THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 118, 2016, pp. 148–158
DOI: 10.1650/CONDOR-15-80.1

RESEARCH ARTICLE

Occupancy and habitat use of the endangered Akikiki and Akekee on Kauai Island, Hawaii

Lucas A. H. Behnke,[1,2,a]* Liba Pejchar,[1] and Lisa H. Crampton[2]

[1] Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA
[2] Department of Land and Natural Resources, Kauai Forest Bird Recovery Project, State of Hawaii, Hanapepe, Hawaii, USA
[a] Current address: The Nature Conservancy, Hawaii Program, Lihue, Hawaii, USA
* Corresponding author: lbehnke@tnc.org

Submitted May 11, 2015; Accepted October 1, 2015; Published December 10, 2015

ABSTRACT

Limited resources for biodiversity conservation demand strategic science-based recovery efforts, particularly on islands, which are global hotspots of both endemism and extinction. 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 investigation of the habitat characteristics influencing range-wide occupancy of these species. We surveyed Akikiki and Akekee and habitat covariates within 5 study areas on the Alakai Plateau of Kauai along a gradient of forest conditions. 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 positively correlated with occupancy for both species, which suggests the damage done by hurricanes in 1982 and 1992 may be one factor 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 gardnerianum*) 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 areas. These results highlight the need to protect habitat in the regions where Akikiki and Akekee occupancy is highest, and restore habitat in other parts of their range. These actions should occur in concert with the mitigation of other known threats to Hawaiian honeycreepers such as avian disease. Without significant investment to address these threats and protect suitable habitat for these species, it is unclear how long these birds will persist.

Keywords: Hawaiian forest birds, invasive species, *Loxops caeruleirostris*, *Oreomystis bairdi*, range contraction, habitat degradation, endangered species, feral ungulates

Ocupación y uso de hábitat de las especies amenazadas *Oreomystis bairdi* y *Loxops caeruleirostris* en la isla Kauai, Hawaii

RESUMEN

Los limitados recursos para la conservación de la biodiversidad demandan esfuerzos estratégicos basados en ciencia, particularmente en islas que son puntos calientes de endemismo y extinción. *Oreomystis bairdi* y *Loxops caeruleirostris* son especies críticamente amenazadas de la isla hawaiana de Kauai. Los declives poblacionales recientes y la contracción de su distribución geográfica estimuló la investigación sobre las características del hábitat que influyen en la ocupación del área de distribución de estas especies. Estudiamos a *O. bairdi* y *L. caeruleirostris* y las covariables de su hábitat en cinco áreas de estudio en la meseta Alakai de Kauiai a lo largo de un gradiente de condiciones de bosque. Las tasas de ocupación para ambas especies se incrementaron de occidente a oriente a lo largo de la meseta (*O. bairdi* $\psi = 0.02 \pm 0.07$ to 0.55 ± 0.21; *L. caeruleirostris*: $\psi = 0.03 \pm 0.10$ to 0.53 ± 0.33), pero fueron bajas a través de sus distribuciones. La altura del dosel se correlacionó positivamente con la ocupación en ambas especies, lo que sugiere que el daño causado por huracanes en 1982 y 1992 podría ser un factor que restringe a estas aves a los remanentes de bosque más intactos. Los censos de vegetación revelaron varias diferencias clave en la composición de los bosques y la estructura entre áreas, lo que indica que ocurren cambios más amplios en la meseta. Las plantas invasoras como *Hedychium gardnerianium* fueron dominantes en la porción occidental de la isla, mientras que hubo un declive correspondiente en la cobertura de plantas nativas. Por el contrario, el disturbio en el suelo causado por ungulados asilvestrados fue mayor en áreas dominadas por plantas nativas hacia el oriente. Estos resultados resaltan la necesidad de proteger el hábitat en las regiones donde la ocupación de *O. bairdi* y *L. caeruleirostris* es más alta, y de restaurar el hábitat en otras partes de su distribución. Estas acciones deben ocurrir en concierto con la mitigación de otras amenazas conocidas contra los mieleros hawaianos, como las enfermedades. Sin una inversión significativa para enfrentar estas amenazas y proteger el hábitat idóneo para estas especies, no es claro por cuánto tiempo puedan persistir.

Palabras clave: aves de bosque hawaianas, contracción de la distribución, degradación de hábitat, especies amenazadas, especies invasoras, *Loxops caeruleirostris*, *Oreomystis bairdi*, ungulados asilvestrados

INTRODUCTION

The loss of Hawaii's endemic birds is well documented (Perkins 1903, Olson and James 1982, Gorresen et al. 2009); since the arrival of humans, 68% of Hawaii's 109 endemic bird species have gone extinct (Scott et al. 2001, Reed et al. 2012). Of the remaining species, 33 are listed as federally endangered, and several of these are likely already extinct (Elphick et al. 2010, USFWS 2015). 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 nonnative mammals, and introduced diseases such as avian malaria (Scott et al. 1986, 2001, Pratt et al. 2009, VanderWerf 2009). These well-known causes of decline, combined with climate change and stochastic events such as hurricanes, threaten the persistence of Hawaii's endemic forest birds (Benning et al. 2002). These threats are particularly acute on relatively low-elevation islands such as Kauai where all native forest is exposed to at least seasonal transmission of avian disease (Atkinson et al. 2014).

Six extant forest bird species are endemic to Kauai, including 2 honeycreepers recently listed as federally endangered under the U.S. Endangered Species Act. The 2010 listing of the Akekee or Kauai Akepa (*Loxops caeruleirostris*; Figure 1A) and Akikiki or Kauai Creeper (*Oreomystis bairdi*; Figure 1B), previously a candidate species for over a decade, was prompted by declines in abundance and apparent 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 area with relatively intact native montane forest that comprises the summit of the island (Foster et al. 2004; Figure 1C). Akikiki feed primarily on arthropods by gleaning and flaking bark along the boles and branches of live and dead canopy and understory trees (Foster et al. 2000), and Akekee forage primarily in the canopy of ohia (*Metrosideros polymorpha*) by using their slightly crossed bill to pry open terminal leaf nodes to extract invertebrates including spiders, psyllids, and caterpillars (Lepson and Pratt 1997). These 2 distinct foraging strategies may lead to different patterns of habitat use across their current range. Understanding these patterns in light of current and past disturbance events (e.g., hurricane damage and invasive species; Figure 1D) is important, particularly because management interventions to improve habitat quality may be more feasible than mitigating disease in this system in the near term.

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. Although there are no quantitative data on the habitat requirements, key threats, or potential conservation measures for these 2 species, research on other Hawaiian endemic birds has illuminated many of the causal mechanisms of decline (Pratt et al. 2009). Understanding the factors influencing habitat use (e.g., proportion of native and introduced vegetation, predation, and disease) is urgently needed to implement meaningful conservation action. Acquiring this information before these birds become too scarce for recovery is critical, as illustrated by the recent extinction of the Poouli (*Melamprosops phaeosoma*) on another Hawaiian Island (VanderWerf et al. 2006).

The primary objective of this study was to determine spatial patterns of occupancy and predictors of habitat use of Akikiki and Akekee across their known range on the Alakai Plateau, as defined by Foster et al. (2004) and Camp and Gorresen (2010). 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). This approach allows biologists to assess population dynamics across a large spatial scale with multiple species of concern (Bailey et al. 2007). We estimated and compared probability of occupancy at 5 sites across the range of Akikiki and Akekee to assess spatial trends, which could be correlated with changes in habitat and/or disease prevalence. At the sites where occupancy was high enough to do so, we coupled these data with vegetation surveys and measures of habitat disturbance by nonnative ungulates to provide insight into predictors of current habitat use. Our second objective was to examine potential differences in structure and composition across the Alakai Plateau to provide additional insight into avian species distribution patterns in this last remaining contiguous native forest on Kauai (USGS 2011). Finally, we build on our results to recommend research and management priorities for these species.

METHODS

Study Area

This study was conducted in the Alakai Wilderness Preserve, Kokee State Park, and Na Pali Kona Forest

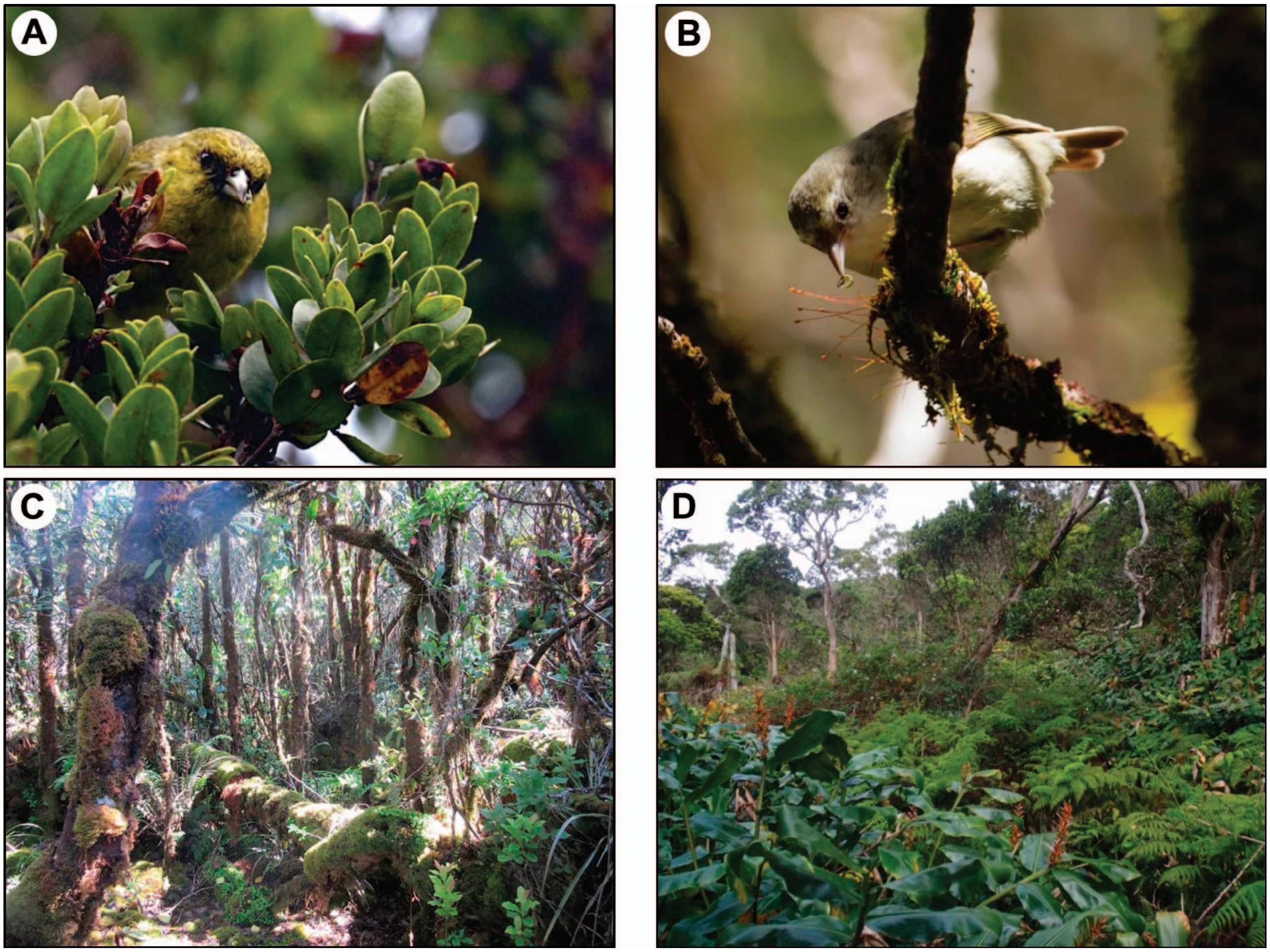

FIGURE 1. Photographs of the study species and contrasting habitat conditions, Kauai, Hawaii. **(A)** Akekee (*Loxops caeruleirostris*), photo by Lucas Behnke. **(B)** Akikiki (*Oreomystis bairdi*), photo by Robby Kohley. **(C)** Relatively intact native forest with high mean canopy cover typical of EAK. Photo by Maria Costantini. **(D)** Degraded forest with invasive ginger and blackberry typical of KWK. Photo by Ruby Hammond.

Reserve on the Alakai Plateau of Kauai Island, Hawaii (22°05′N 159°30′W; Figure 2). 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 plateau transitions from wet montane forest dominated by ohia in the east, receiving ∼900 cm of rain per year, to the relatively mesic mixed ohia–koa (*Acacia koa*) in the west with rainfall of 190 cm per year (Giambelluca et al. 2013).

Sampling Design

We measured occupancy of Akikiki and Akekee from March to July 2012, and described habitat characteristics at 5 sites in 3 study regions (Figure 2). We chose study regions based on recent estimates of the density and 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), had medium to high densities of both Akikiki and Akekee according to recent quantitative data (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 3 regions are dominated by native ohia canopy and a diverse understory of native shrubs and ferns, with varying cover of nonnative plants (Figure 1).

Within each study region, we randomly located 2 non-overlapping 100-ha polygons for our study sites using ESRI ArcGIS (Version 10.1; ESRI, Redlands, California, USA) 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).

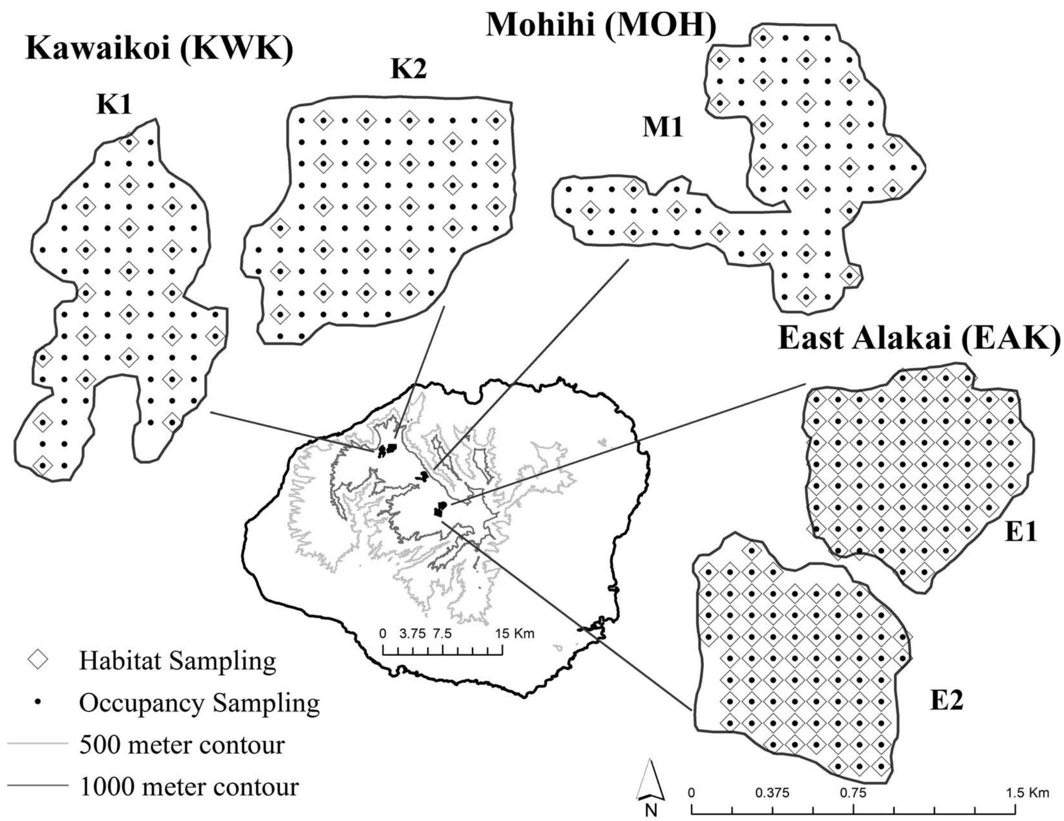

FIGURE 2. Location and distribution of sampling points across 3 study regions (KWK, MOH, EAK) containing the 5 study sites Kawaikoi West (K1), Kawaikoi East (K2), Mohihi (M1), Halehaha (H1), and Halepaakai (H2) on the Alakai plateau on Island of Kauai (Hawaii, USA) where occupancy and habitat surveys were conducted for Akikiki and Akekee.

Due to logistical and topographic constraints, the original 2 study sites at MOH were merged into one (M1), resulting in a total of 5 study sites across the 3 study regions (Figure 2). During a pilot study in 2011, we 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 we found >10 territories or covered 75–100 ha; the amount of area covered in 2011 determined the size of the occupancy study sites in 2012. Within each of the 5 study sites we established a systematic grid of sampling points based on a new random starting location (Figure 2). At each point we conducted occupancy surveys and measured habitat variables.

Occupancy Surveys

Following the sampling guidelines in MacKenzie et al. (2002) and Bailey et al. (2007), we quantified occupancy of Akikiki and Akekee in each study site by conducting repeated surveys at sampling points in each of the 5 study sites ($n = 70$–96). Points were spaced 100 m apart, which slightly exceeded the farthest known distance traveled by a color-banded Akikiki during regular resighting efforts from 2007 to 2010 (Hawaii Division of Forestry and Wildlife personal communication). The placement of our sampling grids intercepted several point–line transects used for long-term population monitoring across the Alakai Plateau, which facilitated comparison of our results to previously collected data (Foster et al. 2004; Camp and Gorresen 2010).

Following MacKenzie and Royle (2005), we surveyed occupancy at each point at least 3 times during the breeding season. At each point, we separated the survey into 2 periods. In the first, we passively surveyed and recorded presence/absence of all bird species for 4 min. In the second period, we recorded only presence or absence of Akikiki and Akekee for an additional 4 min, during which we intermittently broadcasted short (5–10 sec) call or song segments of each species, alternating between species, for a total of ~1 min per species. Detections were so sparse that we pooled both time periods in our analyses. To model detection probability (p), we 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 our 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 our 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

We collected data on habitat characteristics at every other bird survey point at the 3 low-occupancy sites and at every point at the 2 high-occupancy sites ($n = 223$; Figure 2). This sampling design was selected to evaluate the influence of vegetation structure and composition on habitat use by the focal species at the sites where the species were most abundant. Circular vegetation plots measuring 100 m^2 were centered on the sampling points (Camp 2011). At each plot, we measured vegetation variables within 25 m^2 quadrants systematically placed at 4 locations at the edge of the plot in each cardinal direction.

We collected data on ground, shrub, and canopy structure and composition, and feral pig (*Sus scrofa*) disturbance within each vegetation plot. We 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). We estimated total % shrub cover (sct) 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. We estimated total % ground cover (gct) and proportion of native ground cover (gcn) inside a 1 m^2 quadrat on the counterclockwise side of the edge of the plot in each cardinal point. We estimated canopy density (den) at each cardinal point using a spherical densiometer. We estimated canopy height (ht) using an electronic range finder and clinometer. To summarize variables for each plot, we used the mean of measurements taken from each cardinal point (fp1, fp2, ht, den), the mean percent cover from the 4 quadrants (sct, scn), and the mean percent ground cover within the 4 quadrats (gct, gcn). We 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. We also measured the total area (m^2) of relatively recent pig sign (pig) in each plot by summing the area covered by scat, digging, or trails that appeared to be less than 3 months old.

Statistical Analysis

We used Program PRESENCE (Hines 2006) to (1) estimate and compare occupancy (ψ) of the 2 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, we used Akaike's Information Criterion adjusted for small sample size (AIC_c), a likelihood-based information theoretic approach to model selection (Anderson 2008). First we assessed detection probability by constructing models of all combinations of sampling covariates. We 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, we 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, we examined habitat use of each species 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 3 covariates to limit the number of parameters, with the exception of one global (all covariates) model for comparison. Because we were most interested in the relative importance of habitat covariates, we model-averaged parameter estimates (Burnham and Anderson 2002) to reduce bias and account for model selection uncertainty (Doherty et al. 2012). The predictions we examined, based on each species' biology, were that (1) for Akikiki, a subcanopy trunk-and-bole gleaner, occupancy is best predicted by an open understory, tall canopy stature,

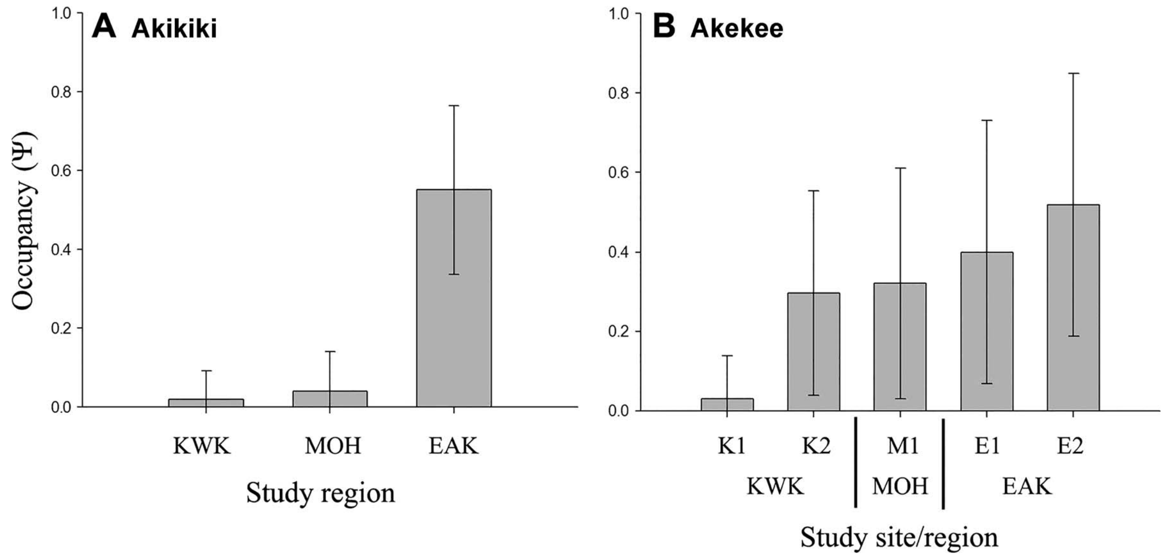

FIGURE 3. Occupancy estimates for Akikiki by study region **(A)** and for Akekee by study site **(B)**. Figures report means ± 95% CI.

and large tree diameter; and (2) Akekee occupancy is best predicted by high canopy cover.

To gain insights into bird distribution where occupancy was too sparse to model against habitat predictors, we 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, we 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 in our study area. We also predicted that disturbance metrics (e.g., invasive plant cover and feral pig disturbance) would decrease from west to east, and be undetectable in the EAK study region. We 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. We 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; IBM, Armonk, New York, USA). Figures and results are presented as untransformed or back-transformed means ± SE.

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 ($-2*\text{Log}L$), 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	$-2*\text{Log}L$	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

RESULTS

Detection Probability and Occupancy across the Study Area

Detection probability was low for both species (Akikiki $p = 0.63 \pm 0.40$; Akekee $p = 0.30 \pm 0.19$). 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. As predicted, we found an increasing trend in estimates of occupancy (ψ) for each species from west to east (Figure 3). 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 substantially greater in the eastern EAK region (ψ: 0.55 ± 0.21) compared with the other 2 regions (KWK ψ: 0.02 ± 0.07 and MOH ψ: 0.04 ± 0.10; Figure 3A). Akekee occupancy increased gradually from west to east across study sites, and only differed substantially between K1 and H2 sites ($\psi = 0.03 \pm 0.10$ and $\psi = 0.53 \pm 0.33$, respectively; Figure 3B).

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

Occupancy of both species varied as a function of tree size within EAK. Akekee and Akikiki occupancy were positively correlated with mean canopy height (Figure 4A,B; Akikiki: $\beta = 479.6 \pm 0.71$, Akekee $\beta = 0.142 \pm 0.074$). Akikiki were

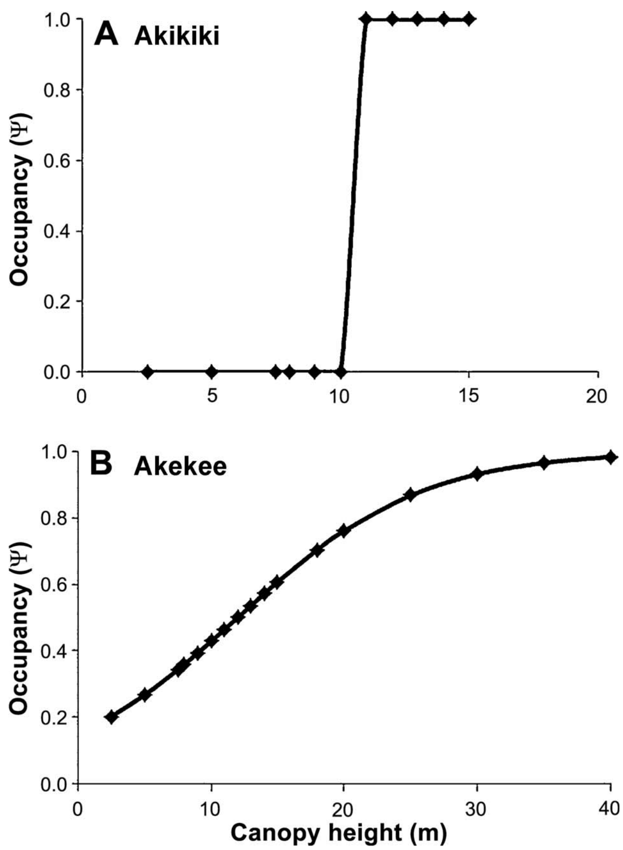

FIGURE 4. Relationship between occupancy (ψ) and model-averaged mean canopy height (ht) for Akikiki **(A)** and Akekee **(B)** in the East Alakai (EAK) study region.

absent from survey points where mean canopy height was 10 m or less (Figure 4A). Mean canopy height was present in 9 of the top 10 models for Akikiki and 3 of the top 4 models for Akekee (Table 2). Maximum diameter at breast height of ohia also was positively correlated with occupancy and was present in 8 of the top 10 candidate models for Akekee ($\beta = 0.019 \pm 0.012$), while canopy density was positively associated with Akikiki occupancy ($\beta = 32.7 \pm 7.9$) and was present in several top models (Table 2).

TABLE 2. Model results for Akikiki and Akekee occupancy (ψ) as predicted by habitat characteristics in the East Alakai (EAK) study region. Models with $\Delta AIC_c > 4$ 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	$-2*\mathrm{Log}L$	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

Comparing Habitat Characteristics among Study Sites

In the MANOVA, habitat characteristics differed significantly across the 5 study sites (Pillai's Trace 1.18, $F = 3188.72$, df = 9, $\alpha = 0.05$). Tests of the between-subjects effects showed significant differences ($\alpha = 0.05$) between 7 of the 9 variables sampled (Table 3). Forest profile, total shrub cover (Figure 5A), native shrub cover (Figure 5B), mean canopy height (Figure 5C), and moss cover all showed significant differences between at least 2 of the sites ($p = <0.001$); total ground cover, and pig sign (Figure 5D) also differed significantly among sites ($p = 0.001$ and $p = 0.002$, respectively). Maximum ohia diameter and canopy density did not differ significantly among sites. The westernmost study site (K1) differed from the other study sites for most structural variables, and contributed to the overall difference between regions.

TABLE 3. MANOVA results showing multivariate effects of study site on habitat variables measured at bird survey stations on the Alakai plateau ($\alpha = 0.05$).

Dependent variable	Abbreviation	Df	F	Sig.	Partial eta squared
Forest profile 1–2 m (%)	fp2	4	5.977	<0.001	0.101
Shrub cover: total (%)	sct	4	7.292	<0.001	0.121
Shrub cover: native (%)	scn	4	88.18	<0.001	0.625
Canopy height: mean (m)	ht	4	11.9	<0.001	0.183
Moss cover: average (%)	moss	4	16.28	<0.001	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

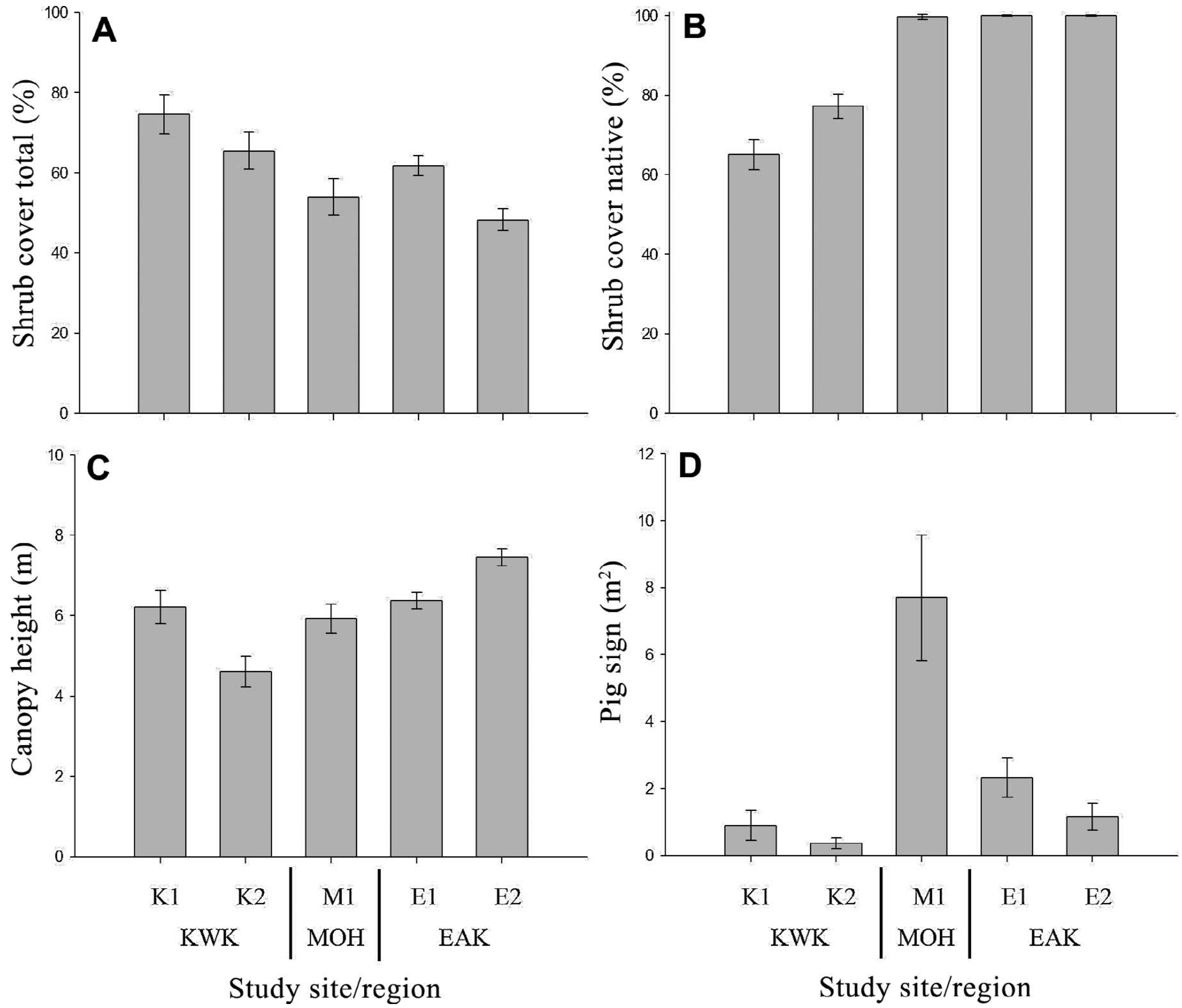

FIGURE 5. The habitat characteristics "shrub cover" **(A, B)**, "canopy height" **(C)**, and "pig sign" **(D)** vary across study sites from west to east on the Alakai plateau. Figures report means ± 95% CI.

DISCUSSION

Akikiki and Akekee, both single-island endemics, have nearly disappeared from their last remaining habitat. Our results demonstrate that occupancy rates within this narrow range are extremely low for both species, even when compared to another endangered Kauai passerine, the Puaiohi (*Myadestes palmeri*), across a similar range (L. H. Crampton personal observation), and other federally listed species in the U.S. (e.g., Golden-cheeked Warbler, *Setophaga chrysoparia*; Reidy et al. 2015). As predicted and corroborated by spatial patterns of bird density, there is a slight increase toward the eastern end of the Alakai Plateau (Foster et al. 2004, Camp and Gorresen 2010). Even compared to surveys published only 11 (Foster et al. 2004) and 5 (Camp and Gorresen 2010) years ago, our results indicate that the range of these species continues to contract. Where Akikiki and Akekee were still present, we 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 appeared to be associated with intermediate occupancy. These range-wide patterns suggest that controlling invasive plants and restoring native plant cover, fencing remaining habitat, and eradicating or reducing the density of feral pigs in this region is critical to the survival of these Hawaiian honeycreepers. Even with significant protection from other threats, avian disease is likely to increasingly limit forest bird range and populations on Kauai (Atkinson et al. 2014); thus other conservation measures, such as mosquito control, captive breeding, and translocation outside of their historical range, should be considered.

The difference between Akikiki occupancy in the central and western regions (KWK, MOH) and the eastern region (EAK) was large and abrupt (Figure 3A). In contrast, Akekee occupancy declined gradually from east to west (Figure 3B). Although these trends are based on only one year of data, which limits our inference, these findings are consistent with the results of long-term bird surveys (Foster et al. 2004). The dissimilar pattern of occupancy among Akikiki and Akekee could be a result of different resource requirements and foraging behavior. For example, as canopy foragers, Akekee can cover large distances more readily than Akikiki in order to access available canopy resources. The cumulative effect of changes in forest structure, spread of nonnative vegetation, disturbance by feral pigs, and the slow recovery of the native forest following Hurricanes Iwa (1982) and Iniki (1992), are other factors that may shape the distribution of both species across the plateau. Additional research on potentially important drivers of survival and reproductive success—such as nest predation by introduced rats, which caused some Akikiki nest failure (Hammond et al. 2015), and avian malaria, which is increasing across this east–west gradient (Atkinson et al. 2014)—is critical to developing a comprehensive strategy for the conservation and recovery of these species.

The relationship between occupancy and habitat characteristics at EAK may provide 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 provides 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 result may indicate that Akikiki prefer mature forest, possibly because of greater availability of food resources, and may explain the near absence of these species from KWK and MOH, where mean canopy height is well below the threshold 10-m canopy height that predicts occupancy at EAK (Figure 4A). The lack of a significant difference between EAK and KWK in other factors apparently important to Akikiki occupancy, such as maximum ohia diameter (mdbh) and canopy cover (den), may indicate that disease transmission also may limit Akikiki occupancy in KWK; malaria prevalence is greater at KWK than EAK (Atkinson et al. 2014). The positive relationship between Akekee occupancy and canopy height and maximum ohia diameter (mdbh) indicates that this species, a canopy-foraging "crossbill" (Lepson and Pratt 1997), may preferentially use habitat with large trees. This observation is consistent with our prediction that Akekee occupancy would be related to canopy density, and 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 in these predictor variables among vegetation plots in the EAK study area. While there was no detectable effect on occupancy within regions, these factors may be important determinants of occupancy among regions, but could not be examined directly because so few birds were detected at regions other than EAK. 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 2 species, especially Akikiki, was lowest. We also found moderate levels of pig sign in the easternmost region (EAK), which we had predicted to contain the most intact native forest, and where we documented the highest occupancy of Akikiki and Akekee.

Management in the MOH and EAK regions, 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 nonnative plant species in Hawaii (Simberloff and Van Holle 1999) and which may create habitat for larval mosquitoes, 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

To build on these findings, we recommend consistent population-level monitoring to detect trends over time, and research to investigate other factors that may synergistically contribute to the decline of these species. Our results suggest that occupancy may provide a useful conservation metric for these and other rare species. 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 Gorresen 2010). By estimating detection probability, we also provided a quantitative measure of the difficulty of detecting these species that could help guide future survey efforts (MacKenzie et al. 2002).

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, we recommend continued investigation of management techniques such as ungulate fencing, invasive plant and rat removal, and attempting mosquito control to limit disease transmission, to evaluate the relative importance of these factors for population dynamics and habitat use. Both the continued control of invasive plants and the removal of feral ungulates from these areas are likely to increase the resiliency of the Alakai Plateau's forests, possibly providing time for the birds themselves to adapt to avian disease (Kilpatrick 2006). For example, the implementation of current plans to fence and remove ungulates from ~3,000 acres surrounding the study region with the highest bird densities (Hawaii Department of Land and Natural Resources 2011) will be critical for halting the degradation of the last strongholds of the Akikiki and Akekee.

Given the low occupancy and increasingly narrow range of these 2 species, we emphasize that immediate conservation action based on the best available science is essential. There is, however, a significant lag time in the recovery of the habitats that support these species. Additionally, 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, Atkinson et al. 2014) and by further limiting availability of food and suitable foraging and nesting habitat. If disease or nonnative predators are the most important threats to these species, habitat management alone will not be sufficient to prevent their extinction on Kauai. In response to this threat, eggs of both species were collected and a captive breeding program was initiated in 2015 (L. H. Crampton personal observation). If the synergistic effects of climate change, disease, and other factors make Kauai uninhabitable, the only option for sustaining Akikiki and Akekee in the wild will be to establish new populations in suitable habitat outside their known historic range where disease and predators are minimal or absent.

ACKNOWLEDGMENTS

P. K. Roberts was instrumental in initially guiding and grant writing for this work. The research would not have been possible without the dedicated full-time and seasonal field staff of the Kauai Forest Bird Recovery Project, including B. Heindl, R. Hammond, L. Solomon, A. Wang, B. Williams, M. Walters, and Americorps interns C. Hagen, J. Liebrecht, and N. Ozaki, as well as volunteer data entry assistance by K. Maling. We are especially grateful for statistical advice from L. Bailey, and for comments that improved earlier drafts of this manuscript from J. Vetter, D. Leonard, R. Camp, and 2 anonymous reviewers.

Funding statement: We thank the U.S. Fish and Wildlife Service Pacific Islands Fish and Wildlife Office, the State of Hawaii Division of Forestry and Wildlife, and the Warner College of Natural Resources at Colorado State University for generously funding this research. None of our funders had any influence on the content of the submitted or published manuscript nor did they require approval of the final manuscript to be published.

Ethics statement: All research was conducted following an IACUC protocol submitted through Colorado State University (Protocol ID: 10-2395A) and followed applicable federal and state regulations and permitting procedures.

Author contributions: L.A.H.B., L.P., and L.H.C. conceived the idea and design. L.A.H.B. collected the data. L.A.H.B., L.P., and L.H.C. wrote the paper. L.A.H.B. analyzed the data. L.P. and L.H.C. contributed substantial materials, resources, and funding.

LITERATURE CITED

Anderson, D. R. (2008). Model Based Inference in the Life Sciences: A Primer on Evidence. Springer, New York, NY, USA.

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 USA 99:14246–14249.

Bibby, C. J., N. D. Burges, D. A. Hill, and S. H. Mustoe (2000). Bird Census Techniques, 2nd ed. Academic Press, London, United Kingdom.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York, NY, USA.

Camp, R. J. (2011). Standard operating procedure (SOP) #8, documenting landbird habitat, Version 1.00. In Landbirds Vital Sign Monitoring Protocol–Pacific Island Network (R. J. Camp, T. K. Pratt, C. Bailey, and D. Hu). Natural resources report NPS/PWR/PACN/NRR. National Park Service, Oakland, CA, USA.

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

Doherty, P. F., G. C. White, and K. P. Burnham (2012). Comparison of model building and selection strategies. Journal of Ornithology 152:317–323.

Elphick, C. S., D. L. Roberts, and J. M. Reed (2010). Estimated dates of recent extinctions for North American and Hawaiian birds. Biological Conservation 143:617–624.

Foster, J. T., J. M. Scott, and P. W. Sykes Jr. (2000). Akikiki (*Oreomystis bairdi*). In The Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.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.

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 (T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, B. L. Woodworth, Editors). Yale University Press, New Haven, CT, USA. pp. 108–193.

Hammond, R. H., L. H. Crampton, and J. T. Foster (2015). Breeding biology of two endangered forest birds on the island of Kauai, Hawaii. The Condor: Ornithological Applications 117:31–40.

Hines, J. E. (2006). PRESENCE2 – Software to estimate patch occupancy and related parameters. USGS-PWRC, Laurel, MD, USA. http://www.mbr-pwrc.usgs.gov/software/presence.html

Kilpatrick, A. M. (2006). Facilitating the evolution of resistance to avian malaria (*Plasmodium relictum*) in Hawaiian birds. Biological Conservation 128:475–485.

LaPointe, D. A., C. T. Atkinson, and S. I. Jarvi (2009). Managing disease. In Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna (T. K. Pratt, C. T. Atkinson, P. C. Banko, J. D. Jacobi, and B. L. Woodworth, Editors). Yale University Press, New Haven, CT, USA. pp. 405–424.

Lepson, J. K., and H. D. Pratt (1997). Akekee (*Loxops caeruleirostris*). In The Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bna.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.

Noon, B. R., L. L. Bailey, T. D. Sisk, and K. S. McKelvey (2012). Efficient species-level monitoring at the landscape scale. Conservation Biology 26:432–441.

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. In Fauna Hawaiiensis, Vol. I, pt. IV (D. Sharp, Editor). University Press, Cambridge, England. pp. 365–466.

Pratt, T. K., C. T. Atkinson, P. C. Banko, J. D. Jacobi, and B. L. Woodworth (Editors) (2009). Conservation Biology of Hawaiian Forest Birds: Implications for Island Avifauna. Yale University Press, New Haven, CT, USA.

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.

Reidy, J. L., F. R. Thompson, C. Amundson, and L. O'Donnell (2015). Landscape and local effects on occupancy and densities of an endangered wood-warbler in an urbanizing landscape. Landscape Ecology doi:10.1007/s10980-015-0250-0.

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.

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

Simberloff, D., and B. Von Holle (1999). Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions 1:21–32.

U.S. Fish and Wildlife Service (2015). Environmental Conservation Online System (ECOS): Listed Species Believed or Known to Occur in Hawaii. http://ecos.fws.gov/tess_public/reports/species-listed-by-state-report?state=HI&status=listed.

U.S. Geological Survey (2011). Gap Analysis Program (GAP): National Land Cover, Version 2.0.

VanderWerf, E. A., J. J. Groombridge, J. S. Fretz, and 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.

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.