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ORIGINAL PAPER

Linking occupancy surveys with habitat characteristics to estimate abundance and distribution in an endangered cryptic bird

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Abstract Accurate estimates of the distribution and abundance of endangered species are crucial to determine their status and plan recovery options, but such estimates are often difficult to obtain for species with low detection probabilities or that occur in inaccessible habitats. The Puaiohi (*Myadestes palmeri*) is a cryptic species endemic to Kaua'i, Hawai'i, and restricted to high elevation ravines that are largely inaccessible. To improve current population estimates, we developed an approach to model distribution and abundance of Puaiohi across their range by linking occupancy surveys to habitat characteristics, territory density, and landscape attributes. Occupancy per station ranged from 0.17 to 0.82, and was best predicted by the number and vertical extent of cliffs, cliff slope, stream width, and elevation. To link occupancy estimates with abundance, we used territory mapping data to estimate the average number of territories per survey station (0.44 and 0.66 territories per station in low and high occupancy streams, respectively), and the average number of individuals per territory (1.9). We then modeled Puaiohi occupancy as a function of two remote-sensed measures of habitat (stream sinuosity and elevation) to predict occupancy across its entire range. We combined predicted occupancy with estimates of birds per station to produce a global population estimate of 494 (95% CI 414–580) individuals. Our approach is a model for using multiple independent sources of information to accurately

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track population trends, and we discuss future directions for modeling abundance of this, and other, rare species.

Keywords Endangered species · Hawai'i · Habitat modeling · Occupancy estimates

Introduction

Understanding population dynamics, effective conservation planning, and evaluating responses to management rely on accurate estimates of abundance and population size (e.g. Johnson et al. 2006; King et al. 2006; McCartney et al. 2006). The collection of these types of data, especially for rare species, is often labor-intensive, high impact, expensive, and even unfeasible. In such cases, occupancy can be used as a surrogate approach to evaluate population trends for management purposes (reviewed in MacKenzie et al. 2006). If information on the relationship between occupancy and abundance is available, it can be used to estimate abundance from occupancy data. Occupancy estimation, which accounts for differences in detection probability, is also an excellent tool for quantifying habitat use, distribution and range, and changes in these parameters over time and space (Crampton et al. 2011; Scott et al. 2002). In this context, occupancy modeling is likely to be most useful when it also considers the amount of suitable habitat (MacKenzie et al. 2006). A well-designed occupancy survey will thus survey suitable and unsuitable habitat, collect data on habitat characteristics, and attempt to describe the relationship between habitat variable, abundance, occupancy and detection probability. Here we present results from the survey protocol we developed to estimate occupancy, and ultimately model range and population size, of a cryptic, patchily-distributed passerine, the Puaiohi (*Myadestes palmeri*).

The endangered Puaiohi, also known as the small Kaua'i thrush, is endemic to Kaua'i, Hawai'i. Once found island-wide, it is currently restricted to the rain forests of the remote, high-elevation plateau in Kaua'i's interior, where it nests in cliff face recesses along deeply incised streams (Snetsinger et al. 2005). The thrush's low numbers and highly restricted range influenced the decision to list the species as federally endangered in 1967 (Udall 1967; USFWS 2006), but a robust population estimate has yet to be achieved given the species' cryptic nature, rarity, and predilection for inaccessible, meandering stream habitats. Traditional distance survey methods for estimating abundance, such as variable circular point counts and line transects, are not feasible in the channelized, non-linear stream environment (Foster et al. 2004). Researchers have made varying assumptions to place the population at approximately 300–500 individuals, extrapolating from surveys in a subset of its range (Woodworth et al. 2009). The lack of a population estimate that is systematic and repeatable has impeded efforts to document species' trends and monitor the impact of management efforts, such as a captive-bred release program implemented between 1999 and 2012. Thus in 2011, we began systematic occupancy surveys as an alternative method to monitor Puaiohi population trends (Royle and Dorazio 2006), aiming to model abundance and population size using habitat and density data.

Our objectives were to (1) estimate Puaiohi occupancy with respect to habitat characteristics, (2) link occupancy probability to bird densities to estimate abundance in the surveyed areas, and (3) determine if remotely sensed data captured this relationship sufficiently to permit extrapolation of occupancy and abundance across the plateau to estimate global population size and range. Our results provide a baseline to measure future changes in distribution and abundance, and can be refined as new remote sensing or field data become available to more precisely estimate population size and range in the future. This study shows the power of combining occupancy surveys with additional information (habitat characteristics, territory density) to estimate population parameters of great conservation need, and can serve as a model for other rare, difficult-to-survey species.

Methods

Study area and survey transect locations

Our study encompassed most of the current range of Puaiohi, an area of <20 km^2 in wet (>6000 mm rain/year) and mesic montane forest from 1056 to 1413 m elevation in the remote southern and central Alakaʻi Plateau of Kauaʻi Island, Hawaiʻi, USA (Scott et al. 1986; Snetsinger et al. 1999). Dominant canopy plants include ʻōhiʻa (*Metrosideros polymorpha*), koa (*Acacia koa*), ʻōlapa (*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), ʻōhia ha (*Syzygium sandwicensis*), kāwaʻu (*Ilex anomala*), and kōlea (*Myrsine lessertiana*), while the diverse understory includes ʻōhelo (*Vaccinium calycinum*), and kanawao (*Broussaisia argute*) (Snetsinger et al. 1999). The plateau is deeply incised by many streams, making access by foot and vehicle very difficult. Most of the Puaiohi's range falls in the state-owned Nā Pali Kona Forest Reserve and the Alakaʻi Plateau Wilderness Area. However, some potential habitats in the southern part of the range occur on private land to which we were unable to gain access.

We centered our surveys on streams as Puaiohi are rarely detected far from streams. We identified 221.6 km of potentially occupied streams on the plateau (above 1050 m), of which we categorized 17 accessible stream segments (hereafter simply called "streams") likely to support either a high or low density of Puaiohi based on previous experience with this area (Fig. 1). From 2011 to 2013, we randomly selected two to three streams in each density category to survey each year, for a total of twelve streams constituting 27.2 km of streams (12.2% of all streams >1050 m in elevation; Table 1). One high density stream, MOH, was surveyed in all three years.

Based on analysis of previous territory maps (Division of Forestry and Wildlife, DOFAW, unpubl. data), which indicated Puaiohi territories average 100 m in length along streams, we spaced survey stations 150 m apart to minimize the chance of detecting the same individual from >1 survey stations. A starting location for surveys was determined by randomly choosing a direction (up or downstream) from an access point, and using a random number generator to determine the initial distance from the access point. We then used a rangefinder and hip chain to establish survey stations along the actual stream course. If we thought that loud stream noise (e.g. rapids) would interfere with Puaiohi detections, we skipped the station and established the next station a further 150 m downstream. Typically, we established 20 stations along each stream section for a total of approximately 3 km of surveys. However, occasionally we could not fit 20 stations into a single stream (e.g. due to short side streams, presence of major waterfalls), in which case we would combine several shorter segments in close proximity to each other into a single 20-station composite survey route for the purposes of analysis (i.e. streams KOA and WKO).

Occupancy surveys

Each station was surveyed five times during peak Puaiohi breeding season (March–mid-June). Surveys on each transect were evenly distributed across the breeding season, with

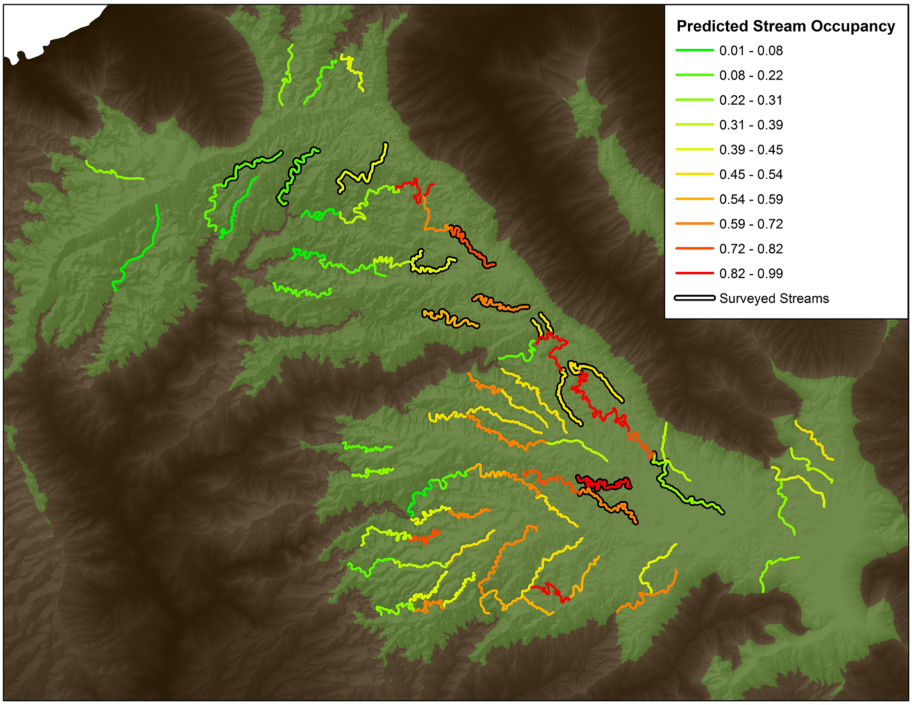

Fig. 1 Map of Puaiohi range showing surveyed streams (outlined in *black*) and predicted occupancy of surveyed and unsurveyed streams above 1050 m on the Alaka'i Plateau, Kaua'i, HI, 2011–2013

Table 1 Length and percentage of streams (by elevation) on the Alaka'i Plateau used for surveys, estimating Puaiohi populations, and calculating total amount of streams

	Elevation range						
	Total	1050–1140 m		1140–1340 m		>1340 m	
	(km)	Length (km)	% of streams	Length (km)	% of streams	Length (km)	% of streams
Surveyed streams	27.2	4.5	17	19.6	72	3.1	11
Streams used for population estimate	146.2	45.8	31	87.0	60	13.4	9
All streams	221.6	88.3	40	107.3	48	26.1	12

The middle elevation range, 1140–1340 m ASL, represents the range in which all Puaiohi detections occurred during this study, although Puaiohi have historically been detected at lower elevations. The lower and upper elevations represent the minimum and maximum elevations surveyed. Surveyed streams were streams on which occupancy surveys were conducted. Streams used in population estimates are all streams documented in the State of Hawaii GIS stream layer that are greater than 1500 m in length, while "All streams" represent all of the streams between 1050 and 1340 m ASL in elevation, regardless of length. "% total streams" is the percentage of the total length of streams in that row (e.g. surveyed streams) occurring at that elevation, such that percentages add up to 100% across rows. If streams crossed more than one elevation category, we accounted for the length occurring in each category approximately 1–2 surveys per transect per month. To minimize the potential of observers remembering where they had previously detected Puaiohi, multiple observers surveyed a large number of stations alternating among streams in each year, and observers were instructed to try to be "blank slates" at each visit to a station. We used a multi-interval survey protocol to assess the balance between effort and detection probability for future surveys. At each survey station, we passively listened and watched for Puaiohi for two consecutive 4 min intervals (intervals 1 and 2). We then played 30 s of high quality recordings (calls or songs) of wild Puaiohi, followed by 1 min of observation, a second 30 sec playback period of different songs/calls, a second min of observation, then a third 30 sec playback of yet different songs/calls, and a final 5 min observation period (intervals 3–5; total survey time was 16.5 min/station). During a survey and between stations different recordings of wild Puaiohi were randomly alternated throughout. Upon initial detection of a Puaiohi, we recorded the survey interval (1–5), distance from the surveyor and a code indicating if the bird was either first seen, first heard then seen, or heard only. Each individual was only recorded once per survey unless it was detected in both a passive interval and a playback interval, in which case it was recorded twice.

We recorded variables that could affect detection probability to incorporate into occupancy models. Specifically, survey date and time, observer, wind speed, rainfall intensity, cloud cover (%) were recorded at every survey. We recorded wind using the Beaufort scale of 0–5, where 0 = calm conditions, 1 = light breeze of 1–3 mph, 2 = slight breeze of 4–7 mph, 3 = gentle breeze of 8–12 mph, 4 = moderate breeze of 13–18 mph, and 5 = winds of over 19 mph. For rain we used a scale of 0–4, where 0 = no rain, 1 = mist/fog, 2 = light drizzle, 3 = light rain, and 4 = heavy rain. Stream noise was recorded as 0–4 scale where 0 = no noise, 1 = light noise, noise at a distance, 2 = light babbling, 3 = heavy babbling where birds can still be heard at a distance, 4 = loud/falls nearby/difficult to hear any birds not in close proximity. Surveys were postponed until another day if wind, rain, or stream noise were at maximum levels.

Habitat characteristics

Given Puaiohi nest site preferences for cliff faces, we measured topographic features at survey points that we hypothesized might influence Puaiohi occupancy, in particular to capture the vertical nature (cliffs vs. shallow banks) and complexity of streams (Online Resource Table S1). Specifically, we counted the number of cliff walls and side streams and drainages that might increase complexity within a 150 m radius around survey stations. Cliff walls were defined as any vertical or overhanging surface (75–105 degree slope) with total vegetative cover measuring less than 0.5 m in length or height. Side streams were defined as streams which met the surveyed stream at the same height and had the same substrate as the surveyed stream, whereas side drainages had a different substrate type than the surveyed route. We measured bank full width as the point at which the flow just begins to enter the active floodplain (i.e. the width of the stream at channel-forming flow stage). We recorded majority substrate size within 2 m upstream and downstream of the point (Online Resource Table S1; Barbour et al. 1999). We took clinometer measurements to the bottom and top of the cliffs on either side of the station and measured the distance to the cliff top and bottom with a rangefinder. We used these measurements to calculate cliff vertical extent (for each side of the drainage), cliff slope (for each side of the drainage), cliff length (for each side of the drainage), and the top and bottom gap width of the cliffs (Online Resource Fig. S2) (Barbour et al. 1999; Greeney 2009; Sullivan et al. 2006). For the analysis, we used the maximum value of all of these metrics at each station. We calculated a symmetry ratio for cliff slope as the ratio of the larger to smaller value, and employed this ratio as an interaction term in models to indicate whether stream banks were gently sloping on both sides or steep on both sides (i.e. a channelized section).

Several additional habitat characteristics were derived in GIS. The sinuosity of each stream was calculated from the State of Hawaii stream layer (http://files.hawaii.gov/dbedt/op/gis/data/darstreams.shp.zip) using Hawth's Tools (Beyer 2004) in ArcGIS 9.3 as the straight line distance from beginning to end of the stream divided by the total length of the stream. If a survey transect consisted of two separate stream segments that did not flow consecutively, then the sinuosity of that transect was calculated as the sum of the straight line distances for each segment divided by the sum of the total length of each segment. The elevation at each occupancy station was extracted from a digital elevation model (DEM) (http://www.soest.hawaii.edu/coasts/data/kauai/dem.html) in ArcMap 10.2. These elevations were then averaged across all the occupancy stations on the stream to get the average elevation of the stream.

Territory mapping and density

To estimate densities of birds on occupied streams, we territory mapped according to methods described in Bibby et al. (2000) on three high occupancy (HHA and HPK from 2007 to 2011, MOH from 2011 to 2013) and two low occupancy streams (KWKN from 2010 to 2011 and KWKE in 2011). Each stream was surveyed from 6 to 10 times per year; during each survey, observers marked the location (in UTMs with a handheld GPS) of all Puaiohi detected, resighted color bands, recorded behavior, and if possible noted sex and age. When possible, nests were also located. Special attention was paid to breeding and territorial behaviors (e.g. counter singing) that would help sex birds and identify territory boundaries. Banded Puaiohi occurred on all streams where territory mapping was conducted except KWKE, with approximately 33, 67 and 100% of the territories containing banded birds on HHA, HPK and KWKN, respectively, but fewer than 25% of territories held by banded birds on MOH. Territories were delineated by plotting detections in ArcMap 10.1, using information on color banded birds, nests, territorial behavior, and natural breaks in distribution, and overlaid on the occupancy survey stations. We used a spatial join in ArcMap 10.2 to count the number of stations per territory, and calculated an average value per stream per year. Mapping of territories also helped us determine the numbers of Puaiohi per territory on the two streams with the most intensive surveys, HPK and HHA (2007–2009).

Occupancy analysis

Occupancy models were fit in R version 3.1.1 (R Core R_Core_Team 2016) using the unmarked package (Fiske and Chandler 2011). We modeled observed detections as a two-stage process of occupancy, the probability that a survey station was occupied (Ψ); and detection probability (p), conditional that a station was occupied. Occupancy models estimate logit-transformed Ψ and p as linear functions of covariate measurements (MacKenzie et al. 2002, 2006). For model selection we removed six stations with incomplete information. In addition, we removed one station where the gap width at the canyon top was >75 m, because this value was an outlier 50% larger than the next-largest measurement.

To identify important predictor variables we used information theoretic multimodel inference as described by Burnham and Anderson (2002). We first ran sets of models representing all possible combinations of predictors of just p and just Ψ, independently. Because there was considerable model uncertainty, we retained all Ψ- and p-only models with ΔAICc < 4, then examined all 1275 combinations of those models estimating both p and Ψ. We again applied the ΔAICc < 4 cutoff to select a subset of these combined models (see Online Resource Table S3) and calculated model-averaged parameter estimators and 95% confidence intervals for each predictor of p and Ψ in these models (Burnham and Anderson 2002).

Day of year, a quadratic term for day of year, observer, pre- or post-playback, visit number (1–5), and rain were used as potential covariates to estimate detection probability. During each visit to a survey station, observers recorded Puaiohi detections over five intervals, but for analysis these intervals were condensed into a pre- and post-playback observation for each visit. Seventeen unique observers participated in occupancy surveys, but ten of them contributed relatively few observations (each <5% of the total observations). These ten observers were combined into a single category totaling 32% of observations, leaving eight categories of observer. The two detection phases were modeled as independent detection observations at each station, with pre- or post-playback as a potential detection predictor.

Predicting occupancy for unsurveyed streams

In ArcMap 10.2, we identified all unsurveyed streams of ≥1050 m in elevation (the lowest elevation surveyed during occupancy surveys) on the Alaka'i Plateau, and ≥1500 m in length to accommodate the creation of 10–20 "stations" at 150 m intervals to match inter-station distance of surveyed streams. Streams >3000 m in length (i.e. maximum length for surveyed streams) were split into segments ≥1500 m. We were not able to estimate variables such as cliff slope and gap width for unsurveyed streams given the low resolution of available Digital Elevation Models. Therefore, we calculated average elevation and sinuosity of each unsurveyed stream as surrogate measures of important stream morphology. These metrics were calculated on 146 km of streams, which account for approximately 66% of the total length of streams within the study area (Fig. 1, Table 1). These variables were not calculated for 34% (75 km) of streams that did not meet our length requirement, but 57% of these streams were below 1140 m in elevation, the minimum elevation at which we detected Puaiohi.

To predict average Puaiohi occupancy of unsurveyed streams across the Alaka'i Plateau, we hypothesized that average occupancy would increase with increasing sinuosity (creating more cliff habitat) and be greatest at middle elevations, where stream structure, vegetation structure and composition, and climate are thought to be most suitable for Puaiohi. To test this hypothesis, we used an information theoretic approach in R 3.1.1 to run models testing average elevation, average elevation^2, and sinuosity plus two-way interactions as predictors of average estimated occupancy for each of the 12 surveyed streams (Table 2, Online Resource Table S4). We used a general linear model with a normal distribution and a logit link function to constrain predicted occupancies between 0 and 1. Because there was very little model uncertainty (see Results and Online Resource Table S4), we then applied the best model to predict average occupancy for all streams >1500 m in length (surveyed and unsurveyed) across the range of the species for a range-wide occupancy estimates.

Table 2 Streams surveyed for Puaiohi occupancy in the Alaka'i Plateau, Kaua'i Island, Hawai'i, with total number of stations surveyed and the number of stations at which a Puaiohi was detected by year (2011–2013)

Stream	# Stations	2011	2012	2013	Mean estimated occupancy (95% CI)	
EAF–East Alakai Fence	20		0		0.21	(0.11–0.30)
EKOA–East Koaie	20			12	0.47	(0.35–0.60)
HHA–Halehaha	21	16			0.82	(0.70–0.93)
HPK–Halepaakai	21	17			0.71	(0.60–0.82)
KKN–Kauaikinana	20		0		0.17	(0.08–0.27)
KOA–Koaie	19		8		0.46	(0.34–0.59)
KWKE–East Kawaikoi	20	8			0.39	(0.28–0.50)
KWKN–North Kawaikoi	20	2			0.19	(0.14–0.25)
MMO–Mid-Mohihi	20			8	0.53	(0.41–0.64)
MOH–Mohihi	20	16	18	18	0.75	(0.62–0.88)
UUK–Upper Kawaikoi	20			14	0.69	(0.55–0.84)
WKO–Waiakoali	20		14		0.50	(0.37–0.63)

Average modeled per station occupancy (with 95% CI) is shown for each reach. The estimate for 2011 from Mohihi Stream is presented, as this was the estimate used in occupancy models. The global estimate across all three years was 0.75 (0.67–0.82)

Population model

To estimate the population of Puaiohi *(P)* across the Alaka'i Plateau above 1050 m in elevation, we multiplied average predicted occupancy per stream *(PO)* by the number of stations/stream *(NS),* density of territories/station *(TD),* and number of birds per territory (*NBT*) for both high and low density streams and summed:

$$P = \sum_{HDS}^{stream} PO * NS * HiTD * NBT + \sum_{LDS}^{stream} PO * NS * LoTD * NBT$$

Using the predicted range-wide occupancy estimates (above) for each stream >1500 m in length, we classified streams as high occupancy (occupancy >0.5, HDS), or low occupancy (LDS). We then used territory mapping information to apply high or low (*LoTD* and *HiTD*, respectively) territory/station ratio estimates to low and high occupancy streams, respectively, and multiplied each by the number of birds per territory (NBT), to estimate the number of birds per occupied station in high and low occupancy streams. When multiplied by predicted occupancy, we derived estimates of the total number of breeding birds per stream. Summing across all streams produced an estimate of the total population size. We calculated confidence with the above formula and substituting the 95% confidence limits of predicted occupancy for upper and lower estimates. Estimates are presented as means with 95% (CI).

Results

We surveyed 241 distinct stations on 12 streams (Table 2, Fig. 1); after we removed stations for which there were missing data or outliers, we modeled occupancy on 234 stations. Puaiohi were detected at 149 stations (62%), during 679 of 3009 (23%) survey periods (pre- and post-playback counted separately). Minimum and maximum elevations at which Puaiohi were detected were 1141 m and 1339 m, respectively. No Puaiohi were detected on two streams, with the remaining streams having 2–18 stations with detections per survey period (Table 2). Mean estimated occupancy rates of surveyed streams ranged from 0.17 to 0.82, with mean estimated occupancy of all surveyed stations being 0.49 (95% CI 0.45–0.53; Table 2). Slightly more detections occurred during playback periods: Puaiohi were detected in 381/1516 playback periods (25%) and only 298/1493 passive periods (20%).

Occupancy model fit and model covariates

Twenty-two of the combined p and Ψ models were within $\Delta 4AIC_c$ of the best model (Online Resource Table S3). Thirteen parameters were included in the top models, but model averages of these parameters suggested that only seven were informative predictors based on model-averaged 95% CI not containing 0: number of cliff walls, maximum cliff vertical extent, maximum slope, stream bank width, and elevation were informative predictors of Ψ; and pre- vs. post-playback and visit were informative predictors of p (Table 3).

One of the strongest covariates affecting occupancy was number of cliffs per station, with the odds of a station being occupied increasing by 1.31 for each additional cliff (Table 3); this variable occurred in all top 22 models. Probability of site occupancy also was positively associated with maximum vertical extent (also in all top models) and slope of the bordering cliffs, with the odds of occupancy increasing 1.1 for every additional meter of vertical extent and 1.03 for every additional degree of slope. Occupancy was strongly negatively related with stream width, indicating that streams that are too wide are not as likely to be occupied (odds ratio = 0.87), and moderately positively correlated with elevation (Table 3).

Table 3 Model averaged parameter values predicting Puaiohi detection and occupancy probabilities from the top 22 models with delta $\Delta AIC_c < 4.0$ (see Online Resource Table S3 for full model results)

Parameter	Estimate	SE	Mean	Min	Max
p					
Playback (Y/N)	0.4123*	0.1053			
Visit (1–5)	−0.1896*	0.0542			
Year day	0.0016	0.0026			
psi					
Stream width (m)	−0.1413*	0.0631	4.2	0.3	16.5
Maximum slope (^{o})	0.0273*	0.0139	64	10	114
Maximum vertical extent (m)	0.0926*	0.0279	13	1	58
# Cliff walls	0.2732*	0.0577	6	0	30
Elevation (m)	0.0051*	0.0022	1224	1056	1414
Slope symmetry	−0.1491	0.1720	1.8	1	18
# Side streams	0.1014	0.0943	2	0	16
Top gap width (m)	0.0144	0.0240	23	5	74

Model intercept for p = −0.200 and for psi = −9.566

* Indicates that 95% CI does not overlap with 0. Only parameters found in more than 1 of the 22 models were included in this table

Detection probability was strongly affected by whether or not the detection interval was preceded by playback, with probability of detection 0.45 (95% CI 0.36–0.54) and 0.55 (95% CI = 0.59–0.70) for pre-playback and post-playback intervals, respectively (considering the two periods independently; Table 3). The odds of detecting a bird increased by 1.51 when playback was used. Of initial detections, 305 (73%) were in the pre-playback interval, while an additional 110 (27%) first-time detections occurred in the post-playback period; the addition of new detections along with birds re-detected from the pre-playback period resulted in the post-playback detection rate being higher. The probability of detection decreased with each subsequent visit, which could be a function of habituation to surveys or seasonal changes (e.g. less responsive post-breeding individuals); however, visitation to each stream was spread across the survey period, so all streams were surveyed in both early and late time periods.

Predicted occupancy and population abundance

Predicted occupancy on unsurveyed streams ranged from 0.15 (95% CI 0.09–0.25) to 0.90 (95% CI 0.79–0.96; Fig. 1). Of the set of models containing remote sensing variables used to predict occupancy on unsurveyed streams, the model containing sinuosity, elevation, and elevation^2 received the majority of support ($w_i = 0.99$), with all three predictors significant at the 95% level. Sinuosity ($\beta = 2.20$, 95% CI 1.59–2.80) was positively associated with occupancy, while elevation had a quadratic relationship with maximum effect on occupancy effect at mid-elevations (peak at 1253 m; $\beta_{\mathrm{elevation}} = 0.316$, 95% CI 0.24–0.39; $\beta_{\mathrm{elevation}^2} = -0.000126$, 95% CI 0.000097–0.00016). Model predictions agreed with 75% of predictions based on 2002–2005 field observations (USGS and DOFAW, unpubl. data) when streams were divided into two categories, high and low occupancy. When predictions differed, the model predicted high occupancy, whereas the other sources predicted low occupancy.

Territories were bigger on low occupancy streams (LDS) than high occupancy streams (HDS: 2.4 ha vs. 0.9 ha, respectively), and therefore encompassed longer stretches of stream and more stations (2.25 stations/territory on LDS vs. 1.51 stations/territory on HDS, which is equivalent to 0.44 and 0.66 territories/station, respectively). Although a helper (third individual) was present on 8% of territories at MOH in 1996–1997 (Snetsinger et al. 2005), we never observed helpers, and pairing density was 89–96% at HPK/HHA in 2007–2009. Thus for our population model we used 1.9 breeding birds/territory. Multiplying the model-predicted occupancies across the plateau with the different territory/station ratios for LDS and HDS, and 1.9 birds per territory, we estimated the total population size for Puaiohi at 494 (95% CI 414–580) birds.

Discussion

Accurate distribution and abundance metrics are a critical element in evaluating population stability and effectiveness of conservation activities, but can be costly and daunting to obtain (Williams et al. 2002). Our study not only tested a survey protocol for a cryptic, difficult-to-survey rare species, but also provided the first quantitative descriptions of habitat use for the Puaiohi, while minimizing the impact that extensive surveys would have on an area that supports many endangered plants and animals (USFWS 2004, 2006). A single island endemic, and always considered uncommon, the Puaiohi was listed as endangered in 1967 (Udall 1967). It has been studied continuously since the mid-1990s, when—on the heels of two major hurricanes—it was thought to number only a few dozen individuals (Snetsinger et al. 1999). Yet because of its secretive nature and the remote, rugged terrain it inhabits, a robust population estimate has eluded researchers, and thus there has been no way to assess trends and the success of management efforts, which have included a captive breeding and release program. By combining occupancy estimates of surveyed streams with demographic data and GIS information from the many inaccessible streams, we were able to produce a population estimate for this species, the first one generated for the entire species' range. This estimate, long a goal under the species' recovery plan (USFWS 2006), will provide a benchmark for Puaiohi conservation. This approach of combining different types of survey and demographic data to generate such an estimate is applicable for other rare, inaccessible species.

Occupancy estimates on surveyed streams

Occupancy estimates ranged widely among surveyed streams: from 17 to 82% considering detection probability. On several streams, Puaiohi were detected at the majority of stations, whereas on other streams no Puaiohi were detected. Within low occupancy streams, occupied stations were clustered together, typically at the top of the stream, although occasionally, occupied stations were scattered throughout the stream. Generally, these among- and within-stream patterns correspond with historical Puaiohi locations (USGS and DOFAW unpubl. data).

Puaiohi prefer to nest on small, recessed, ledges on cliffs (Snetsinger et al. 1999), and the characteristics most closely associated with occupancy reflected the availability of potential nesting substrate. For example, important variables for predicting occupancy included the number of cliff walls within 150 m of the survey station, and maximum slope and maximum vertical extent of the cliff wall at the survey location; all contribute to the amount and quality of cliff habitat. The negative correlation of occupancy with stream width, and positive correlation with elevation, may indicate a preference for locations where streams are small and narrow, and not as big and deep as in the lower drainages.

Estimated detection probability was fairly low, as commonly noted for this cryptic species (Snetsinger et al. 1999; VanderWerf et al. 2014): 45% during pre-playback surveys (over eight mins of passive surveys), increasing slightly to 55% with the addition of playback surveys. This low probability underscores the necessity of a rigorous survey protocol with multiple visits for this species (MacKenzie et al. 2006). However, detection probability decreased with each additional visit, suggesting some habituation of Puaiohi to the observers and/or playback, and indicates that the return on investment decreases with additional visits. Also, the pre-playback data suggest that the passive period could be shortened to a single interval, or eliminated, to make surveys more efficient given the logistical difficulties of reaching many of the streams. Shorter surveys per station and fewer visits may lower detection rates, but can allow more areas to be surveyed or more frequent surveys to assess long-term trends.

An important assumption of occupancy models is that occupancy and detection at each station along a stream are independent of each other (MacKenzie et al. 2006). Puaiohi are territorial (Snetsinger et al. 1999) and a bird at an occupied station could prevent an adjacent station from being occupied—even if it is otherwise ideal habitat. This behavioral effect would reduce estimates of occupancy. On the other hand, conspecific attraction might increase the probability that an adjacent station were occupied, and indeed, both occupancy surveys and territory mapping suggested that adjacent stations were often occupied by different individuals, especially on high density streams. Thus we believe that the spacing of survey stations minimized any effects of territorial behavior. On low density streams, the incorporation of multiple stations in one territory appeared to reflect a lack of competition, rather than exclusion of some birds by a dominant individual. We also assumed that pre- and post-playback detection periods at a station were independent of each other to estimate the added benefit of playback methods. Since post-playback detection periods necessarily followed pre-playback periods, it is possible that detections early in a site's visit biased observers, making them more likely to detect birds during the post-playback phase. This tendency would enhance the estimated effect of playback, but the substantial number of additional detections post-playback supports the increased detection rate.

Estimation of occupancy on unsurveyed streams

Our correlation of remote-sensed information (elevation and sinuosity) with occupancy estimates of surveyed streams allowed us to predict occupancy across the entire range of Puaiohi, much of which is inaccessible. While high resolution remote-sensed data were unavailable, our use of sinuosity (a predictor of topographic complexity) and a quadratic relationship with stream elevation (a proxy for topography, weather, and vegetation structure and composition) produced good concordance with historical information on the Puaiohi (USGS and DOFAW unpubl. data). Sinuosity was used to model the hypothesis that as the number of bends in a stream increases so will the number of cliff walls and side drainages that provide preferred Puaiohi nesting habitat; sinuous streams are less likely to have wide, unforested flood plains. Elevation showed a quadratic effect on occupancy, peaking at mid-elevation.

We hypothesize that quadratic elevation is a useful predictor of occupancy across all streams in the study area because drainages higher and lower than those surveyed may be less suitable for Puaiohi. Forests at low elevations are often degraded and filled with invasive species, and have higher rates of disease transmission (Atkinson et al. 2014; Behnke 2014). Historically, Puaiohi were known from lower elevation streams on the plateau (Perkins 1913) and prehistorically from at sea level (Burney et al. 2001), so apparently the restriction to higher elevation streams is recent. One possibility is a lower incidence of temperature-sensitive avian diseases (which arrived in Kaua'i in the last century) above 1200 m, although there is evidence that Puaiohi may be less impacted by avian malaria than the native honeycreepers (Atkinson et al. 2001, 2014; VanderWerf et al. 2014). Additionally, elevation may be a surrogate for the quality of the vegetation, with weeds and scrubby vegetation being more prevalent in wider, lower elevation streams (Behnke et al. 2016; Behnke 2014). Preliminary data suggest that Puaiohi do not feed on non-native fruit (L. Pejchar pers. comm) and may avoid degraded forests. On the other hand, high elevation streams are characterized by flat, meandering headwaters with vegetation that tends to differ in both structure and composition due to the more extreme weather patterns (lower temperatures, higher rainfall; Atkinson et al. 2014, Behnke et al. 2016; DOFAW, unpubl. data). Therefore, the abundance and diversity of native, fruiting trees and shrubs necessary for Puaiohi would likely be greatest at mid-level elevations.

Using this relationship, we were then able to predict occupancy on streams, many of which are inaccessible, across two-thirds of the Puaiohi's presumed range. These predictions expand the potential range of Puaiohi, especially into the eastern portions of the Alaka'i, but also highlight that Puaiohi are unlikely to be found at elevations below 1140 m or above 1340 m. Past surveys (1997–2005) and expert predictions of high vs. low occupancy (T. Savre, B. Heindl, pers. obs.), which were based on topographic maps and direct experience of the terrain and some of the streams, generally validated model results for unsurveyed streams. Where these sources differed from model results, previous surveys and expert opinion indicated lower occupancy, suggesting that the model has a tendency to overestimate occupancy, perhaps because it does not account for factors such as vegetation composition and structure. We can now prioritize streams for surveys in future years to verify model predictions, and provide new information to improve future iterations of the model.

Population modeling

Our population estimate of 494 (95% CI 414–580) breeding Puaiohi falls within the range of two previous, less rigorous, estimates: (1) 300–500 birds, which was extrapolated from 1995 to 1998 surveys on 12% of the streams included here (Woodworth et al. 2009); and (2) 270–525 birds, which was based on 2003–2005 surveys of 32% of the streams (DOFAW, unpubl. data). The latter surveys mapped 183 territories across those streams and assumed a low pairing rate of 1.6 (observed on some streams) to produce the lower figure in this range. For the higher figure, the surveyors projected their surveys—based on presumed habitat quality and a pairing ratio of 1.9 (the figure used in our estimate)—to predict an additional 95 territories in unsurveyed areas (Woodworth et al. 2009). Snetsinger et al. (1999) hypothesized that the Puaiohi population was growing in the years immediately after Hurricane Iniki in 1992, but these figures suggest that the Puaiohi population was relatively stable over the period of time between these different surveys.

Our estimate encompasses only 66% of the length of the known (mapped) streams on the Alaka'i Plateau >1050 m in elevation. The remaining streams were too small to be used in the analysis given the resolution of our currently available topographic data. Some of these small streams at mid-elevation were surveyed in 2003–2005 and contained several territories (DOFAW, unpubl. data); furthermore it is possible that a few Puaiohi occur in major escarpments far from streams. If small streams and non-stream habitat support many Puaiohi, then our population estimate is biased low. However, 57% of the small streams were <1140 m elevation (the lowest elevation at which Puaiohi were detected), and thus would be unlikely to contribute many individuals to our estimate. Thus, we believe we have produced a reasonable range-wide point estimate of the breeding population, and the first to have confidence intervals.

Although the proxy variables we employed to estimate occupancy on unsurveyed streams are useful for a coarse scale analysis, to further refine our population estimate we need finer scale habitat classification, better vegetation data, and better topographic mapping. Habitat delineation would likely be accomplished by combining high resolution multispectral imagery of the plateau with intensive on the ground, species-level vegetation sampling. LiDAR imaging would allow important topographic variables, such as the number of cliffs and cliff vertical extent, to be remotely sensed across the entire range (Davies and Asner 2014). It would also allow us to estimate canopy height and abundance of fruiting trees, as proximity of food resources to nesting habitat is likely an important consideration in territory placement (Davies and Asner 2014). Furthermore, LiDAR would increase our knowledge of the number and extent of streams and drainages across the entire plateau. Current hydrography layers are based upon a 10 m resolution DEM, and it is likely that many drainages and streams are not visible at this resolution. Finally, many of these variables are static, but presumably gradual changes in habitat (such as encroachment of invasive species) and annual stochasticity (such as frequency of flooding) may be important elements for predicting Puaiohi occupancy, and should be included in future models.

Conclusion

Uncertainty in the distribution, density, and population trends of Puaiohi has stymied conservation planning for this species. There are many endangered species in Hawai'i, and knowledge of whether Puaiohi are declining or stable, and what factors might influence distribution and trends, is important for prioritizing limited conservation resources for this species and others. The expansion of habitat degradation upslope (through the spread of invasive weeds, land development, climate change, or catastrophic disturbance) could be one of the most serious threats to the Puaiohi population. Our ability to actively monitor these changes, and the response of the Puaiohi population, is critical to ensuring its continued survival. Additionally, the ability to identify high occupancy streams will allow managers to prioritize those areas for habitat protection and restoration. Our model is an important step in better understanding the distribution and abundance of Puaiohi, and helps illustrate where additional information (such as plant community measurements) is needed to improve model predictions. We believe that our approach of combining occupancy surveys with multiple sources of information to better understand a cryptic species is an approach that is applicable to many endangered species around the world.

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