THESIS

HABITAT USE AND CONSERVATION IMPLICATIONS FOR AKIKIKI (OREOMYSTIS BAIRDI) AND AKEKEE (LOXOPS CAERULEIROSTRIS), TWO ENDANGERED HAWAIIAN HONEYCREEPERS

Submitted by

Lucas Alan Hallman Behnke

Department of Fish, Wildlife and Conservation Biology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 2014

Master's Committee:

Advisor: Liba Pejchar

Lisa Crampton
Lisa Angeloni
David Theobald

ABSTRACT

HABITAT USE AND CONSERVATION IMPLICATIONS FOR AKIKIKI (OREOMYSTIS BAIRDI) AND AKEKEE (LOXOPS CAERULEIROSTRIS), TWO ENDANGERED HAWAIIAN HONEYCREEPERS

Limited resources for biodiversity conservation warrant strategic science-based recovery efforts, particularly on islands, which are global hotspots of both endemism and extinction. The diverse assemblages and the extreme isolation of the islands of the Hawaiian archipelago make them a unique laboratory for development of a coherent strategy for recovery of rare species and for large-scale systems conservation efforts. The Akikiki (*Oreomystis bairdi*) and the Akekee (*Loxops caeruleirostris*) are critically endangered honeycreepers endemic to the Hawaiian island of Kauai. Recent declines and range contraction spurred this study, the first systematic scientific investigation of these little known species. I conducted occupancy sampling for Akikiki and Akekee and vegetation surveys at plots within five study areas on the Alakai plateau of Kauai to assess range-wide occupancy and habitat use. Occupancy rates for both species increased from west to east along the plateau (Akikiki: $\psi = 0.02 \pm 0.07$ to 0.55 ± 0.21 Akekee: $\psi = 0.03 \pm 0.10$ to 0.53 ± 0.33), but were low throughout the ranges of both species. Canopy height was correlated with occupancy for both species, which suggests the damage done by hurricanes in 1982 and 1992 may be restricting these birds to the most intact forest remaining. Vegetation surveys revealed several key differences in forest composition and structure between areas, indicative of broader changes occurring across the plateau. Invasive plants such as Himalayan ginger (*Hedychium gardnerianium*) were dominant in the western portion of the plateau, where there was a corresponding decline in native plant cover. Conversely, ground disturbance by feral ungulates was higher in more eastern native-dominated plots. These results highlight the need to control ungulates and limit habitat degradation in the regions with the highest occupancy of Akikiki and Akekee. Without significant investment to address these threats and protect and restore suitable habitat for these species, it is unclear how long these birds will persist.

ACKNOWLEDGEMENTS

I would like to acknowledge funding and support from the U.S. Fish and Wildlife Service-Pacific Islands Fish and Wildlife Office *Preventing Extinction* grant as well as funding and logistical support from the State of Hawaii Department of Land and Natural Resources-Division of Forestry and Wildlife and its remarkable conservation project, the Kauai Forest Bird Recovery Project. This work was made possible with the support and encouragement of two project coordinators: Dr. Pauline Roberts helped me find my place on Kauai and opened the door to a graduate education; and Dr. Lisa Crampton, Cali, saw that I made my way through. As my committee member, supervisor, and frisbee tossing partner she kept me on track and confident, relatively speaking. I am particularly grateful to Ruby Hammond for being my better half during my first field season and for dedicating herself so completely to helping these birds through her own thesis work. Likewise, Barbara Heindl has put up with my shenanigans for years and without her, I would probably still be out up in the Alakai collecting vegetation data. The rest of the crew from KFBRP, you know who you are, put up with me through the some of the roughest fieldwork I could have possibly designed for them, and all for the love of some 15-gram flying cotton balls.

I would like to thank my committee members, Drs. Lisa Angeloni and Dave Theobald whose assistance and support helped shape this thesis, as well as Drs. Kate Huyvaert and Boris Kondratieff who contributed to my proposal and helped me to (mostly) manage my own expectations. Dr. Larissa Bailey provided invaluable assistance in the design and analysis of my occupancy data, and she did it while smiling and rolling strikes. The entire Fish, Wildlife and Conservation Biology Department community is incredibly special. The faculty is not only

world-renowned but remarkably approachable; the graduate students are diverse, brilliant, passionate and fun-loving; and the Friday Afternoon Club is still one of the most inspiring “clubs” that I have ever had the privilege to participate in.

I owe an ocean of gratitude to my advisor, Liba Pejchar. Her unfailing support and positive attitude have buoyed me through this incredible process. Her Liba-Lab has been inspiring to take part in as an aspiring conservation biologist and she is an amazing role model, though perhaps an impractical standard, for academic and conservation professionals. I could not have hoped for a better advisor.

None of this would have been possible without the love, support and occasional fieldwork, of my family. My parents, Marie and John have put up with the trials and tribulations of their prodigal son for years and their support could not have been more appreciated, even if it could potentially have been more shrewdly invested. My wiser sister Lynette showed up out of nowhere at Snooze the day of my seminar, to my delight. My younger sister Tessa Behnke, let me tag along with her to CSU, kept me sane in the lab, fixed my slides when they were most definitely crooked, and came all the way to Kauai to lend a helping hand with fieldwork. She has a bright future ahead of her.

Finally but not lastly, I would like to thank my beautiful wife, Jessica Lynn Hallman Behnke. Thank you for the love and support, the eternal confidence, for pushing me to achieve those things that only you seem to believe I can, and of course for the patient dog co-parenting that has changed both our lives for the remarkable. I look forward to sleeping more soundly and surfing more often with you in the near as well as distant future.

PREFACE

With biodiversity under threat worldwide, it is important to prioritize research and management efforts to make best use of limited conservation funds. Understanding the relative importance of key threats to rare and declining species is the first step in implementing effective conservation actions.

Islands in particular have hosted an alarming proportion of all extinctions in recent history (Myers 1993), and without adequate management and monitoring, the losses are likely to continue (Brooke et al. 2007). Islands are susceptible to rapid habitat degradation from land use change and invasive species, yet due to their isolation, have historically hosted large numbers of endemic species (Steinbauer et al. 2012). The unique assemblages of oceanic islands also offer insight into broad ecological patterns, and represent one of the proving grounds of biodiversity evolution and conservation. Adaptive radiation, co-evolution and the process of community assembly on islands is, at a very basic level, an example of the generation of diversity on the planet (Boyer 2010).

With the contentious title of “extinction capital of the world”, the Hawaiian Islands exemplify the loss of diversity in the Pacific Islands. Hawaii’s once diverse and unique assemblage of avifauna has lost more than 50% of its endemic species (Olson and James 1982). Factors contributing to the decline of Hawaii’s forest birds are relatively well known. Scott et al. (1986), building on a strong foundation of research, laid out a plan for conservation action that identified habitat degradation, disease and predation as the key threats to forest bird persistence. Those threats have each been the subject of subsequent research and have resulted in some relatively successful conservation actions, including exclusion and removal of ungulates to prevent and counteract habitat loss, large-scale habitat restoration, and targeted efforts in predator control (Pratt et al. 2009, VanderWerf 2009).

Broad application of this knowledge to alleviate threats to all Hawaiian forest birds has, however, proven problematic. Potential management activities must be conducted at scales relevant to ecological processes that may vary greatly among islands and species. Currently over 95% of Hawaii's avifauna face a combination of threats, many of which cannot be eliminated, but which may be mitigated by large-scale conservation partnerships (Reed et al. 2012). Prioritizing management actions in the face of limited resources, political will, and time is important for all forest birds, including those for which even basic life history information is not known. This is particularly true in Hawaii; although Hawaii has more endangered bird species than any other state in the United States, it receives relatively little funding for endangered species research and recovery (Leonard 2008).

The ecological threats facing the avifauna of Kauai are similar to those facing species occupying the other main Hawaiian Islands. Kauai is unique, however, in that the historic avian assemblage was intact through the 1960's (Richardson and Bowles 1964). Although the range contraction of Kauai's native forest birds was acute by the mid 1970's, only one species, the Kauai Akialoa (*Hemignathus procerus*) went undetected in the Alakai Wilderness Area during an expedition in 1975. The members of this expedition found that all forest birds were effectively confined to the wet montane forest of the Alakai plateau (Conant et al. 1998); but few believed that this seemingly intact community was under imminent threat.

Since that time, hurricanes Iwa (1982) and hurricane Iniki (1992) have struck Kauai, affecting nearly all remaining native bird habitat. Non-native vegetation rapidly encroached on the forest damaged and fragmented by the hurricanes. As a result, Kauai is now at the frontline of conservation in Hawaii. Four more species, the Kauai Oo (*Moho braccatus*), Ou (*Psittirostra psittacea*), Kamao (*Myadestes myadestinus*), and Nukupuu (*Hemignathus lucidus hanapepe*) are thought to have gone extinct in the decades following the hurricanes. Of the eight remaining forest bird species, until recently only one, the Puaiohi (*Myadestes palmeri*), was listed as Federally Endangered under the U.S. Endangered Species Act. Early in 2010, two more species were listed as Endangered, the Akikiki (*Oreomystis bairdi*) and the Akekee (*Loxops caeruleirostris*).

Owing to their unprotected conservation status (until recently they were not listed as endangered or threatened), isolation, and relatively low densities, neither the Akikiki nor the Akekee has been the subject of rigorous scientific study. Each has been the subject of taxonomic debate and short biological notes (Eddinger 1972, VanderWerf and Roberts 2008), yet very little quantitative work has been done on breeding biology, habitat requirements, key threats, or potential conservation measures.

The Akikiki and the Akekee are both insectivorous passerines in the family Fringillidae, endemic to Kauai. Both appear to have similar habitat requirements, predominantly foraging and breeding in wet, montane forest dominated by ohia lehua (*Metrosideros polymorpha).* Each appears to have become less abundant or to have disappeared from the more mesic mixed ohia-koa (*Acacia koa*) forest.

The Akikiki, also known as the Kauai Creeper, feeds primarily by gleaning, flecking, and probing from the bole and branches of trees and from understory plants including kawau (*Ilex anomala*), olapa (*Cheirodendron trigynum*) and *Clermontia faurei* (Foster et al. 2000). The predominant prey items recorded are insects, insect larvae and spiders (Foster et al. 2000), with specific mention of “looper” caterpillars (Geometridae) by Perkins (1903). VanderWerf and

Roberts (2008) reported the first observations of digging into dead wood by Akikiki. They also presented observations of nesting behavior for the species. Almost all nests to date have been found above 5 m and as high as ~15 m in ohia and averaged ~ 10 m (VanderWerf and Roberts 2008, Hammond 2014).

The Akekee predominantly feeds on spiders, psyllids, and caterpillars (Lepson and Pratt 1997) while foraging in the terminal leaf nodes of ohia. Its bill is functionally similar to crossbills (*Loxia* spp.), being asymmetric and allowing it to pry open leaf nodes to extract prey. Very little is known about the nesting biology of the species, as only one nest has been described (Eddinger 1972). As recently as 2005, only eight nests, at an average of over 10 m in height, had been found but none of these were monitored. More recently, nests have been located over 11 m (Lepson and Pratt 1997, Hammond 2014).

Both the Akikiki and the Akekee are currently believed to be restricted to the high Alakai plateau, also known as the Alakai Swamp, from approximately 1,000 to 1,593 m in elevation. Data on the lower extent of their elevation range is lacking, so this may actually over-represent the current range of these species. Forest bird surveys conducted between 1976 and 2008 have been variable in survey effort, and limited to the plateau to which native forest birds were believed to be restricted by the time the first surveys were initiated. Despite the limitations of historic survey methods and data availability, it is likely that the range of both the Akikiki and the Akekee is currently less than 40 km^2. This figure represents less than half of the 88 km^2 range observed in 1976 (Sincock unpubl data, Foster et al. 2004).

Population-level trends in abundance have also been difficult to estimate accurately for these rare species. Camp and Gorresen (2010) found that both species likely experienced range contraction and declined in abundance from 1989 to 2008. The current estimate of abundance for

Akikiki is 3,865 birds (95% CI = 2,566—5,429; mean density * 39 km^2) and Akekee abundance is estimated at 7,887 birds (95% CI = 5,220—10,833; mean density * 127 km^2) (Camp and Gorreson 2010).

Pressure from Hawaii's researchers and local conservation advocates concerned about the range contraction of Akekee and the persistently small population of Akikiki led to their recent listing under the U.S. Endangered Species Act (VanderWerf and American Bird Conservancy 2007). The observed population declines, and the resulting change in conservation status, has catalyzed efforts to explore the factors underlying the decline of these two species while reasonably sized populations still exist.

The major threats to the Akikiki and Akekee are likely to be similar to those identified for all Hawaiian forest birds. Some combination of habitat quality, food availability, introduced avian disease, and predation is probably contributing to declines in population and contraction in range. Climate change is of particular concern for these species, because increased temperature is likely to increase the transmission of avian disease within their limited range, and may also impact the vegetation communities on which they depend (Benning et al. 2002). The relative importance of the factors impacting population and range size, however, are unknown for these species. Identifying the degree to which these explanatory factors are related to survival and fecundity is critical for recovering the Akikiki and the Akekee. To meet this objective, we need much better information on how these birds are occupying and using habitat across their current and former range. This science-based "triage" approach to collecting data on species distributions and habitat use, identifying key threats, and suggesting appropriate recovery measures could be adapted to other species in Hawaii and beyond.

TABLE OF CONTENTS

CHAPTER ONE: *OCCUPANCY AND HABITAT USE OF THE ENDANGERED AKIKIKI AND AKEKEE ON KAUAI ISLAND*

CHAPTER ONE

OCCUPANCY AND HABITAT USE OF THE ENDANGERED AKIKIKI AND AKEKEE ON KAUAI ISLAND

INTRODUCTION

The loss of Hawaii's endemic birds is well documented and in gross disproportion to land area (Perkins 1903, Olson and James 1982, Gorresen et al. 2009). Since the arrival of humans, 68% of Hawaii's 109 endemic birds have gone extinct (Scott et al. 2001, Reed et al. 2012), and an additional 33 species are listed as federally endangered (USFWS 2013). Thus, Hawaii hosts over 30% of all listed bird species in the United States, despite representing only 0.25% of its land mass.

The primary drivers of past extinctions and threats to Hawaii's extant forest birds are habitat loss and degradation, predation by non-native mammals, and introduced diseases such as avian malaria (Scott et al. 1986, Scott et al. 2001, Pratt et al. 2009). These, combined with climate change, and stochastic events such as hurricanes, threaten the persistence of Hawaii's endemic forest birds, particularly on relatively low-elevation islands such as Kauai where introduced avian disease limits their ranges (Benning et al. 2002).

Six extant forest bird species are endemic to Kauai, including two honeycreepers recently listed as federally endangered under the U.S. Endangered Species Act. The listing of the Akikiki or Kauai Creeper (*Oreomystis bairdi*), previously a candidate species for over a decade, and the Akekee or Kauai Akepa (*Loxops caeruleirostris*) in 2010 was prompted by declines in abundance and potential range contraction (Foster et al. 2004, VanderWerf and American Bird Conservancy 2007, Camp and Gorresen 2010). Both species are restricted to the Alakai plateau, a remote and relatively intact high-elevation native montane wet forest in the center of the island (Foster et al. 2004). Akikiki feeds primarily on arthropods by gleaning and flecking bark along the boles and branches of live and dead canopy and understory trees (Foster et al. 2000), and Akekee forages primarily in the canopy of ohia lehua (*Metrosideros polymorpha*) by using its slightly-crossed bill to pry open terminal leaf nodes to extract invertebrates including spiders, psyllids, and caterpillars (Lepson and Pratt 1997). These two distinct foraging strategies may lead to different patterns of habitat use across their current range.

Given the lack of protected status prior to 2010, the remoteness of their current range, and low population densities, neither species has been the subject of rigorous scientific study. The scientific literature on these species is limited to species accounts (Akekee: Lepson and Pratt 1997, Akikiki: Foster et al. 2000), taxonomic descriptions (Pratt 1989, 1992), short biological notes (Eddinger 1972, VanderWerf and Roberts 2008), and a brief unpublished M.S. study on habitat preferences (Powell 2008). There are no quantitative data on the breeding biology, habitat requirements, key threats, or potential conservation measures for these two species, although research on other Hawaiian endemic birds has illuminated many of the causal mechanisms of decline (Pratt et al. 2009). Research focused on these rare species is urgently needed to assess habitat use and potential threats and to implement meaningful conservation actions. This information is needed before these birds become too scarce for recovery, a situation illustrated by the recent extinction of the Poouli (*Melamprosops phaesoma*) on another Hawaiian Island (VanderWerf et al. 2006).

The primary objective of this study was to determine the occupancy and habitat use of Akikiki and Akekee across their current range on the Alakai plateau (Foster et al. 2004, VanderWerf 2009). Due to their flexibility, cost-effectiveness, and relative ease of interpretation, occupancy metrics have increasingly been used for assessing the status and distribution of species of conservation concern (Noon et al. 2012). I estimated probability of occupancy and coupled these data with vegetation surveys and measures of habitat disturbance by non-native ungulates to provide insight into current habitat use. My second objective was to examine potential differences in forest dynamics across the Alakai plateau to provide additional insight into species distribution patterns in this last remaining contiguous native forest on Kauai (USGS 2011).

METHODS

Study Area

This study was conducted in the Alakai Wilderness Preserve, Kokee State Park, and Na Pali Kona Forest Reserve on the Alakai plateau of Kauai Island, Hawaii (22°05′N 159°30′W; Figure 1). The plateau is bounded to the east by the highest point on the island, Mt. Kawaikini (~1600 m), and by Kokee State Park to the west where the elevation reaches just over 1000 m. The forest on the Alakai plateau transitions from wet montane forest dominated by ohia lehua (*Metrosideros polymorpha*) in the east, receiving ~900 cm of rain per year, to the relatively mesic mixed ohia-koa (*Acacia koa*) in the west with a rainfall of 190 cm per year (Giambelluca et al. 2013).

Sampling Design

I measured occupancy of Akikiki and Akekee from March to July 2012, and described habitat characteristics, at five sites in three study regions (Figure 1). I chose study regions based on density estimates and the current estimated range of Akikiki and Akekee (Foster et al. 2004, Camp and Gorresen 2010), and took logistics (i.e., accessibility and existing research infrastructure) into consideration. Two study regions, East Alakai (EAK) and Mohihi (MOH), were predicted to have medium to high densities of Akikiki and Akekee (Foster et al. 2004, Camp and Gorresen 2010). The third study region, Kawaikoi (KWK), previously supported medium densities of Akikiki and Akekee (Foster et al. 2004), but few birds were observed during subsequent surveys in 2005 and 2008 (Camp and Gorresen 2010). Although KWK is more mesic than EAK or MOH, all three regions are dominated by native ohia lehua canopy and a diverse understory of native shrubs and ferns, with varying cover of non-native plants.

Within each study region, I randomly located two non-overlapping 100 ha polygons, or study sites, in ESRI ArcGIS (Version 10.1 ESRI Inc. 2012) and generated a random point within each polygon as a starting point for area searches. Two study sites were established at KWK (K1 and K2) and EAK (E1 and E2). Due to logistical and topographic constraints, the original two study sites at MOH were merged into one (M1), resulting in a total five study sites across the three study regions (Figure 1). During a pilot study in 2011, I searched and mapped territories (Bibby et al. 2000) outward in all directions from the random starting point within each study site, as permitted by topography, until I found $\geq$ 10 territories or covered between 75 and 100 ha; the amount of area covered in 2011 determined the size of the occupancy study sites in 2012. Within each of the five study sites I established a systematic grid of sampling points based on a new random starting location. At each point I conducted occupancy surveys and measured explanatory habitat variables (Figure 1).

Occupancy Surveys

Following the sampling guidelines in MacKenzie et al. (2002), I quantified occupancy of Akikiki and Akekee in each study site by conducting surveys at sampling points in each of the five study sites (n = 70-96). Points were spaced 100 m apart, which slightly exceeded the furthest known distance traveled by a color-banded Akikiki during regular re-sighting efforts from 2007 to 2010 (Hawaii Division of Forestry and Wildlife, unpubl data). This sampling design was also consistent with prior population monitoring in the region and allowed comparison of my results to previously collected data (Foster et al. 2004; Camp and Gorresen 2010).

Following MacKenzie and Royle (2005), I surveyed occupancy at each point at least three times during the breeding season. At each point, I broke the survey into two periods. In the first, I passively surveyed and recorded presence/absence of all bird species for four minutes. In the second period, I recorded only presence or absence of Akikiki and Akekee for an additional four minutes using audio playback of calls and songs of each focal species broadcasted for ~1 minute. To model detection probability (p), I also recorded sampling covariates including observer, sustained wind speed, highest gust speed, precipitation, and cloud cover.

Two primary assumptions of standard single-season occupancy modeling are that occupancy at a particular survey point, ψ_i, is constant for the entire season and that sampling points are independent (Mackenzie et al. 2002). The assumption of constant occupancy is likely to have been met based on personal observation and long-term bird survey data (Camp and Gorresen 2010). If, as in the case of a species with a particularly large home range, survey points cannot be assumed to be independent or occupancy during the season is not constant (i.e., an individual is away from a survey location when it is sampled), then the interpretation of ψ and p must be adapted (Mackenzie et al. 2006). Although the sampling design used in this study was based on previously observed movement of the focal species, during the study both Akikiki and Akekee were observed moving longer distances than the 100 m between sampling points, leading to my interpretation of ψ as “use” of a particular point within the study site, and p as “detection given that the sampling point was “used”. Thus my use of the term “occupancy” is not specifically intended as a metric of abundance, but rather as a measure of relative habitat use across the landscape.

Vegetation Surveys

I used a stratified sampling design to capture vegetation characteristics at two scales: 1) all five study sites across the Alakai plateau, and 2) the two study sites within EAK, the region predicted to have the highest density of Akikiki and Akekee. The vegetation surveys in EAK were conducted at a finer scale to evaluate the influence of vegetation structure and composition on habitat use by the focal species. Specifically, I collected data on habitat characteristics at every other bird survey point at the three low-occupancy sites and at every point at the two high-occupancy sites ($n = 223$; Figure 1). Circular vegetation plots measuring 100 m^2 were centered on the sampling points (Camp 2011). At each plot, I measured vegetation variables within 25 m^2 quadrants systematically placed at four locations at the edge of the plot in each cardinal direction.

I collected data on ground, shrub, and canopy structure and composition, and measured feral pig disturbance within each vegetation plot. I measured forest profile, an index of understory density, as the proportion of a modified Robel pole obscured by vegetation at heights of 0-1 m (fp1) and 1-2 m (fp2) when viewed from each cardinal direction while placed at the center of the plot (Robel et al. 1970). I estimated total % shrub cover (sct) estimated within each quadrant as cover of vegetation greater than 1 m tall, and the proportion of native shrub cover (scn) was also estimated for each quadrant. I estimated total % ground cover (gct) and proportion of native ground cover (gcn) inside a 1 m^2 quadrat on the counter-clockwise side of the edge of the plot in each cardinal point. I estimated canopy density (den) at each cardinal point using a spherical densiometer. I estimated canopy height (ht) using an electronic range finder and clinometers. To summarize variables for each plot, I used the mean of measurements taken from each cardinal point (fp1, fp2, ht, den), the mean percent cover from the four quadrants (sct, scn), and the mean percent ground cover within the four quadrats (gct, gcn). I measured moss cover (moss) on all trees greater than 10 cm diameter at breast height by taking an estimate of the tree surface area covered by moss from breast height to 1 m above breast height. The mean of all moss measurements recorded in the plot was calculated and used in analyses. Maximum diameter at breast height (mdbh) from each plot was also used in analyses. I also measured the total area (m^2) of pig sign (pig) in each plot by summing the area covered by scat, digging, or trails that appeared to be less than three months old.

Statistical Analysis

I used Program PRESENCE (Hines 2006) to: 1) estimate and compare occupancy (ψ) of the two focal species among study regions and sites based on the most parsimonious model for each species (Anderson 2008), and 2) investigate relationships between habitat and occupancy in the EAK region while accounting for detection probability (p). For each focal species, I used Akaike's Information Criterion adjusted for small sample size (AIC_c), a likelihood-based information theoretic approach to model selection. First I assessed detection probability by constructing models of all combinations of sampling covariates. I then used the resulting best model ($\Delta AIC_c = 0$) to construct sets of covariates using region, site, and habitat to predict occupancy, while holding detection probability constant for each species. To investigate occupancy probability across the range of Akikiki and Akekee, I compared region and site as covariates to determine the best model for each species. The specific predictions tested were that 1) occupancy is lower in the west (KWK), higher in the east (EAK), and intermediate at MOH for both species (models with region as the covariate); and 2) that regional trends in occupancy are more detectable than differences between study sites.

For the EAK study region where detections were most frequent, I examined habitat use by constructing models with normalized covariate data from habitat surveys as predictor variables and occupancy as the dependent variable. The normalized value was the difference between a given value and the mean of the sample, divided by the standard deviation. Given the small sample size, these models were restricted to three covariates to limit the number of parameters, with the exception of one global (all covariates) model for comparison. Because I was most interested in the relative importance of habitat covariates, I model-averaged parameter estimates (Burnham and Anderson 2002) to reduce bias and account for model selection uncertainty (Doherty et al. 2012). The predictions I examined, based on each species' biology, were that 1) Akikiki occupancy is best predicted by understory vegetation and other structural metrics, as well as a combination of disturbance metrics; and 2) Akekee occupancy is best predicted by canopy vegetation metrics.

To gain insights into bird distribution, I also analyzed differences in habitat characteristics (dependent variables) among the study sites across the Alakai plateau (independent variable) in a Multivariate Analysis of Variance (MANOVA). Based on prior observation, I predicted that habitat structure (e.g. canopy height and canopy density) would vary across the plateau, with forest stature generally increasing from west to east. Conversely, I predicted that disturbance metrics (e.g. invasive plant cover and feral pig sign) would increase from east to west, and be undetectable in the EAK study region. I used an arcsine transformation of habitat variables involving count or percentage data to meet the assumption of normality. Data based on continuous measurements (canopy height and diameter at breast height) were not transformed. I used Pillai's Trace statistic to assess significance, followed by post-hoc one-way Analysis of Variance (ANOVA) using Least Significant Differences (LSD) and t-tests ($\alpha = 0.05$) in SPSS (PASW Statistics 18). Figures and results are presented as untransformed or back-transformed means ± SE.

RESULTS

Occupancy of Akikiki and Akekee across the Study Area

As predicted, I found an increasing trend in estimates of occupancy (ψ) for both species from west to east. For Akikiki, the region covariate was included in the best model of ψ, and the best model for Akekee included the site covariate (Table 1). Akikiki occupancy was greater in the eastern EAK region ($\psi = 0.55 \pm 0.21$) compared with the other two regions (KWK $\psi = 0.02 \pm 0.07$ and MOH $\psi = 0.04 \pm 0.10$; Figure 2A). Akekee occupancy increased gradually from west to east across study sites, and only differed significantly between K1 and H2 sites ($\psi = 0.03 \pm 0.10$ and $\psi = 0.53 \pm 0.33$, respectively; Figure 2B).

Detection probability (p) was low for both species (Akikiki $p = 0.63 \pm 0.40$; Akekee $p = 0.30 \pm .019$). It was negatively affected by highest gust speed during the survey period for both species, and by survey month for Akekee. For Akekee, p was highest in May, slightly lower in March-April and lowest in June.

Occupancy as a Function of Habitat Variables in the East Alakai Region

Occupancy of both species varied as a function of tree height within EAK. Both Akikiki and Akekee occupancy were positively correlated with mean canopy height (Figure 3; Akikiki: $\beta = 479.6 \pm 0.71$, Akekee $\beta = 0.142 \pm 0.074$). Mean canopy height (ht) was present in nine of the top ten models for Akikiki and three of the top four models for Akekee (Table 2, Appendix A-

B). Maximum diameter at breast height (mdbh) of ohia lehua also was positively correlated with occupancy and was present in eight of the top 10 candidate models for Akekee ($\beta = 0.019 \pm 0.012$), while canopy density (den) was positively associated with Akikiki occupancy ($\beta = 32.7 \pm 7.9$) and was present in several top models (Table 2, Appendix C).

Comparing Habitat Characteristics among Study Sites

In the MANOVA, habitat characteristics differed significantly across the five study sites (Pillai's Trace 1.176, F = 3188.72, df = 9, $\alpha = 0.05$). Tests of the between-subjects effects showed significant differences ($\alpha = 0.05$) between seven of the nine variables sampled (Table 3). Forest profile (fp2), total shrub cover (sct; Figure 4A), native shrub cover (scn; Figure 4B), mean canopy height (ht; Figure 4C), and moss cover (moss) all showed highly significant differences between at least one of the sites ($p = <0.001$); total ground cover (gct), and pig sign (pig; Figure 4D) also differed significantly among sites ($p = 0.001$ and $p = 0.002$, respectively). Maximum ohia diameter (mdbh) and canopy density (den) did not differ significantly among sites. The western-most study site (K1) differed from the other study sites for most structural variables, and contributed to the overall difference between regions.

DISCUSSION

Akikiki and Akekee are now restricted to a small proportion of the only island on which they occur. My results demonstrate that occupancy rates within this narrow range are extremely low for both species across most of their range, and as predicted, there is a slight increase toward the eastern end of the Alakai plateau. Given data from historical surveys (Foster et al. 2004, Gorresen et al. 2010), my findings are a strong indication that the range of these species continues to contract. Where Akikiki and Akekee were still present, I documented a correlation between occupancy and forest characteristics such as canopy height. Across the range of these species, native shrub cover was associated with higher occupancy, and feral pig sign was associated with intermediate occupancy. These range-wide patterns suggest that controlling invasive plants and restoring native plant cover, eradicating feral pigs, and giving full protection to remaining mature forest, is critical to the survival of these Hawaiian honeycreepers.

Akikiki and Akekee, both single-island endemics, have nearly disappeared from their last remaining habitat. Occupancy rates for these federally listed species are dramatically lower than those of another endangered Kauai endemic passerine, the Puaiohi (*Myadestes palmeri*), across a similar range (L.H. Crampton personal communication). The difference between Akikiki occupancy in the central and western regions (KWK, MOH) and the eastern region (EAK) was large and abrupt. In contrast, Akekee occupancy declined gradually from east to west. These trends are consistent with the results of long-term bird surveys (Foster et al. 2004). The dissimilar pattern of occupancy likely results from the different resource requirements of the species, or the ability of Akekee, canopy foragers, to cover large distances more readily in order to access available canopy resources. Nonetheless, the cumulative effect of changes in forest structure, spread of non-native vegetation, unfettered invasion of feral pigs, and the slow recovery of the native forest following Hurricanes Iwa (1982) and Iniki (1992) may all shape the distribution of both species across the plateau. Ongoing research on factors other than habitat characteristics that could affect Akikiki and Akekee survival and reproductive success, such as predation by introduced rats (Hammond 2014) and avian malaria (Atkinson et al. 2014), will be critical to developing a comprehensive strategy for the conservation and recovery of these species.

The relationship between occupancy and habitat characteristics at EAK provides insights into habitat use of these species across the plateau, which could not be measured directly because occupancy was too low outside of this study region. Habitat data from EAK indicated that canopy height and density were strongly associated with occupancy for Akikiki. This species is primarily an understory, branch and bole foraging "creeper" (Foster et al. 2000), so it is not surprising that canopy density may be an important predictor of occupancy, closed-canopy ohia forest may provide a high degree of foraging structure. Contrary to our predictions, however, canopy height appears to be a better indicator of occupancy than understory density. This may indicate that Akikiki prefer mature forest, possibly because of availability of food resources. The positive relationship between Akekee occupancy and canopy height and maximum ohia diameter (dbh) indicates that this species, a canopy foraging "crossbill" (Lepson and Pratt 1997), may preferentially use habitat with large trees. This observation is not inconsistent with my prediction that Akekee occupancy would be related to canopy density, but further indicates that large, mature trees are particularly important resources for this species.

The weak relationship between weed cover, disturbance and occupancy in the EAK region may be attributable to the low variation among vegetation plots in the study area. While there was not a detectable effect on occupancy at the within region scale, these factors may be important determinants of occupancy at the among region scale, but could not be examined directly because so few birds were detected at the other regions. Vegetation characteristics and ungulate disturbance did vary across the range of these species, with the lowest proportions of native plant cover found in the westernmost region (KWK) and the highest incidence of pig sign in the more central region (MOH), i.e., in the regions where occupancy of these two species was lowest. Contrary to my prediction, I also found a relatively high proportion of pig sign in the easternmost region (EAK), which was predicted to be the most pristine and was the site where I documented the highest occupancy of Akikiki and Akekee.

Management in this area, including weed control but not ungulate removal, has likely slowed the invasion of habitat-modifying plants such as Himalayan ginger (*Hedychium gardnerianum*) and strawberry guava (*Psidium cattleianum*). The evidence of damage by pigs, which are vectors for the spread of non-native species in Hawaii (Simberloff and Van Holle 1999), is of immediate concern. Lack of active ungulate management in this region may facilitate the spread of invasive species and continued degradation of an area that currently supports the highest occupancy of Kauai's rarest forest birds.

RECOMMENDATIONS FOR RESEARCH AND MANAGEMENT

My results confirmed that the range of these two Hawaiian honeycreepers is highly restricted and occupancy is extremely low. I also found that habitat characteristics, such as canopy height and density and emergent trees, were associated with higher habitat use, and that invasive plants are prevalent in regions where few birds were detected. Further, the unexpected high density of feral ungulates in the region with highest occupancy of Akikiki and Akekee could precipitate the spread of invasive plants into the best remaining habitat for these birds.

To build on these findings, I recommend consistent population-level monitoring to detect trends over time, and research that addresses other factors that could be acting synergistically to contribute to the decline of these species. My results suggest that occupancy as a state variable may provide a useful conservation tool for rare species. This approach allows biologists to assess population dynamics across a large spatial scale with multiple species of concern (Bailey et al. 2002). Traditional line-transect point counts provide important baseline data on range and population size of Kauai's forest bird community (Foster et al. 2004, Gorresen et al. 2009). However, as these and other species become increasingly rare and more difficult to detect, the amount of effort and funding necessary to provide good estimates of population size and habitat use with this method becomes untenable (Camp and Gorreson 2009). By estimating detection probability, I also provided a quantitative measure of the difficulty of detecting these species (MacKenzie et al. 2002) that could help guide future survey efforts.

In addition to monitoring Akikiki and Akekee to assess trends over time and the effectiveness of future management actions, research to address knowledge gaps on other threats to these species is of high priority. Specifically, I recommend using both observational and experimental techniques (e.g. ungulate fencing and eradication, rat removal, mosquito control to limit disease transmission) to evaluate the relative importance of these factors for population dynamics and habitat use.

However, given the low occupancy and increasingly narrow range of these two species, I emphasize that immediate conservation action based on the best available science is also essential. Climate change is predicted to exacerbate existing stressors to Kauai's forest birds through increased disease transmission (Benning et al. 2002, LaPointe et al. 2009) and by further limiting food availability and suitable foraging and nesting habitat. This study quantified the presence of invasive plants and the impact of ungulates across the Alakai plateau including the core range of Akikiki and Akekee. Both the continued control of invasive plants and the removal of feral ungulates from these areas may increase the resiliency of the Alakai's forests, possibly providing time for the birds themselves to adapt to the increased prevalence of disease. For example, the implementation of current plans to fence and remove ungulates from this area

(Hawaii Department of Land and Natural Resources 2011) will be critical to halting the degradation of the last strongholds of the Akikiki and Akekee.

There is, however, a significant lag time in the recovery of the habitats that support these species. Additionally, if disease or non-native predators are the most important threats to these species, habitat management alone will not be sufficient to prevent their extinction on Kauai. Under these circumstances, the only option left for Akikiki and Akekee would be to establish new populations in suitable habitat outside their known historic range where disease and predators are absent.

FIGURES

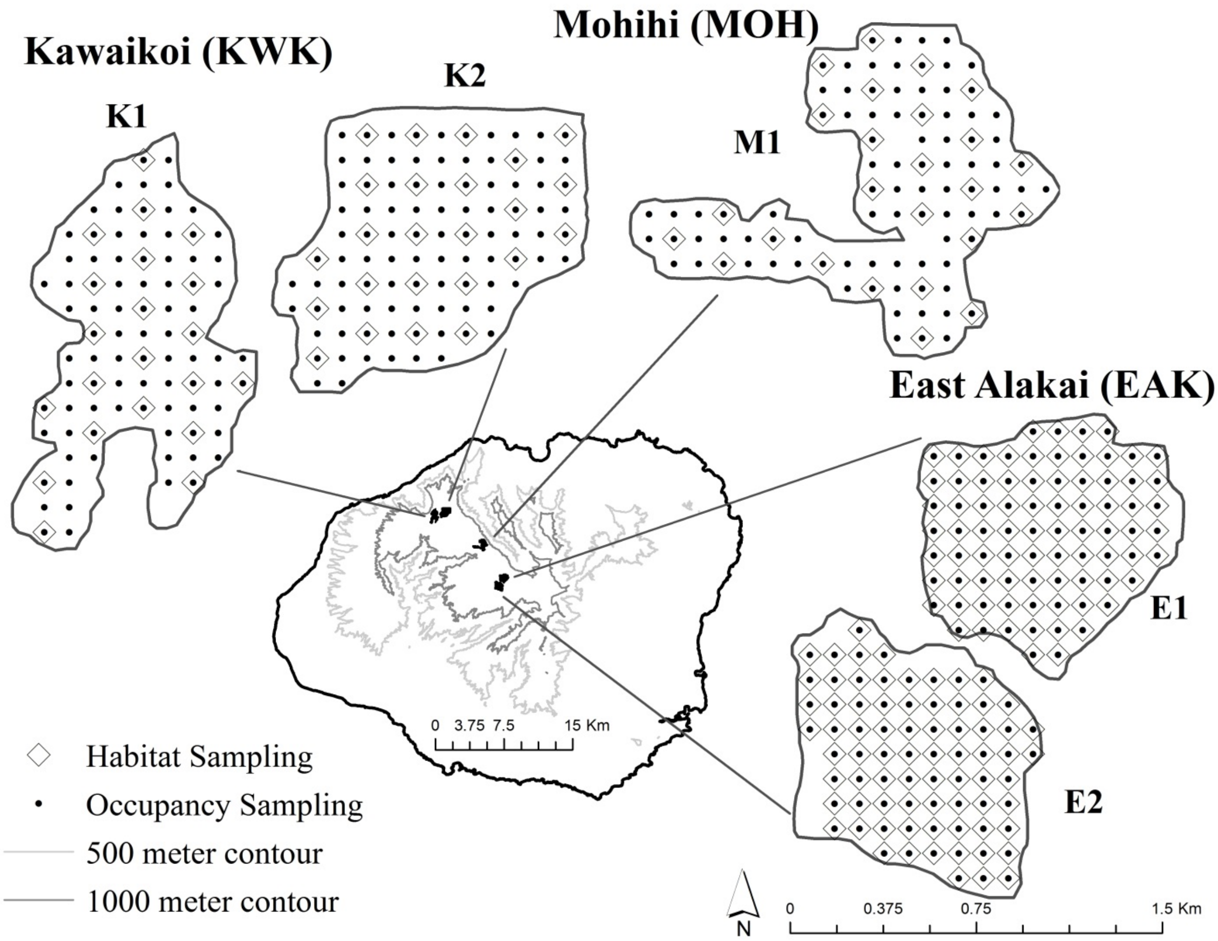

Figure 1. Location and distribution of sampling points across three study regions (KWK, MOH, EAK) containing the five study sites Kawaikoi West (K1), Kawaikoi East (K2), Mohihi (M1), Halehaha (H1) and Halepaakai (H2) on the Alakai plateau on Island of Kauai (Hawaii, U.S.) where occupancy and habitat surveys were conducted for Akikiki and Akekee.

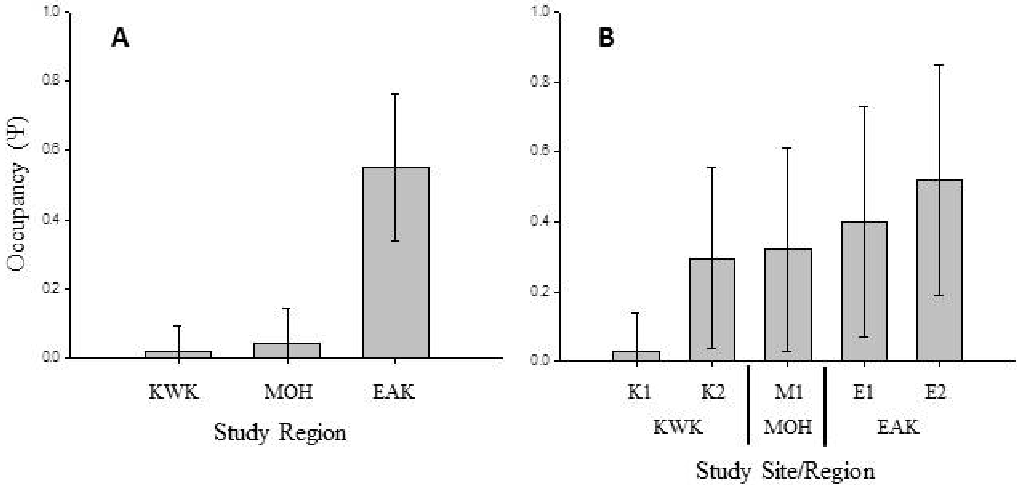

Figure 2. Occupancy estimates for Akikiki by study region (**A**) and for Akekee by study site (**B**). Figures report means ± 95% CI.

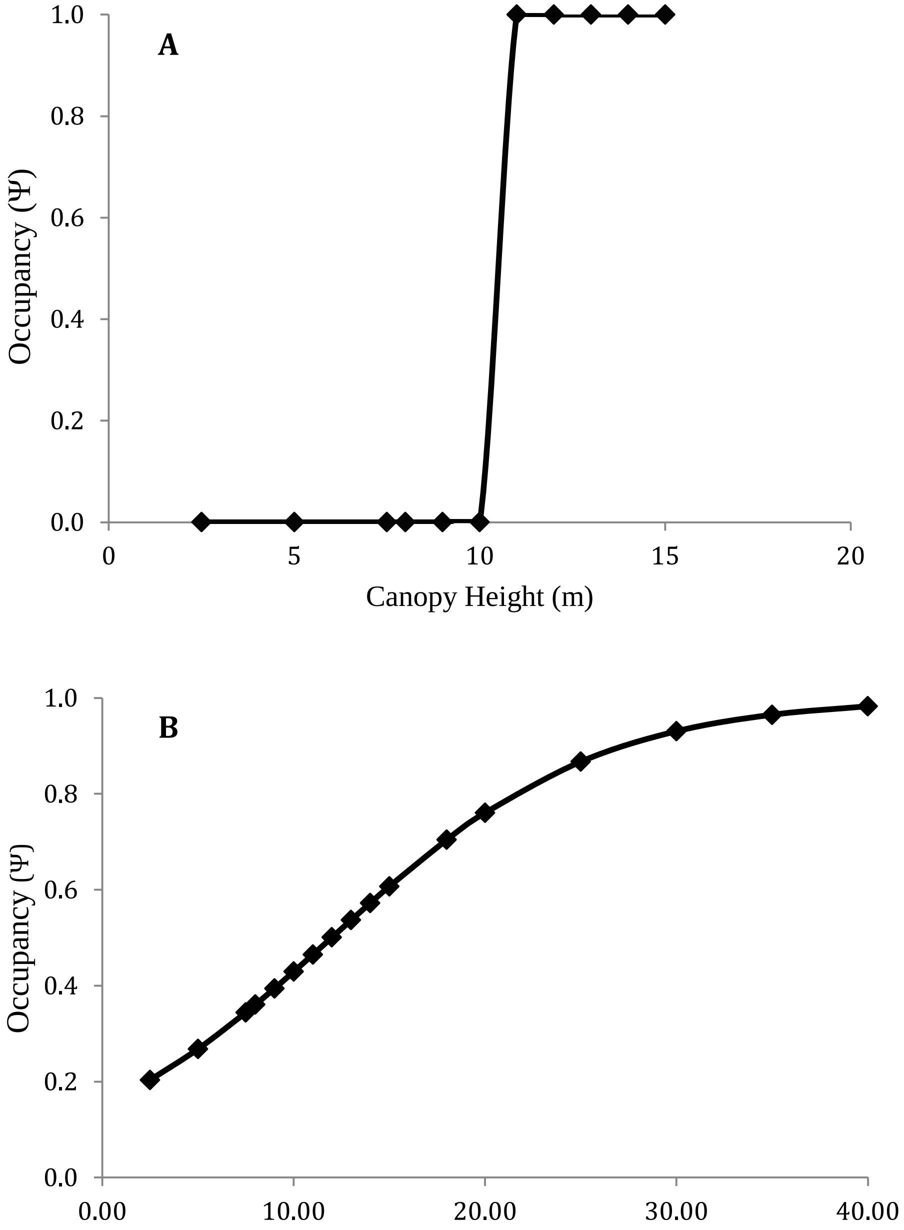

Figure 3. Relationship between occupancy (ψ) and model-averaged mean canopy height (ht) for Akikiki (**A**) and Akekee (**B**) in the East Alakai (EAK) study region.

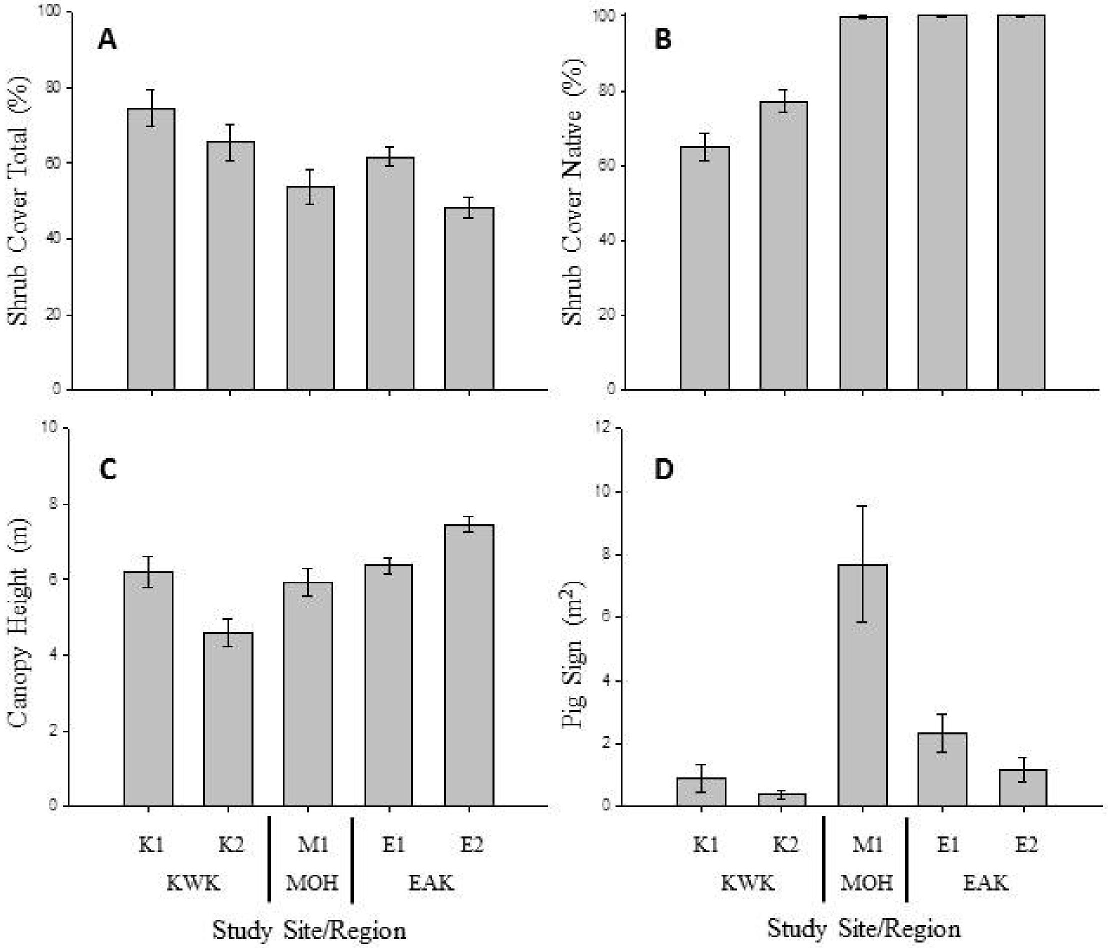

Figure 4. The habitat characteristics ‘shrub cover’ (**A**, **B**), ‘canopy height’ (**C**) and ‘pig sign’ (**D**) vary across study sites from west to east on the Alakai plateau. Figures report means ± 95% CI.

TABLES

Table 1. Model results for occupancy (ψ) across the range of Akikiki and Akekee. Results are by species and include model sets comparing survey data grouped by region (n = 3) and by site (n = 5) with the number of estimated parameters (K), the maximized log-likelihood (-2*Log*L*), the simple difference of second-order Akaike's Information Criterion adjusted for small sample size (ΔAIC_c) and the Akaike weight (w_i) for each model.

Species	Model	K	-2*Log*L*	ΔAIC_c	w_i
Akikiki	ψ(region),*p*(g)	6	253.8	0	0.83
	ψ(site),*p*(g)	8	252.81	3.16	0.17
Akekee	ψ(site),*p*(g+month)	11	531.2	0	0.99
	ψ(region),*p*(g+month)	9	545.09	9.68	0.01

Table 2. Model results for Akikiki and Akekee occupancy (ψ) as predicted by habitat characteristics in the East Alakai (EAK) study region. Models with $\Delta\text{AIC}_c > 4$ have been excluded, with the exception of the global model for Akekee, which contains all covariates. See Table 1 for column header definitions. See Table 3 for definition of model parameters.

Species	Model	*K*	-2*Log*L*	ΔAIC_c	w_i
Akikiki	ψ(fp2+ht),*p*(g)	5	208.04	0.00	0.22
	ψ(global),*p*(g)	11	194.79	0.24	0.19
	ψ(sct+den+ht),*p*(g)	6	206.49	0.62	0.16
	ψ(den+ht),*p*(g)	5	209.46	1.42	0.11
	ψ(den+ht+pig),*p*(g)	6	208.55	2.68	0.06
	ψ(gct+sct+den),*p*(g)	6	208.60	2.73	0.06
	ψ(ht),*p*(g)	4	213.54	3.36	0.04
	ψ(gct+ht),*p*(g)	5	211.44	3.40	0.04
	ψ(ht+pig),*p*(g)	5	211.63	3.59	0.04
Akekee	ψ(ht+mdbh),*p*(g+month)	9	278.60	0.00	0.26
	ψ(ht+pig+mdbh),*p*(g+month)	10	277.80	1.49	0.12
	ψ(mdbh),*p*(g+month)	8	283.41	2.54	0.07
	ψ(ht+moss),*p*(g+month)	9	281.24	2.64	0.07
	ψ(pig+mdbh),*p*(g+month)	9	281.89	3.29	0.05
	ψ(mdbh+gct),*p*(g+month)	9	282.13	3.53	0.04
	ψ(gct+mdbh),*p*(g+month)	9	282.13	3.53	0.04
	ψ(ht),*p*(g+month)	8	284.79	3.92	0.04
	…				
	ψ(global),*p*(g+month)	15	274.29	9.98	0.00

Table 3. Multivariate effects of study site on habitat variables measured at bird survey stations on the Alakai plateau (α= 0.05).

Dependent Variable	Abbreviation	*df*	*F*	Sig.	Partial Eta Squared
Forest Profile 1-2m (%)	fp2	4	5.977	<.001	0.101
Shrub Cover- Total (%)	sct	4	7.292	<.001	0.121
Shrub Cover- Native (%)	scn	4	88.183	<.001	0.625
Canopy Height- Mean (m)	ht	4	11.9	<.001	0.183
Moss Cover- Average (%)	moss	4	16.282	<.001	0.235
Ground Cover- Total (%)	gct	4	5.014	0.001	0.086
Pig Sign (m^2)	pig	4	4.507	0.002	0.078
Canopy Density (%)	den	4	1.491	0.206	0.027
Ohia Diameter- Maximum (cm)	mdbh	4	0.951	0.436	0.018

LITERATURE CITED

Anderson, D.R. (2008). Model based inference in the life sciences: a primer on evidence. Springer, New York, USA.

Atkinson, C. T. and K. L. Woods (1995). Wildlife disease and conservation in Hawaii: Pathogenicity of avian malaria (*Plasmodium relictum*) in experimentally infected Iiwi (*Vestiaria coccinea*). Parasitology 111:S59-S69.

Atkinson, C. T. and M. D. Samuel (2010). Avian malaria *Plasmodium relictum* in native Hawaiian forest birds: epizootiology and demographic impacts on 'apapane (*Himatione sanguinea*). Journal of Avian Biology 41:357-366.

Atkinson, C. T., R. B. Utzurrum, D. A. Lapointe, R. J. Camp, L. H. Crampton, J. T. Foster and T. W. Giambelluca (2014). Changing climate and the altitudinal range of avian malaria in the Hawaiian Islands – an ongoing conservation crisis on the island of Kauai. Global Change Biology. doi: 10.1111/gcb.12535

Bailey, L.L., J.E. Hines, J.D. Nichols and D.I. MacKenzie (2007). Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. Ecological Applications 17:281-290.

Benning, T.L., D. LaPointe, C.T. Atkinson and P.M. Vitousek (2002). Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. Proceedings of the National Academy of Sciences of the United States of America. 99:14246-14249.

Boyer, A. G. (2010). Consistent ecological selectivity through time in Pacific island avian extinctions. Conservation Biology 24:511-519.

Brooke, M. D., G. M. Hilton (2007). Prioritizing the world's islands for vertebrate-eradication programmes. Animal Conservation 10:380-390.

Burnham, K.P. and D.R. Anderson (2002). Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, USA.

Camp, R.J. (2011). Standard operating procedure (SOP) #8, Documenting landbird habitat, Version 1.00. In Camp, R.J., T.K. Pratt, C. Bailey, and D. Hu. 2009. Landbirds vital sign monitoring protocol- Pacific island network. Natural resources report NPS/PWR/PACN/NRR. National Park Service, Oakland, CA.

Camp, R. J. and P.M. Gorreson (2010). Design of forest bird monitoring for strategic habitat conservation on Kauai Island, HI. U.S. Fish and Wildlife Service. Portland, Oregon, USA.

Department of Land and Natural Resources, State of Hawaii (2011). The rain follows the forest: a plan to replenish Hawaii’s source of water. http://dlnr.hawaii.gov/rain/files/2014/02/The-Rain-Follows-the-Forest.pdf

Eddinger, C. R. (1972). Discovery of the nest of the Kauai Akepa. Wilson Bulletin 84:95-97.

Foster, J. T., J. M. Scott and P. W. Sykes, Jr. (2000). Akikiki (*Oreomystis bairdi*), The Birds of North America Online (A. Poole, Editor). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.eres.library.manoa.hawaii.edu/bna/species/552

Foster, J. T., E. J. Tweed, R.J. Camp, B.L. Woodworth, C.D. Adler and T. Telfer (2004). Long-term population changes of native and introduced birds in the Alakai Swamp, Kaua'i. Conservation Biology 18:716-725.

Fretz, J. S. (2002). Scales of food availability for an endangered insectivore, the Hawaii Akepa. The Auk 119:166-174.

Giambelluca, T.W., Q. Chen, A.G. Frazier, J.P. Price, Y.L. Chen, P.-S. Chu, J.K. Eischeid, and D.M. Delparte (2013). Online Rainfall Atlas of Hawaii. Bulletin of The American Meteorological Society 94:313-316, doi: 10.1175/BAMS-D-11-00228.1.

Gorresen, P.M., R.J. Camp, M.H. Reynolds, B.L. Woodworth and T.K. Pratt (2009). Status and trends of native Hawaiian songbirds. In Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna (Pratt TK, Atkinson CT, Banko PC, Jacobi JD, Woodworth BL, Editors). Yale University, CT, USA.

Hammond, R.H. (2014). Factors affecting nesting success of forest birds on Kauai Island (Master’s thesis). Northern Arizona University, Flagstaff, AZ.

LaPointe, D.A., C.T. Atkinson and S.I. Jarvi (2009). Managing disease. In Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna (Pratt TK, Atkinson CT, Banko PC, Jacobi JD, Woodworth BL, Editors). Yale University, CT, USA.

Lepson, J.K. and H. D. Pratt (1997). Akekee (*Loxops caeruleirostris*), The Birds of North America Online (A. Poole, Editor). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu.eres.library.manoa.hawaii.edu/bna/species/295

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle and C. A. Langtimm (2002). Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

MacKenzie, D.I. and J.A. Royle. (2005) Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105-1114.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. P. Pollock, L. L. Bailey, and J. E. Hines (2006). Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, CA, USA.

Myers, N. (1993). Questions of mass extinction. Biodiversity and Conservation 2:2-17.

Olson, S. L. and H. F. James (1982). Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before Western contact. Science 217:633-635.

Perkins, R. C. L. (1903). Vertebrata. Pages 365-466 in Fauna Hawaiiensis. Vol. I, pt. IV (Sharp, D. Editor) Univ. Press, Cambridge, England.

Powell, A. (2008). Habitat use of the Akikiki *Oreomystis bairdi* (Aves; Drepanidinae): A Hawaiian forest bird in decline. M.Sc. thesis, University of East Anglia, Norwich, UK.

Pratt T.K., C.T. Atkinson, P.C. Banko, J.D. Jacobi, B.L. Woodworth (Editors) (2009). Conservation Biology of Hawaiian forest birds: Implications for island avifauna. Yale University, CT, USA.

Ralph, C. J. and S.G. Fancy (1994). Demography and movements of the endangered Akepa and Hawaii Creeper. The Wilson Bulletin 106:615-628.

Reed, J.M., D.W. Desrochers, E.A. VanderWerf and J. M. Scott (2012). Long-term persistence of Hawaii's endangered avifauna through conservation-reliant management. BioScience 62:881-892.

Richardson, F. and J.B. Bowles (1964). A survey of the birds of Kauai, Hawaii. Bernice P. Bishop Museum Bulletin 227:1-51.

Robel, R. J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management, 23:295-297.

Scott, J. M., S. Mountainspring, F. L. Ramsey, and C. B. Kepler (1986). Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Studies in Avian Biology 9:1-431.

Scott J.M, S. Conant and C. Van Riper III (Editors) (2001). Evolution, Ecology, and Management of Hawaiian Birds: A Vanishing Avifauna. Cooper Ornithological Society. Studies in Avian Biology 22.

Simberloff, D., and B. Von Holle (1999). Positive interactions of nonindigenous species: invasional meltdown? Biological invasions 1:21-32.

US Geological Survey, Gap Analysis Program (GAP). May 2011. National Land Cover, Version 2.0

VanderWerf, E.A., J.J. Groombridge, J.S. Fretz, K.J. Swinnerton (2006). Decision analysis to guide recovery of the poouli, a critically endangered Hawaiian honeycreeper. Biological Conservation 129:383-392.

VanderWerf, E. A., and American Bird Conservancy (2007). Petition to list the Akikiki or Kauai Creeper (O*reomystis bairdi*) and the Akekee or Kauai Akepa (*Loxops caeruleirostris*) as endangered or threatened under the U.S. Endangered Species Act. Submitted to the U.S. Fish and Wildlife Service, October 2007. 18 pp.

VanderWerf, E. A. and P. K. Roberts (2008). Foraging and nesting of the Akikiki or Kauai Creeper (*Oreomystis bairdi*). Wilson Journal of Ornithology 120:195-199.

VanderWerf, E. A. (2009). Importance of nest predation by alien rodents and avian poxvirus in conservation of Oahu Elepaio. Journal of Wildlife Management 73:737-746.

APPENDICES

Appendix A. Complete model results of habitat use analysis for Akikiki occupancy (ψ) as predicted by habitat characteristics in the East Alakai (EAK) study region. See Table 1 for column header definitions. See Table 3 for definition of model parameters.

Model	K	-2*Log$L$	ΔAIC$_c$	w_i	Model Likelihood
psi(fp2+ht),*p*(g)	5	208.04	0.00	0.22	1.00
psi(global),*p*(g)	11	194.79	0.24	0.19	0.89
psi(sct+den+ht),*p*(g)	6	206.49	0.62	0.16	0.73
psi(den+ht),*p*(g)	5	209.46	1.42	0.11	0.49
psi(den+ht+pig),*p*(g)	6	208.55	2.68	0.06	0.26
psi(gct+sct+den),*p*(g)	6	208.60	2.73	0.06	0.26
psi(ht),*p*(g)	4	213.54	3.36	0.04	0.19
psi(gct+ht),*p*(g)	5	211.44	3.40	0.04	0.18
psi(ht+pig),*p*(g)	5	211.63	3.59	0.04	0.17
psi(ht+moss),*p*(g)	5	213.15	5.11	0.02	0.08
psi(ht+mdbh),*p*(g)	5	213.18	5.14	0.02	0.08
psi(sct+ht),*p*(g)	5	213.25	5.21	0.02	0.07
psi(ht+pig+mdbh),*p*(g)	6	211.28	5.41	0.01	0.07
psi(sct+pig),*p*(g)	5	214.83	6.79	0.01	0.03
psi(sct+den),*p*(g)	5	215.56	7.52	0.01	0.02
psi(fp2+sct),*p*(g)	5	217.81	9.77	0.00	0.01
psi(sct),*p*(g)	4	220.37	10.19	0.00	0.01
psi(gct+pig),*p*(g)	5	218.31	10.27	0.00	0.01
psi(den+pig),*p*(g)	5	218.43	10.39	0.00	0.01
psi(den),*p*(g)	4	220.90	10.72	0.00	0.00
psi(pig),*p*(g)	4	221.65	11.47	0.00	0.00
psi(gct+sct),*p*(g)	5	219.65	11.61	0.00	0.00
psi(sct+moss),*p*(g)	5	219.72	11.68	0.00	0.00
psi(fp2+gct+sct),*p*(g)	6	217.57	11.70	0.00	0.00
psi(sct+mdbh),*p*(g)	5	219.77	11.73	0.00	0.00
psi(gct+den),*p*(g)	5	220.38	12.34	0.00	0.00
psi(fp2+den),*p*(g)	5	220.61	12.57	0.00	0.00
psi(den+moss),*p*(g)	5	220.90	12.86	0.00	0.00
psi(den+mdbh),*p*(g)	5	220.90	12.86	0.00	0.00

psi(fp2+pig),*p*(g)	5	221.39	13.35	0.00	0.00
psi(fp2),*p*(g)	4	223.60	13.42	0.00	0.00
psi(pig+moss),*p*(g)	5	221.65	13.61	0.00	0.00
psi(pig+mdbh),*p*(g)	5	221.65	13.61	0.00	0.00
psi(.),*p*(.)	2	228.65	14.27	0.00	0.00
psi(gct),*p*(g)	4	224.55	14.37	0.00	0.00
psi(mdbh),*p*(g)	4	224.80	14.62	0.00	0.00
psi(moss),*p*(g)	4	224.80	14.62	0.00	0.00
psi(fp2+gct),*p*(g)	5	222.77	14.73	0.00	0.00
psi(fp2+moss),*p*(g)	5	223.60	15.56	0.00	0.00
psi(fp2+mdbh),*p*(g)	5	223.60	15.56	0.00	0.00
psi(pig+mdbh+moss),*p*(g)	6	221.64	15.77	0.00	0.00
psi(mdbh+moss),*p*(g)	5	224.40	16.36	0.00	0.00
psi(gct+mdbh),*p*(g)	5	224.54	16.50	0.00	0.00
psi(gct+moss),*p*(g)	5	224.54	16.50	0.00	0.00
psi(moss+fp2+gct),*p*(g)	6	222.65	16.78	0.00	0.00
psi(mdbh+moss+fp2),*p*(g)	6	223.41	17.54	0.00	0.00

Appendix B. Complete model results of habitat use analysis for Akekee occupancy (ψ) as predicted by habitat characteristics in the East Alakai (EAK) study region. See Table 1 for column header definitions. See Table 3 for definition of model parameters.

Model	*K*	-2*Log*L*	ΔAIC_c	w_i	Model Likelihood
psi(ht+mdbh),*p*(g+month)	9	278.60	0.00	0.26	1.00
psi(ht+pig+mdbh),*p*(g+month)	10	277.80	1.49	0.12	0.47
psi(mdbh),*p*(g+month)	8	283.41	2.54	0.07	0.28
psi(ht+moss),*p*(g+month)	9	281.24	2.64	0.07	0.27
psi(pig+mdbh),*p*(g+month)	9	281.89	3.29	0.05	0.19
psi(mdbh+gct),*p*(g+month)	9	282.13	3.53	0.04	0.17
psi(gct+mdbh),*p*(g+month)	9	282.13	3.53	0.04	0.17
psi(ht),*p*(g+month)	8	284.79	3.92	0.04	0.14
psi(sct+mdbh),*p*(g+month)	9	283.13	4.53	0.03	0.10
psi(den+mdbh),*p*(g+month)	9	283.16	4.56	0.03	0.10
psi(fp2+mdbh),*p*(g+month)	9	283.40	4.80	0.02	0.09
psi(pig+mdbh+moss),*p*(g+month)	10	281.28	4.97	0.02	0.08
psi(gct+ht),*p*(g+month)	9	283.64	5.04	0.02	0.08
psi(den+ht),*p*(g+month)	9	284.04	5.44	0.02	0.07

psi(moss),*p*(g+month)	8	286.63	5.76	0.01	0.06
psi(ht+pig),*p*(g+month)	9	284.40	5.80	0.01	0.06
psi(sct+ht),*p*(g+month)	9	284.74	6.14	0.01	0.05
psi(fp2+ht),*p*(g+month)	9	284.75	6.15	0.01	0.05
psi(.),*p*(g+month)	7	289.69	6.59	0.01	0.04
psi(mdbh+moss+fp2),*p*(g+month)	10	283.14	6.83	0.01	0.03
psi(pig+moss),*p*(g+month)	9	285.51	6.91	0.01	0.03
psi(den+ht+pig),*p*(g+month)	10	283.30	6.99	0.01	0.03
psi(gct+moss),*p*(g+month)	9	285.73	7.13	0.01	0.03
psi(sct+den+ht),*p*(g+month)	10	283.88	7.57	0.01	0.02
psi(den+moss),*p*(g+month)	9	286.26	7.66	0.01	0.02
psi(gct),*p*(g+month)	8	288.59	7.72	0.01	0.02
psi(sct+moss),*p*(g+month)	9	286.38	7.78	0.01	0.02
psi(pig),*p*(g+month)	8	288.65	7.78	0.01	0.02
psi(fp2+moss),*p*(g+month)	9	286.61	8.01	0.00	0.02
psi(sct),*p*(g+month)	8	289.41	8.54	0.00	0.01
psi(den),*p*(g+month)	8	289.50	8.63	0.00	0.01
psi(gct+pig),*p*(g+month)	9	287.33	8.73	0.00	0.01
psi(fp2),*p*(g+month)	8	289.65	8.78	0.00	0.01
psi(moss+fp2+gct),*p*(g+month)	10	285.71	9.40	0.00	0.01
psi(den+pig),*p*(g+month)	9	288.13	9.53	0.00	0.01
psi(gct+den),*p*(g+month)	9	288.30	9.70	0.00	0.01
psi(fp2+pig),*p*(g+month)	9	288.31	9.71	0.00	0.01
psi(sct+pig),*p*(g+month)	9	288.49	9.89	0.00	0.01
psi(gct+sct),*p*(g+month)	9	288.54	9.94	0.00	0.01
psi(fp2+gct),*p*(g+month)	9	288.56	9.96	0.00	0.01
psi(global),*p*(g+month)	15	274.29	9.98	0.00	0.01
psi(sct+den),*p*(g+month)	9	289.09	10.49	0.00	0.01
psi(fp2+sct),*p*(g+month)	9	289.40	10.80	0.00	0.00
psi(fp2+den),*p*(g+month)	9	289.48	10.88	0.00	0.00
psi(gct+sct+den),*p*(g+month)	10	288.16	11.85	0.00	0.00
psi(fp2+gct+sct),*p*(g+month)	10	288.52	12.21	0.00	0.00

Appendix C. Model-averaged β estimates ± SE for models relating occupancy with habitat characteristics in the EAK study region. Model averaging was conducted on all models with a weight of >.01.

Species	Variable	β ± SE
Akikiki	Psi Intercept	-4883 ± 11.3
	Height (ht)	479.6 ± 0.71
	Canopy Density (den)	32.7 ± 7.9
	Forest Profile 1-2m (fp2)	9.4 ± 4.5
	Total Shrub Cover (sct)	-9.1 ± 5.2
	Pig Sign (pig)	9.0 ± 2
	Total Ground Cover (gct)	-3.3 ± 0.07
	Max Diameter At Breast Height (mdbh)	1.1 ± 0.001
	Moss Cover (moss)	-1.01 ± 0.001
Akekee	Psi Intercept	-1.725 ± 0.783
	Height (ht)	0.142 ± 0.074
	Max Diameter At Breast Height (mdbh)	0.019 ± 0.012
	Pig Sign (pig)	-0.006 ± 0.006
	Ground Cover Total (gct)	0.001 ± 0.0006
	Canopy Density (den)	-0.0007 ± 0.0004
	Moss Cover (moss)	-0.0002 ± 0.0003
	Total Shrub Cover (sct)	-0.0002 ± 0.0003
	Forest Profile 1-2m (fp2)	0.00002 ± 0.0003