Breeding biology of two endangered forest birds on the island of Kauai, Hawaii

Author(s): Ruby L. Hammond, Lisa H. Crampton, and Jeffrey T. Foster
Source: The Condor, 117(1):31-40. 2015.
Published By: Cooper Ornithological Society
URL: http://www.bioone.org/doi/full/10.1650/CONDOR-14-75.1

THE CONDOR
Ornithological Applications
www.cooper.org

Volume 117, 2015, pp. 31–40
DOI: 10.1650/CONDOR-14-75.1

RESEARCH ARTICLE

Breeding biology of two endangered forest birds on the island of Kauai, Hawaii

Ruby L. Hammond,[1,2]* Lisa H. Crampton,[2] and Jeffrey T. Foster[1,3]

[1] Northern Arizona University, Flagstaff, Arizona, USA
[2] Kauai Forest Bird Recovery Project, Hanapepe, Hawaii, USA
[3] University of New Hampshire, Durham, New Hampshire, USA
* Corresponding author: ruby.l.hammond@gmail.com

Submitted May 2, 2014; Accepted October 27, 2014; Published January 7, 2015

ABSTRACT

Two forest bird species endemic to the island of Kauai in the Hawaiian Archipelago were listed under the U.S. Endangered Species Act in 2010 due to recent population declines. This research represents the first comprehensive breeding biology study of both species, the ʻAkikiki or Kauai Creeper (*Oreomystis bairdi*) and ʻAkekeʻe or Akekee (*Loxops caeruleirostris*). The 2-year study was initiated in 2012 to determine if low nesting success may be a cause of their population declines. We monitored 20 ʻAkikiki and 8 ʻAkekeʻe nests to assess basic nesting biology parameters (e.g., brood size; nest height; length of construction, incubation, and nestling periods) and to derive estimates of nesting success and investigate causes of failure. In general, ʻAkikiki and ʻAkekeʻe breeding biology was similar to other insectivorous Hawaiian honeycreepers. Mean nest height for ʻAkikiki and ʻAkekeʻe was high (9.2 ± 2.3 m SD and 11.1 ± 2.3 m SD, respectively) compared to most Kauai forest birds. Nesting success, calculated using program MARK, was 0.77 ± 0.12 SE for ʻAkikiki and 0.71 ± 0.17 SE for ʻAkekeʻe. Three ʻAkikiki and 2 ʻAkekeʻe nests failed. One ʻAkikiki nest failed due to nest predation and the other 2 to unknown causes. One ʻAkekeʻe nest failed due to poor nest attendance and the other to hatching failure. Nest sample sizes were small and should be considered with caution; however, these results suggest that low nesting success may not be a primary cause of decline in these species. Future research on both species should assess post-fledging, juvenile, and adult survival as potential causes of their populations' declines. Determining which demographic parameters currently have the largest negative impact on these populations is imperative for guiding effective management actions to conserve these species.

Keywords: ʻAkekeʻe, ʻAkikiki, bird, breeding biology, conservation, Kauai, nest, endangered

Biología reproductiva de dos aves de bosque en peligro de extinción en la isla de Kauaʻi

RESUMEN

Dos especies de aves de bosque endémicas de la isla de Kauai del archipiélago de Hawái fueron listadas bajo la Ley de Especies en Peligro de EEUU en 2010 debido a su reciente disminución poblacional. Esta investigación representa el primer estudio integral de la biología reproductiva de ambas especies, *Oreomystis bairdi* y *Loxops caeruleirostris*. Un estudio de dos años fue iniciado en 2012 para determinar si el bajo éxito reproductivo puede ser una causa de sus disminuciones poblacionales. Veinte nidos de *O. bairdi* y 8 nidos de *L. caeruleirostris* fueron monitoreados para evaluar los parámetros básicos de la biología de anidación (e.g., tamaño de la nidada; altura del nido; duración de la construcción, de la incubación y del volantón) y para derivar estimaciones del éxito de anidación e investigar las causas de fracaso. En general, la biología reproductiva de *O. bairdi* y *L. caeruleirostris* fue similar a la de otras especies insectívoras hawaianas de mieleros. La altura media del nido de *O. bairdi* y *L. caeruleirostris* fue alta (9.2 ± 2.3 m DE y 11.1 ± 2.3 m DE, respectivamente) comparada con la mayoría de las aves del bosque de Kauaʻi. El éxito de anidación, calculado usando el programa MARK, fue 0.77 ± 0.12 EE para *O. bairdi* y 0.71 ± 0.17 EE para *L. caeruleirostris*. Un total de 3 nidos de *O. bairdi* y 2 nidos de *L. caeruleirostris* fallaron. Un nido de *O. bairdi* fue depredado y los otros 2 fracasaron por causas desconocidas. Un nido de *L. caeruleirostris* fracaso por baja asistencia y el otro debido al fracaso de la eclosión. Los tamaños de muestra de los nidos fueron pequeños y los resultados deben ser considerados con precaución. Sin embrago, estos resultados sugieren que el bajo éxito de anidación no sería una causa primaria de disminución en estas especies. Las futuras investigaciones para ambas especies deben evaluar la supervivencia luego del emplumamiento, la supervivencia del juvenil y la del adulto como causas potenciales de sus disminuciones poblacionales. Es vital determinar qué parámetros demográficos actualmente tienen el mayor impacto negativo en estas poblaciones para guiar las acciones de manejo efectivas que permitan conservar estas especies.

Palabras clave: aves, biología reproductiva, conservación, en peligro, Kauai, *Loxops caeruleirostris*, nido, *Oreomystis bairdi*

INTRODUCTION

Recently ranked as the most important ecoregion for bird species conservation by BirdLife International (Buchanan et al. 2011), forests of the Hawaiian Archipelago harbor more than 30% of endangered bird species in the U.S. (Leonard 2008). Due to population declines since the 1970s, 2 Hawaiian honeycreepers endemic to the island of Kauai, the ʻAkikiki or Kauai Creeper (*Oreomystis bairdi*) and ʻAkekeʻe or Akekee (*Loxops caeruleirostris*), were recently listed under the U.S. Endangered Species Act. Estimates of ʻAkikiki population size declined from 6,832 ± 966 SE in 1973 (Gorresen et al. 2009) to 1,472 ± 680 SE in 2000 (Foster et al. 2004), and ʻAkekeʻe population size declined from 5,066 ± 840 SE in 1973 (Gorresen et al. 2009) to 3,111 ± 591 SE in 2008 (VanderWerf 2012a). More recent surveys suggest additional population declines and range contractions in both species (U.S. Geological Survey and Hawaii Division of Forestry and Wildlife personal communication). Although incidental data have been collected (e.g., nest descriptions, infrequent monitoring of nests and family groups, resighting of color-banded birds; Eddinger 1972a, 1972b, Foster et al. 2000, Powell 2007a, VanderWerf and Roberts 2008), the causes of decline for both species are unknown, and most studies have focused on estimating population density (Scott et al. 1986, Foster et al. 2004, Gorresen et al. 2009). As for other Hawaiian forest birds (USFWS 2006), introduced avian diseases (van Riper et al. 1986, Atkinson and LaPointe 2009), habitat loss (Vitousek et al. 1987, Loope et al. 2001), introduced mammalian predators (Atkinson 1977, VanderWerf 2012b, VanderWerf et al. 2014), and stochastic events such as hurricanes (Conant et al. 1998) have been hypothesized to have contributed to recent declines.

Fossil evidence suggests the historical range of the ʻAkikiki was islandwide, but no ʻAkeke'e fossils have been found in lowland areas, suggesting ʻAkeke'e may have always been limited to montane forests (Olson and James 1982). Both species are currently restricted to largely undisturbed forest above 1,000 m in elevation (USFWS 1983, Scott et al. 1986). ʻAkikiki are insectivorous and obtain prey primarily in the subcanopy by gleaning, probing, and excavating (Foster et al. 2000, Powell 2007a, VanderWerf and Roberts 2008; R. L. Hammond personal observation). ʻAkekeʻe use their crossed bills to pry open leaf buds of the dominant tree in wet forests of Kauai, the ʻōhiʻa (*Metrosideros polymorpha*), to obtain invertebrate prey, (Lepson and Freed 1997). ʻAkikiki and ʻAkekeʻe are often observed foraging in mixed-species flocks along with other honeycreepers, such as ʻAnianiau or Anianiau (*Magumma parva*) and Kauaʻi ʻAmakihi or Kauai Amakihi (*Hemignathus kauaiensis*).

Assessing the biology and demography of both species is crucial to understanding and mitigating their population declines. The purpose of this study is to provide the first comprehensive reproductive assessment of these species. The first objective was to provide descriptive nesting data for ʻAkikiki and ʻAkekeʻe because few descriptions of their nests and breeding biology exist in the literature (Eddinger 1972a, 1972b, Pratt 1989, Foster et al. 2000, Powell 2007a, VanderWerf and Roberts 2008). The aspects of breeding biology that were examined were nest placement; length of construction, incubation and nestling period lengths; adult provisioning; and brood size. The second objective was to determine if low nesting success is a potential cause of their population declines, and if so, what factors are limiting nesting success.

METHODS

Study Area

Field studies were conducted at the remote Halepaakai field site in the central mountains of Kauai (Figure 1). The 100 ha study area lies between 1,205 and 1,400 m in elevation and consists of largely intact ʻōhiʻa-dominant wet forest. Halepaakai is located ~5 km west of Mount Waialeale, where mean annual precipitation is ~10 m (Giambelluca et al. 2013). This section of forest is encompassed by the Alakai Wilderness and is considered the best remaining habitat for indigenous forest bird species on Kauai.

Nest Searching and Monitoring

Nest searching and monitoring were conducted from March through June of 2012 and 2013, which is the peak of the breeding season for both species based on observations made in 2011 (R. L. Hammond personal observation). Halepaakai was divided into 4 subplots, and observers searched for nests following methods in Martin and Geupel (1993). Nests were monitored using a spotting scope located 10–25 m from nests to minimize disturbance and to improve observations of these high-canopy nesters. Nests were monitored every 2–3 days until termination, except when monitored near hatching or fledging, in which case they were typically monitored every 1–2 days. Nests were defined as successful when they fledged at least one chick (Martin and Geupel 1993) and failed when no chicks fledged. Even with spotting scopes, precise estimates of fledge dates were difficult to obtain. To avoid incorrectly assigning fates to nests, nests that terminated within 5 days of the projected fledge date with no obvious evidence of predation (e.g., chick remains in nest, disheveled nest) and those for which fledglings could not be located were characterized as unknown fate because chicks younger than 5 days from fledging were easily characterized as too young to fledge.

Fledglings were sought for up to 1 week after a nest was found empty and presumed to have fledged. A 70 m radius

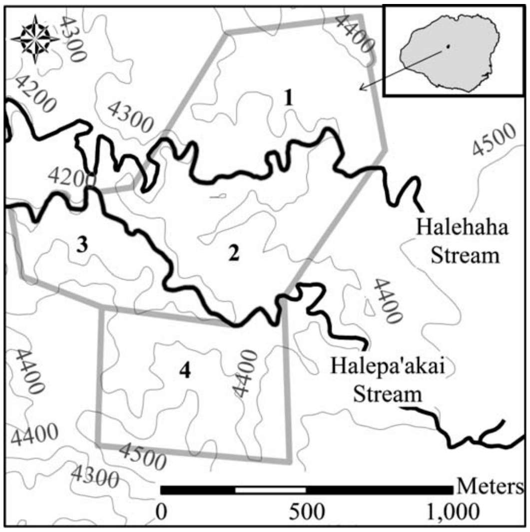

FIGURE 1. Halepaakai study area, depicting subplot boundaries, 100-foot contours, and major stream courses.

around nests was searched because fledglings of multiple honeycreeper species at Halepaakai (including ʻAkikiki) are capable of such movements on the first day of fledging (R. L. Hammond personal observation). Family groups from successful nests were monitored after fledging for the remainder of the season to determine juvenile dependency length.

Cause of failure was investigated using an SM-202T (Teklink Security, Ontario, CA, USA) wireless camera mounted on a telescoping 9 m pole, and nests were collected to further investigate failures when video was inconclusive. Presence of rodent feces, eggshell fragments, chick remains, and disturbance of nest material were used to identify predation events. To determine if weather directly caused nest failures, observers searched for eggs and nestlings that might have been ejected from nests when failures occurred within 2 days of a storm event (i.e. >40 mm of precipitation; Kuntz 2008). After nests terminated, nest height was measured using a clinometer.

Clutch size was not measured because of difficulty accessing nests and the need to minimize disturbance, but brood size was measured based on the number of chicks in nests that survived to the late nestling stage. Brood sizes and nest contents (i.e. eggs found in nests after a sole chick fledged) were used to estimate egg hatching rate (i.e. the proportion of total eggs laid that hatched). Hatching rate was estimated assuming that every nest initially contained 2 eggs (because brood sizes for both species were typically 2; see Results). A second, more conservative, estimate was also calculated by assuming that inaccessible nests that failed to hatch, or contained only one chick, originally contained one egg.

For each species, we calculated mean nest height ±SD; mean length of nest construction, incubation, and nestling periods ±SD; and brood size. Nests found in the building stage that did not progress to incubation were not used in these calculations. Nests were used to estimate incubation and nestling period lengths only when they were monitored for the entire period. Incubation was defined as the length in days from the date egg laying began to the earliest date on which hatching evidence (e.g., female popping on nest, feeding young, removing eggshells or fecal sacs) was recorded. Both species probably lay a 2-egg clutch at a rate of one egg daily (Eddinger 1972a, 1972b, VanderWerf and Roberts 2008). In 2012, hatching dates were estimated for nests found before incubation based on data from closely related species to target critical monitoring periods: Hawaii Creeper (*Loxops mana*; Lepson and Woodworth 2002) for ʻAkikiki, and ʻĀkepa or Hawaiian Akepa (*Loxops coccineus*; Lepson and Freed 1997) for ʻAkekeʻe. In 2013, hatching dates were projected from the start of incubation using the mean estimate for incubation period length derived from the 2012 breeding season. Nestling period lengths were defined as the length in days from the estimated hatching date to the first date of fledging. Fledging dates were projected from estimated hatching dates by using nestling period lengths of closely related species in 2012 or by using mean nestling period lengths from 2012 for nests in 2013 to target critical monitoring periods for catching fledgling events. Range estimates for incubation and nestling periods may be high or low by 1–3 days; exact hatching and fledging dates were rarely known because nests were not checked every day, the inside of nests were not visible to confirm hatching, and fledglings were rarely seen leaving the nest. Observations recorded during monitoring were compiled to draw inferences about male and female roles in the nesting cycle (e.g., nest building, incubation, provisioning of female and young). ArcMap 10.0 (ESRI, Inc.) was used to estimate nearest-neighbor nest distances (±SD) when home ranges of 2 simultaneously breeding pairs abutted.

ʻAkikiki at Halepaakai were captured and color-banded opportunistically or as part of a different study to estimate occupancy and habitat use since 2008 (L. A. Benhke personal communication). As a result, 2 pairs consisting of one banded member and 3 pairs with both members marked were monitored during this study. These color-banded birds were used to determine if pairs exhibited inter- and intra-annual mate fidelity and to document double-brooding and renesting attempts.

Statistical Analysis

Only nests that progressed to the incubation period and had known fates were used for statistical analysis. Nests' monitoring data were compiled for each species and used to derive estimates of nesting success ±SE using program MARK (White and Burnham 1999), which uses a maximum likelihood method of estimating a daily survival

TABLE 1. ʻAkikiki and ʻAkekeʻe nest fates at Halepaakai (A = abandoned, S = successful, F = failed, D = depredated, O = failure not attributed to predation, C = nest failed with unknown cause, U = unknown fate). Daily survival rate (DSR) ± SE and cumulative estimates of nesting success ± SE derived from the null model (i.e. constant DSR with no additive effects) and listed with confidence intervals in parentheses.

	n	A	S	F	D	O	C	U	DSR	Nesting success
2012										
ʻAkekeʻe	6	0	4	2	0	2	0	0	0.986 ± 0.010 (0.945–0.996)	0.60 ± 0.22 (0.16–1.03)
ʻAkikiki	11	1	6	3	1	0	2	1	0.986 ± 0.008 (0.957–0.995)	0.59 ± 0.18 (0.23–0.95)
2013										
ʻAkekeʻe	2	0	2	0	0	0	0	0	1.0	1.0
ʻAkikiki	9	2	7	0	0	0	0	0	1.0	1.0
Both years										
ʻAkekeʻe	8	0	6	2	0	2	0	0	0.990 ± 0.007 (0.963–0.998)	0.71 ± 0.17 (0.36–1.05)
ʻAkikiki	20	3	13	3	1	0	2	1	0.993 ± 0.004 (0.978–0.998)	0.77 ± 0.12 (0.53–1.00)

rate (DSR) for nests based on exposure days (Mayfield 1961). The generalized linear modeling framework provided in program MARK was used to build competing models of DSR that incorporated individual covariates.

The variables of nest height, nest age, and time across the breeding season (i.e. a linear or quadratic time trend as the breeding season progresses) were selected a priori and used to build 6 models for each species. Nest height might be an important predictor of nesting success if lower nests are more susceptible to rodent predation (Woodworth and Pratt 2009), as has been shown in the Oʻahu ʻElepaio or Oahu Elepaio (*Chasiempis ibidis*; VanderWerf 2012b). Alternatively, nests high in the canopy may have lower success if weather is a primary cause of nest failure (Simon et al. 2000, Kuntz 2008; Maui Forest Bird Recovery Project personal communication) because they are more exposed to severe weather events. Nest age was considered for examination to determine if nest failure was more likely to occur early or late in the nesting cycle. The linear (time) and quadratic ($time^2$) models of nesting success across the breeding season were considered to assess temporal effects potentially correlated with factors such as weather, food availability, and predators. Small sample sizes prevented the modeling of inter-annual effects on DSR. A global model was included to evaluate the additive effects of all variables modeled. The null model, having no additive effects to DSR, was used to derive estimates of constant DSR for each species, and these estimates were used to calculate cumulative estimates of nesting success for the entire nesting period by exponentiating the respective DSR to the mean nest period estimates from this study (see Results). For each species, a cumulative estimate of nesting success was calculated for each year and cumulatively for both years, and variances were calculated using the delta method (Powell 2007b). Akaike's Information Criteria with a small sample size correction (AIC_c) was used for model selection, and the model with the lowest AIC_c was considered best. Because no model in either model set received substantial support over other models in the set (i.e. ≥90%), model uncertainty was addressed by reporting parameter estimates for variables in each confidence set (Burnham and Anderson 2002).

RESULTS

ʻAkikiki

We located 20 ʻAkikiki nests during the study (Table 1). Nest construction began in early March, with most pairs showing signs of building by mid-March, and the last evidence of construction was observed in mid-May. All 20 ʻAkikiki nests were placed in ʻōhiʻa trees; 16 nests were placed in small branches just beneath the canopy, 3 were placed on a horizontal branch, and 1 was built next to the trunk. ʻAkikiki nest heights ranged from 4.5–16.6 m, with a mean of 9.2 ± 2.6 m ($n = 17$). Seven active nests were found when a neighboring pair's nest had already been located and was concurrently active. One of these nests was the nearest-neighbor for 2 nests, with the 2 different nearest-neighbor nests being active at different periods of time during its nest cycle. Nearest-neighbor nest distance was estimated at 268 ± 85 m ($n = 4$, range 194–363 m).

Nest construction lasted from 13 to >20 days based on 4 nests found near construction initiation. On one occasion a male was confirmed helping with nest construction. Incubation ranged from 13 to 20 days with a mean of 16.5 ± 2.7 days ($n = 7$), and the nestling period ranged from 16 to 23 days with a mean of 19.0 ± 2.3 days ($n = 7$). Males were never observed helping with incubation. Putative males often fed putative females at or near the nest during nest construction, incubation, and early in the nestling period. Both parents fed nestlings, but putative females received food from the putative male at the nest and transferred it to the chicks on the day of and day after hatch, after which time males fed nestlings directly.

Brood size was 2 chicks for 11 nests and 1 chick for 4 nests. Of the 1-chick nests, 2 nests contained 1 unhatched egg, and the other nests could not be accessed to determine clutch size. One of the unhatched eggs was

TABLE 2. Confidence model sets of daily survival rate (DSR) for nests of ʻAkikiki and Akekeʻe monitored in 2012 and 2013.

Model	*K*	ΔAIC_c	w_i
ʻAkikiki			
$S_{time}{}^{2,a}$	3	0.00	0.82
S_{null}	1	4.96	0.07
$S_{nest\ ht}$	2	6.00	0.04
S_{time}	2	6.35	0.03
$S_{nest\ age}$	2	6.98	0.02
ʻAkekeʻe			
$S_{nest\ ht}{}^{b}$	2	0.00	0.30
$S_{time}{}^{2}$	3	0.63	0.22
S_{null}	1	0.73	0.21
S_{global}	5	1.82	0.12
$S_{nest\ age}$	2	2.66	0.08
S_{time}	2	2.75	0.08

[a] $AIC_c = 26.86$
[b] $AIC_c = 19.47$

candled and confirmed to be infertile. Fifteen nests could be used to estimate hatching rate. Excluding a nest that failed early in incubation and assuming that 2 eggs were laid in every nest, hatching rate of eggs was as low as 87% but may have been as high as 93% if the 2 inaccessible nests containing only 1 chick originally had only 1 egg.

Monitoring of 3 pairs in which both members were banded suggested that ʻAkikiki were monogamous. The only color-banded pair that was monitored both years appeared to be monogamous throughout the study. Double-brooding was witnessed twice. In 2012, a color-banded pair successfully fledged a single chick that likely died within a week of fledging. This pair's second brood of 2 chicks progressed to the late nestling stage and may have fledged, but fledging was not confirmed because the field crews left at the end of June, prior to the projected fledge date. In 2013, a different color-banded pair was observed fledging 2 broods, and frequent observations of the male foraging with 2 hatch-year (HY) birds suggest males largely assume responsibility for the first brood when pairs double-brood. ʻAkikiki HYs were observed remaining with the family group until field crews left the field site each year, suggesting a juvenile dependency period of more than 3 months. One color-banded family group was observed with a second-year (SY) offspring at Halepaakai in January 2012. The pair's young separated from the parents in March. Based on the similarity of facial patterns of some of the breeding birds to those of HY birds, ʻAkikiki may nest in their second year, and one color-banded SY bird was observed attempting to build a nest without a mate in 2012. A renest may have been attempted for one pair after their first nest failed, but this could not be confirmed because the birds were not color-banded.

Sixteen ʻAkikiki nests had sufficient data for use in candidate modeling, spanning 415 exposure days. Three of these nests failed during the course of the study. One of the nest failures was apparently depredated by a rodent in the late nestling stage, one failed in the incubation stage but could not be accessed to determine a cause of failure, and the third failed in the late nestling stage but was seemingly undisturbed and contained one egg.

The model of quadratic time was the best model (Table 2), suggesting a decrease in nesting success at the middle of the breeding season, and differed from the second-best model by a ΔAIC_c of ≥ 2. The model of quadratic time received 82% of the support in the model set, but 95% confidence intervals (CI) around the parameter estimates included zero for this variable ($\beta_{time} = -2.97 \pm 3.42$, CI = –9.80 to 3.87 and $\beta_{time}{}^{2} = 0.05 \pm 0.06$, CI = –0.07–0.16) and all variables in the confidence set ($\beta_{nest\ height} = -0.25 \pm 0.24$, CI = –0.73–0.22; β_{time} 0.02 ± 0.03, CI = –0.04–0.08; $\beta_{nest\ age} = -0.001 \pm 0.054$, CI = –0.110–0.108), suggesting that a real effect of any variable is uncertain. The cumulative estimate of nesting success for the constant DSR was 0.77 ± 0.12 (Table 1).

ʻAkekeʻe

Eight ʻAkekeʻe nests were found during the study (Table 1). Nest construction probably begins in early March for some pairs based on one nest found in the late building stage on March 16, 2013, but most females in the study (*n* = 6) began incubating in late March or early April, suggesting that nest construction typically begins in mid to late March. All ʻAkekeʻe nests were located in the small branches in the canopy of ʻōhiʻa (*n* = 8), and mean nest height was 11.1 ± 2.3 m (range 8.7–14.5 m, *n* = 8). ʻAkekeʻe were difficult to follow, and nests were located for only a small proportion of breeding pairs in the study area.

Construction duration was not measured because no nests were found earlier than the late building stage. The mean length of the incubation period was 16.9 ± 2.0 days (range 15–19 days, *n* = 4), and the mean nestling period was 18.0 ± 2.3 days (range 16–22 days, *n* = 5). Only females were observed constructing and incubating the nest. Males often provisioned females at or near the nest during construction, incubation, and early in the nestling period. Males fed only females at the nest during hatching day and the day after hatch while females were solely responsible for feeding the hatchlings, but afterward both adults fed the nestlings.

Brood size was 2 chicks in 5 of 6 successful nests; the other successful nest had only 1 chick and it could not be accessed to determine clutch size. Both nest failures terminated during incubation; one was attributed to hatching failure because the female apparently incubated for 1 week after the projected hatching date before abandoning. The other failure was attributed to poor nest attendance by the female and was therefore excluded from hatching rate estimation. Based on 7 nests, hatching rate was 79% if 2 eggs were assumed to have been laid in each nest, but 93% if 1 egg was assumed to have been laid in the nest that failed to hatch and in the nest that fledged only 1 chick.

Breeding behavior and nesting were challenging to fully document for ʻAkekeʻe, and several aspects of their biology remain incompletely known. One pair may have raised a second brood, where the assumed male of a brooding female fed 2 HY birds multiple times at 20–100 m from the nest. Parentage was uncertain, however, because these birds were not color-banded and the female was never seen directly interacting with the family group. It is unclear if ʻAkekeʻe breed in their second year because no birds were color-banded, and they could not be discriminated by age. Fledglings were attended by both adults after departing the nest. Juvenile dependency was possibly as short as 2 months because HY birds were seen traveling and foraging in pairs late in the study period for 20–30 min without an adult nearby. These birds also showed signs of molting juvenile plumage and made only adult calls.

All 8 nests found had known fates and were used to build candidate models based on 207 exposure days. Of 2 total nest failures, one was attributed to poor nest attendance by the female, and one was apparently due to hatching failure.

All models were included in the 95% confidence set, and the model of nest height was the best model but received only 30% of the support in the model set (Table 2). The ΔAIC_c for the nest height model differed from the second-best model (quadratic time) and the third-best model (null) by 0.63 and 0.73, respectively, suggesting that all 3 models have some explanatory value. Additionally, 95% confidence intervals around all parameter estimates included zero ($\beta_{\text{nest height}} = -0.67 \pm 0.51$, CI $= -1.68$ to 0.35; $\beta_{\text{time}} = -0.70 \pm 0.90$, CI $= -2.49$ to 1.10 and $\beta_{\text{time}}{}^{2} = 0.007 \pm 0.010$, CI $= -0.013$ to 0.027; $\beta_{\text{nest age}} = -0.02 \pm 0.07$, CI $= -0.17$ to 0.12; $\beta_{\text{time}} = 0.004 \pm 0.026$, CI $= -0.048$ to 0.055), suggesting that all variables modeled may not be good predictors of DSR. The cumulative estimate of nesting success for constant DSR was 0.71 ± 0.17 (Table 1).

DISCUSSION

Nesting success was higher than expected for both of these declining species. Estimates of nesting success for ʻAkikiki and ʻAkekeʻe were ~25–31% higher than the overall success rate of Hawaiian forest bird nest studies (Woodworth and Pratt 2009). Of the 5 nest failures that occurred during this study, known causes of failure were attributed to predation, poor nest attendance, and hatching failure. No single cause dominated nest failures.

Nest predation did not severely impact nesting success of either species, which was unexpected because predation is considered a primary cause of nest mortality for many birds (Ricklefs 1969, Martin 1992, 1995). Hawaiian forest bird nests are suggested to be highly susceptible to predation by introduced mammals because they evolved in the absence of native mammalian predators (Tomich 1969, Atkinson 1977, Woodworth and Pratt 2009). Rats, primarily black rats (*Rattus rattus*), were implicated in 19% of nest failures ($n = 21$) of the Puaiohi or Small Kauai Thrush (*Myadestes palmeri*), a native thrush that nests in similar habitat on Kauai (Snetsinger et al. 2005). The higher predation rate in Puaiohi might be attributed to their differing breeding behavior compared to Hawaiian honeycreepers, or the differences in vegetation composition between Halepaakai and Snetsinger's study site. Oʻahu ʻElepaio are severely impacted by rodents (VanderWerf 2001), and they might be evolving to build nests at greater heights in response to high rates of nest predation by rodents (VanderWerf 2012b). Oʻahu ʻElepaio is a member of the Monarchidae family, however, and its breeding behavior differs markedly from Hawaiian honeycreepers (Conant 1977, Pratt 2005). Additionally, VanderWerf (2012b) conducted his research in a nonnative forest at low elevation on the island of Oahu that differs substantially in structure and composition from Halepaakai. The research presented here showed no evidence of a relationship between nest height and nesting success. In a larger study of nesting native birds at Halepaakai consisting of 124 nests of 6 species, there was also no relationship between nesting success and nest height (Hammond 2014). ʻAkekeʻe is the highest arboreal-nesting native passerine at Halepaakai, but the ʻAkikiki nest height range overlaps considerably with that of other nesting birds (Hammond 2014).

Substantial rainfall and high winds are common in the Hawaiian Islands, and such events are a major cause of nest mortality for ʻIʻiwi or Iiwi (*Vestiaria coccinea*) on Hawaii (Kuntz 2008) and the Maui Parrotbill (*Pseudonestor xanthophrys*) on Maui (Simon et al. 2000; Maui Forest Bird Recovery Project personal communication) and are thought to be an important factor for the Hawaii Creeper (Lepson and Woodworth 2002). Of the 5 nest failures that occurred during this study, none could be directly attributed to storm events, and nest failures were not more likely to occur in the months when precipitation was greatest (Mar–Apr in 2012 and May–Jun in 2013; R. L. Hammond personal observation). This result may have been due in part to the different topography on Kauai compared to Maui and Hawaii. Halepaakai is located on a plateau with meandering ridges and valleys that may provide pockets of shelter from severe weather events, whereas the aforementioned studies were conducted on windward mountain slopes. Additionally, studies on Maui and Hawaii were conducted at higher elevations, and wind speed increases with elevation in the Hawaiian Islands (Giambelluca and Nullet 1991).

Hatching failure occurred in both species and may become an important factor for these small populations if population bottlenecks lead to inbreeding (Briskie and Mackintosh 2004, Heber and Briskie 2010), but this study found no strong indication that hatching failure was high in ʻAkikiki and ʻAkekeʻe populations. Hatching rates for ʻAkikiki and ʻAkekeʻe, with an assumed 2-egg clutch, were slightly lower than the estimated hatching rate of 91% that occurs in large, contiguous passerine populations (Koenig 1982), but these estimates should be considered cautiously because sample sizes were small. The conservative estimates for ʻAkikiki and ʻAkekeʻe hatching rates in this study were 2% greater than in contiguous populations.

The numbers of nests and nest failures used for modeling were small, and these results are uncertain because the confidence intervals around parameter estimates for all variables bounded zero. The nest height model ranked highest for ʻAkekeʻe, but there was high model uncertainty within the model set. For ʻAkikiki, the model of quadratic time ranked highest, but there was model uncertainty. If the 3 ʻAkikiki nest failures do accurately portray a pattern of decreasing DSR at the middle of the breeding season for this population, temporal variability in factors such as food availability and predator behavior may be responsible. Nest densities were highest at Halepaakai in the middle of the breeding season (Hammond 2014), and higher nest densities might have increased competition inter- and intra-specifically. Density-dependent nest predation (Martin 1988) may have also increased nest failure during the peak of nest activity. Because 2 nests failed due to unknown causes, and few nests failed overall, it was unclear if either of these factors caused the quadratic trend in DSR. To determine if a true temporal pattern exists in the nesting success of ʻAkikiki and what factors drive it, a more robust sample size of nests and a broader investigation of ʻAkikiki ecology is necessary.

The breeding biology of ʻAkikiki and ʻAkekeʻe was similar to that of other members of the honeycreeper family. Hawaiian honeycreepers tend to be socially monogamous (Pratt 2005), and ʻAkikiki followed this trend; however, the lack of color-banded birds prevented an assessment of the ʻAkekeʻe mating system. The duration of the nesting season of ʻAkikiki and ʻAkekeʻe probably extends from early March through July, but some pairs may have nested earlier or later than documented. ʻAkikiki males apparently play a minor role in nest construction, as do some other insectivorous honeycreepers (Eddinger 1970, VanderWerf 1998, Simon et al. 2000), but ʻAkekeʻe males, like the closely related ʻĀkepa (Lepson and Freed 1997), were never seen carrying nest material. One nest documented by Eddinger (1972b) suggests, however, that males sometimes help with construction. All nests in this study were placed in ʻōhiʻa trees, as is typical for most Hawaiian honeycreepers nesting in wet ʻōhiʻa forests (Woodworth and Pratt 2009). Kauaʻi ʻElepaio or Kauai Elepaio (*Chasiempis sclateri*), a native monarch flycatcher, nests in at least 7 native substrates at Halepaakai, suggesting that other tree species are usable (Hammond 2014).

Like other Hawaiian forest birds, ʻAkikiki and ʻAkekeʻe nest cycles were long compared to north temperate taxa. ʻAkikiki and ʻAkekeʻe mean incubation periods were ~4 days longer than the mean estimate for Fringillid relatives of the north-temperate mainland, and nestling periods were 3–4 days longer (Woodworth and Pratt 2009). The range estimates of incubation and nestling period lengths in this paper are relatively large, likely due to the inability of observers to reliably assess exact dates of nest initiation, hatching, and fledging.

ʻAkikiki HYs were never observed dispersing from their natal home range before the end of the field season. In one case, ʻAkikiki juvenile dependency extended into the second year as it does in some other insectivorous honeycreepers, such as the Maui Parrotbill and ʻAkiapōlāʻau or Akiapolaau (*Hemignathus monroi*; Ralph and Fancy 1996, Simon et al. 2000); however, this observation may have been anomalous considering HY Hawaii Creepers were typically observed leaving the family group by October (Lepson and Woodworth 2002). ʻAkekeʻe juvenile dependency might be shorter than for the closely related ʻĀkepa, which can remain with the adults until October (Lepson and Freed 1997). ʻAkekeʻe HYs appear to leave the adults as early as 2 months post-fledging, but close monitoring of multiple pairs is necessary for confirmation. ʻAkikiki double-brood, and ʻAkekeʻe probably double-brood based on observations of one unbanded pair. Both species probably renest when nests fail early in the season (prior to June), but nests were not reused.

Because sample sizes in this study were small, it would be useful to conduct additional nesting studies of both species to confirm the relatively high nesting success rates of both endangered species. Because funding is limited and ʻAkikiki and ʻAkekeʻe populations are difficult to access, however, future research may be more effective if focused on post-fledgling, juvenile, and adult survival. Results presented in this paper suggest that low nesting success may not be a primary cause of decline for ʻAkikiki and ʻAkekeʻe. In addition to having higher nesting success than the overall rate for Hawaiian forest bird nest studies, ʻAkikiki and ʻAkekeʻe nesting success estimates from this study were 32–55% greater than overall estimates from multi-species studies in the temperate mainland (Powell and Steidl 2000, Heltzel and Earnst 2006, Dellinger et al. 2007) and 55–65% higher than mean nesting success of tropical mainland passerines derived from a meta-analysis of multiple studies (Brawn et al. 2011). This difference implies that nesting success is unlikely to be the demographic parameter that is causing ʻAkikiki and ʻAkekeʻe populations to decline, and efforts to increase their nesting success might not be the most effective means of achieving population stability or increasing population numbers.

Hawaiian forest birds share many life history traits with mainland tropical species, such as greater adult survival rates than temperate mainland birds, and apparently greater investment of energy into survival than into reproduction (Martin 1996, Badyaev 1997, Woodworth and Pratt 2009, Tarwater et al. 2011). Lack of stress due to migration and seasonal bottlenecking, in addition to a more constant availability of food resources, may maintain tropical species at population levels close to carrying capacity, such that the need for annual recruitment is lower than in temperate species (Skutch 1985). There is no estimate for ʻAkikiki and ʻAkekeʻe adult survival; however, if this high adult survival trend holds true for ʻAkikiki and ʻAkekeʻe, and considering their apparent high nesting success, survival rates of dependent young, juvenile birds, and adults warrant investigation. Determining if one of these demographic parameters is low may provide access to a more effective means of managing these species. Mitigating the demographic parameter that has the greatest negative effect on the population is imperative to meet the goal of effectively recovering ʻAkikiki and ʻAkekeʻe to self-sustaining populations. Focused management actions that will be expeditious are necessary considering the uncertainty of future funding and the unknown rate at which these populations are declining.

ACKNOWLEDGMENTS

We are most indebted to the passionate field biologists who helped collect these data in this challenging environment: Richard Aracil, Lucas Behnke, Adam Elzinga, Gemma Green, Aaron Hulsey, Joey Leibrecht, Liza Olson, Nicki Ozaki, Allison Salas, Laura Southcott, and Alex Wang. We also thank Tad Theimer for intellectual contributions to this study and for comments on multiple drafts of this manuscript.

Funding statement: Financial support for this project largely came from Hawaii Division of Forestry and Wildlife, Pacific Cooperative Studies Unit, University of Hawaii, United States Fish and Wildlife Service, and Northern Arizona University. No funders had any influence on the content of the submitted manuscript, nor did they require approval of the final manuscript to be published.

Ethics statement: All research was conducted under Northern Arizona University IACUC protocol 11-013 and USFWS federal fish and wildlife permit #MB673451-0.

LITERATURE CITED

Atkinson, I. A. E. (1977). A reassessment of factors, particularly *Rattus rattus*, that influenced the decline of endemic forest birds in the Hawaiian Islands. Pacific Science 31:109–133.

Atkinson, C. T., and D. A. LaPointe (2009). Ecology and pathogenicity of avian malaria and pox. In Conservation Biology of Hawaiian Forest Birds (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. 234–252.

Badyaev, A. V. (1997). Avian life history variation along altitudinal gradients: An example with cardeuline finches. Oecologia 111:365–374.

Brawn, J. D., G. Angehr, N. Davros, W. D. Robinson, J. N. Styrsky, and C. E. Tarwater (2011). Sources of variation in nesting success of understory tropical birds. Journal of Avian Biology 42:61–68.

Briskie, J. V., and M. Mackintosh (2004). Hatching failure increases with severity of population bottlenecks in birds. Proceeding of the National Academy of Sciences USA 101: 558–561.

Buchanan, G. M., P. F. Donald, and S. H. M. Butchart (2011). Identifying priority areas for conservation: A global assessment for forest-dependent birds. PLOS One 6:1–10.

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

Conant, S. (1977). The breeding biology of the Oʻahu ʻElepaio. Wilson Bulletin 89:193–210.

Conant, S., H. D. Pratt, and R. J. Shallenberger (1998). Reflections on a 1975 expedition to the lost world of the Alakaʻi and other notes on the natural history, systematics, and conservation of Kauaʻi birds. Wilson Bulletin 110:1–22.

Dellinger, R. L., P. B. Wood, P. D. Keyser, and G. Seidel (2007). Habitat partitioning of four sympatric thrush species at three spatial scales on a managed forest in West Virginia. The Auk 124:1425–1438.

Eddinger, C. R. (1970). A study of the breeding biology of four Hawaiian honeycreepers (Drepanididae). Ph.D. dissertation, University of Hawaii at Manoa, Honolulu, HI, USA.

Eddinger, C. R. (1972a). Discovery of the nest of the Kauai creeper. The Auk 89:673–674.

Eddinger, C. R. (1972b). Discovery of the nest of the Kauai ʻĀkepa. Wilson Bulletin 84:95–97.

Foster, J. T., J. M. Scott, and P. W. Sykes (2000). ʻAkikiki (*Oreomystis bairdi*). In The Birds of North America 522 (F. B. Gill and A. Poole, Editors). Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington DC, USA.

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 Alakaʻi Swamp, Kauaʻi. 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.

Giambelluca, T. W., and D. Nullet (1991). Influence of the trade-wind inversion on the climate of a leeward mountain slope in Hawaii. Climate Research 1:207–216.

Gorresen, M. P., R. J. Camp, M. D. Reynolds, B. L. Woodworth, and T. K. Pratt (2009). Status and trends of native Hawaiian songbirds. In Conservation Biology of Hawaiian Forest Birds (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. 108–136.

Hammond, R. L. (2014). Factors affecting nesting success of forest birds on Kaua'i Island. M.S. thesis, Northern Arizona University, Flagstaff, AZ, USA.

Heber, S., and J. V. Briskie (2010). Population bottlenecks and increased hatching failure in endangered birds. Conservation Biology 24:1674–1678.

Heltzel, J. M., and S. L. Earnst (2006). Factors influencing nest success of songbirds in aspen and willow riparian areas in the Great Basin. The Condor 108:842–855.

Koenig, W. D. (1982). Ecological and social factors affecting hatchability of eggs. The Auk 99:526–536.

Kuntz, W. A. (2008). The importance of individual behavior to life history and conservation: Breeding and movement biology in the 'I'iwi (*Vestiaria coccinea*). Ph.D. dissertation, University of Hawaii at Manoa, Honolulu, HI, USA.

Leonard, D. L. (2008). Recovery expenditures for birds listed under the US Endangered Species Act: The disparity between mainland and Hawaiian taxa. Biological Conservation 141: 2054–2061.

Lepson, J. K., and L. A. Freed (1997). 'Ākepa (*Loxops coccineus*). In The Birds of North America 294 (F. B. Gill and A. Poole, Editors). Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington DC, USA.

Lepson, J. K., and B. L. Woodworth (2002). Hawaii Creeper (*Loxops mana*). In The Birds of North America 680 (F. B. Gill and A. Poole, Editors). Academy of Natural Sciences, Philadelphia, PA, USA, and American Ornithologists' Union, Washington DC, USA.

Loope, L. L., F. G. Howarth, F. Kraus, and T. K. Pratt (2001). Newly emergent and future threats of alien species to Pacific birds and ecosystems. In Evolution, Ecology, Conservation, and Management of Hawaiian Birds: A Vanishing Avifauna (J. M. Scott, S. Conant, and C. van Riper, III, Editors). Studies in Avian Biology 22:291–304.

Martin, T. E. (1988). Processes organizing open-nesting bird assemblages: Competition or nest predation? Evolutionary Ecology 2:37–50.

Martin, T. E. (1992). Breeding season productivity: What are the appropriate habitat features for management? In Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan and D. W. Johnston, Editors). Smithsonian Institute Press, Washington, DC, USA. pp. 455–473.

Martin, T. E. (1995). Avian life-history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101–127.

Martin, T. E. (1996). Life-history evolution in tropical and south temperate birds: What do we really know? Journal of Avian Biology 27:263–272.

Martin, T. E., and G. R. Geupel (1993). Nest-monitoring plots: Methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

Mayfield, H. F. (1961). Nesting success calculated from exposure. Wilson Bulletin 73:255–261.

Olson, S. L., and H. F. James (1982). Prodromus of the fossil avifauna of the Hawaiian Islands. Smithsonian Contributions to Zoology 365:1–59.

Powell, A. (2007a). Habitat use of the 'Akikiki *Oreomystis bairdi* (Aves: Drepanidinae): A Hawaiian forest bird in decline. M.S. thesis, University of East Anglia, Norwich, UK.

Powell, L. A. (2007b). Approximating variance of demographic parameters using the delta method: A reference for avian biologists. The Condor 109:949–954.

Powell, B. F., and R. J. Steidl (2000). Nesting habitat and reproductive success of southwestern riparian birds. The Condor 102:823–831.

Pratt, H. D. (1989). Species limits in Akepas (Drepanidinae: Loxops). The Condor 91:933–940.

Pratt, H. D. (2005). The Hawaiian Honeycreepers: Drepanidinae. Oxford University Press, Oxford, UK.

Ralph, C. J., and S. G. Fancy (1996). Aspects of the life history and foraging ecology of the endangered 'Akiapōlā'au. The Condor 98:312–321.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

Scott, J. M., S. Mountainspring, F. L. Ramsey, and C. B. Kepler (1986). Forest bird communities of the Hawaiian Islands. Studies in Avian Biology 9.

Simon, J. C., T. K. Pratt, K. E. Berlin, and J. R. Kowalsky (2000). Reproductive ecology of the Maui Parrotbill. Wilson Bulletin 112:482–490.

Skutch, A. F. (1985). Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithological Monographs 36:575–594.

Snetsinger, T. J., C. M. Herrmann, D. E. Holmes, C. D. Hayward, and S. G. Fancy (2005). Breeding ecology of the Puaiohi (*Myadestes palmeri*). Wilson Bulletin 117:72–84.

Tarwater, C. E., R. E. Ricklefs, J. D. Maddox, and J. D. Brawn (2011). Pre-reproductive survival in a tropical bird and its implications for avian life histories. Ecology 92:1271–1281.

Tomich, P. Q. (1969). Mammals in Hawaii. Bishop Museum Press, Honolulu, HI, USA.

U.S. Fish and Wildlife Service (USFWS) (1983). Kauai forest birds recovery plan. USFW, Portland, OR, USA.

U.S. Fish and Wildlife Service (USFWS) (2006). Revised recovery plan for Hawaiian forest birds. USFW, Region 1, Portland, OR, USA.

van Riper, C., III, S. G. van Riper, M. L. Goff, and M. Laird (1986). The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecological Monographs 56:327–344.

VanderWerf, E. A. (1998). Breeding biology and territoriality of the Hawaii Creeper. The Condor 100:541–545.

VanderWerf, E. A. (2001). Rodent control decreases predation on artificial nests in O'ahu 'Elepaio habitat. Journal of Field Ornithology 72:448–457.

VanderWerf, E. A. (2012a). Hawaiian bird conservation action plan. Honolulu, HI, USA.

VanderWerf, E. A. (2012b). Evolution of nesting height in an endangered Hawaiian forest bird in response to a non-native predator. Conservation Biology 26:905–911.

VanderWerf, E. A., L. H. Crampton, J. S. Diegmann, C. T. Atkinson, and D. L. Leonard (2014). Survival estimates of wild and captive-bred released Puaiohi, an endangered Hawaiian thrush. The Condor: Ornithological Applications 116:609–618.

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

Vitousek, P. M., L. L. Loope, and C. P. Stone (1987). Introduced species in Hawaii: Biological effects and opportunities for ecological research. Trends In Ecology and Evolution 2:224–227.

White, G. C., and K. P. Burnham (1999). Program MARK: Survival estimation from populations of marked animals. Bird Study 46:S120–S138.

Woodworth, B. L., and T. K. Pratt (2009). Life history and demography of Hawaiian forest birds. In Conservation Biology of Hawaiian Forest Birds (T. K. Pratt, C. A. Atkinson, P. Banko, J. Jacobi, and B. L. Woodworth, Editors). Yale University Press, New Haven, CT, USA. pp. 194–233.