)	2 mice (12 g, 12 g)	3	32
25	Grassland	1 mouse (12 g)	1 mouse (10 g)	2	22
26	Grassland	6 mice (10 g, 9 g, 12 g, 10 g, 10 g, 10 g)	6 mice (11 g, 12 g, 11 g, 10 g, 10 g, 10 g), 1 rat (60 g)	13	185

Appendix F. Insect (Order Orthoptera) count data per survey site.

ID	Major vegetation type	Insect (Order Orthoptera) type (n/ 500m^2**)**	Insect biomass (g/ 500m^2):
1	Shrubland	1 large cricket (0.7 g), 2 small moths (.1 g ea.)	0.72
2	Shrubland	2 small moths (.1 g ea.)	0.2
3	Grassland	3 small moths (0.1 g ea.), 1 small grasshopper (.1 g), 6 small green katydids (.1 g ea.), 1 large grasshopper (0.7 g)	1.7
4	Grassland	4 small black grasshoppers (0.1 g ea.), 6 small, 1 medium, 3 large green w/black line grasshoppers (0.1 g ea., 0.4 g, 0.7 g ea.)	3.5
5	Cropland	3 large field crickets (0.7 g ea.)	2.1
6	Forest	2 small, striped katydids (.1 g ea.), 8 medium grasshoppers (.4 g ea.)	3.4
7	Forest	6 medium moths (0.4 g ea.)	2.4
8	Grassland	8 small katydids (0.1 g ea.), 5 small grasshoppers (0.1 g ea.), 1 large grasshopper (0.7 g)	2.0
9	Forest	2 small moths (0.1 g ea.), 3 medium grasshoppers (0.4 g ea.)	1.4
10	Cropland	6 large grasshoppers (0.7 g ea.)	3.5
11	Forest	8 small moths (0.1 g ea.), 10 medium moths (0.4 g ea.)	4.8
12	Cropland	0	0
13	Cropland	0	0
14	Grassland	1 medium beetle (0.4 g)	0.4
15	Shrubland	4 medium moths (0.4 g ea.)	1.6
16	Forest	2 medium moths (0.4 g ea.),	5.1

		5 medium termite flies (0.4 g ea.), 15 small katydids (0.1 g ea.), 2 unknown medium orthoptera (0.4 g ea.)	
17	Grassland	2 small moths (0.1 g ea.), 5 medium moths (0.4 g ea.)	2.2
18	Forest	70 small and 30 large grasshoppers (0.1 g and 0.7 g ea.)	28
19	Cropland	10 small flying beetles (0.1 g ea.)	1
20	Forest	4 medium moths (0.4 g ea.), 4 small beetles (0.1 g ea.), 2 small grasshoppers (0.1 g)	2.2
21	Cropland	3 small beetles (0.1 g ea.), 3 medium moths (0.4 g ea.)	1.5
22	Shrubland	11 medium moths (.4 g ea.)	4.4
23	Cropland	3 small moths (0.1 g ea.), 3 large moths (0.7 g ea.)	2.4
24	Forest	21 small grasshoppers (0.1 g ea.), 8 large grasshoppers (0.7 g ea.)	7.7
25	Grassland	6 medium moths (.4 g ea.), 10 small grasshoppers (0.1 g ea.), 3 large grasshoppers (0.7 g ea.)	5.5
26	Grassland	9 medium moths (0.4 g ea.), 1 medium grasshopper (0.4 g), 2 large grasshoppers (0.7 g ea.)	5.4

Appendix G. Owl observations per survey site.

ID	Vegetation type	Owl presence (n, species, distance away)	Behavior	Pueo playback response	Incidental owl observations
1	Shrubland	1 pueo (20 m)	Hunting, perched, flying	Y	1 pueo flew overhead while checking rodent traps on 5/22/19 at 8:30.
2	Shrubland	2 pueo (45 m)	Hunting, flying, perched, wing-clap courtship	Y	N
3	Grassland	1 pueo (60 m)	Flying, hunting, observed wing-clap courtship	Y	N
4	Grassland	2 pueo (40 m), 1 barn owl (20 m)	Observed 1 pueo hunting then perched, another pueo flew from opposite side of field, did courtship display and returned to Eucalyptus grove perch. barn owl flew overhead while playing pueo playback.	Y	1 pueo observed hunting near road and cattle pen at 10:30.
5	Cropland	N	N	N	N
6	Forest	1 barn owl (100 m)	Observed barn owl hunting opposite side of gulch at sunset.	N	N
7	Forest	N	N	N	After survey driving down by the disc golf course, played pueo callback. At 19:40, pueo called and flew out from wattle/eucalyptus grove

					over car then back into forest.
8	Grassland	1 unknown owl (40 m)	Unknown owl flew nearby through Eucalyptus forest near end of survey time	N	While driving home from survey observed 2 barn owls along road perched and 1 pueo in road. All observations were near ‘Ulupalakua Ranch.
9	Forest	N	N	N	Observed pueo flying nearby at sunset in the same area on 9/7/19.
10	Cropland	N	N	N	N
11	Forest	N	N	N	Observed pueo the last morning of survey hunting at 9:00, near road and shrubland at the turnoff towards Hosmer's Grove.
12	Cropland	N	N	N	N
13	Cropland	N	N	N	N
14	Grassland	1 pueo (90 m)	Observed pueo hunting near the cattle pen and road.	N	N
15	Shrubland	1 pueo (100 m)	Observed pueo flying and hunting.	N	N
16	Forest	1 pueo (100 m)	Observed pueo hunting over pasture, came from Eucalyptus grove.	N	Yes, have observed a pair of pueo hunting in the same area any time of day.
17	Grassland	1 pueo (200 m)	Observed pueo flying in the distance over trees.	N	N

18	Forest	N	N	N	N
19	Cropland	N	N	N	N
20	Forest	1 pueo (60 m)	Observed pueo hunting over field.	Y	Yes, have observed a pair of pueo hunting in the same area all times of day.
21	Cropland	1 pueo (90 m)	Responded to pueo calls at the end of the survey.	Y	N
22	Shrubland	2 pueo (150 m)	Observed 2 pueo flying and hunting together in the nearby gulch.	Y	Observed 1 pueo the following morning flying in the same area as the night prior.
23	Cropland	N	N	N	N
24	Forest	N	N	N	N
25	Grassland	unknown owl (30 m)	Observed unknown owl flying and hunting.	N	N
26	Grassland	unknown owl (200 m)	Observed flying near a patch of trees.	N	Ranch owner observed pueo perched at night near survey point a few nights prior to survey.