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RESEARCH ARTICLE

Survival estimates of wild and captive-bred released Puaiohi, an endangered Hawaiian thrush

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ABSTRACT

Estimating and monitoring adult and juvenile survival are vital to understanding population status, informing recovery planning for endangered species, and quantifying the success of management. We used mark–recapture models to estimate apparent annual survival of the Puaiohi (*Myadestes palmeri*), an endangered thrush endemic to the Hawaiian island of Kauai, from 2005 to 2011. Our sample included 87 wild birds and 123 captive-bred birds that were released at various ages. Survival was higher for wild adult males (0.71 $\pm$ 0.09) than for wild adult females (0.46 $\pm$ 0.12). Survival of wild juveniles (0.23 $\pm$ 0.06) was lower than that of wild adults of both sexes, indicating that recruitment may limit population growth. Captive-bred birds released when $<$1 yr old had survival (0.26 $\pm$ 0.21) comparable with that of wild juveniles, but captive-bred birds released at 1–3 yr old had very low survival (0.05 $\pm$ 0.06). Only 8 of 123 (7%) captive birds were seen again after release. Two wild birds resighted five years after marking are the oldest known individuals, being at least six years of age. Malarial infection did not affect survival of wild Puaiohi, unlike many Hawaiian forest birds. The difference between adult male and adult female survival is consistent with rat (*Rattus* spp.) predation of females on the nest as a major source of mortality. As such, attempting to reduce nest predation by controlling rats may be the best available management option. Releasing captive-bred birds has had little effect on the wild population in recent years.

Keywords: avian malaria, captive breeding, endangered species, mark–recapture, *Myadestes palmeri*, population biology, rat predation, reintroduction

Estimaciones de supervivencia de individuos silvestres y cautivos de *Myadestes palmeri*, una especie en peligro de Hawái

RESUMEN

Las estimaciones y el monitoreo de la supervivencia de adultos y juveniles son vitales para entender el estatus poblacional, apoyar planes de recuperación de especies en peligro y cuantificar el éxito del manejo. Usamos modelos de marcado y recaptura para estimar la supervivencia anual aparente de *Myadestes palmeri*, una especie en peligro endémica de la isla hawaiana de Kauai, entre 2005 y 2011. Nuestro muestreo incluyó 87 aves silvestres y 123 aves criadas en cautiverio que fueron liberadas a distintas edades. La supervivencia fue más alta para los machos adultos silvestres (0.71 $\pm$ 0.09) que para las hembras adultas silvestres (0.46 $\pm$ 0.12). La supervivencia de los juveniles silvestres fue aún más baja (0.23 $\pm$ 0.06), indicando que el reclutamiento puede limitar el crecimiento poblacional. Las aves criadas en cautiverio liberadas cuando tenían $<$1 año de edad presentaron supervivencias comparables (0.26 $\pm$ 0.21) a las de los juveniles silvestres, pero las aves criadas en cautiverio liberadas a las edades de entre 1 y 3 años tuvieron una supervivencia muy baja (0.05 $\pm$ 0.06). Solo 8 de 123 (7%) aves cautivas fueron vistas luego de ser liberadas. Dos aves silvestres observadas de nuevo cinco años después de ser marcadas son los individuos conocidos más viejos, de al menos seis años de edad. La infección de malaria no afectó la supervivencia de los individuos silvestres de *M. palmeri*, a diferencia de muchas especies de aves de bosque de Hawái. La diferencia entre la supervivencia de los adultos macho y hembra es consistente con la depredación de hembras en el nido causada por ratas (*Rattus* spp.), como una causa principal de mortalidad. Si es así, los intentos de reducir la depredación de los nidos mediante el control de las ratas puede ser la mejor opción disponible de manejo. La liberación de aves criadas en cautiverio ha tenido un efecto menor en la población silvestre en los últimos años.

Palabras clave: biología poblacional, cría en cautiverio, depredación por ratas, especie en peligro, malaria aviar, marcado–recaptura, *Myadestes palmeri,* reintroducción

INTRODUCTION

Estimates of age- and sex-specific demographic parameters are essential to understanding and managing populations, whether for conservation or resource use (Nur and Sydemann 1999, Sandercock et al. 2000, Martin 2002, VanderWerf 2008). Such data can be used to analyze population trends and viability, indicate habitat quality, identify which sex or life stages are most limiting or sensitive, and determine efficacy of management (VanderWerf 2009, Bulluck et al. 2013, Smith et al. 2013). In the case of species listed under the U.S. Endangered Species Act, such estimates often are a crucial component of the listing, recovery planning, and delisting processes (U.S. Fish and Wildlife Service 2006). For Hawaiian forest birds, many of which have small and declining populations, acquiring demographic data has been identified as a high priority (U.S. Fish and Wildlife Service 2006). However, the very rarity of endangered species often makes it difficult to obtain this information.

The Puaiohi, or Small Kauai Thrush (*Myadestes palmeri*), is a case in point. A medium-sized (37–43 g) thrush endemic to the island of Kauai, Hawaii, USA, it was listed as endangered in 1967 and has been the subject of recovery planning for more than 30 years (U.S. Fish and Wildlife Service 1983, 2006), yet vital demographic data are still lacking. A rare and cryptic bird, it has never been considered common, is difficult to detect, and estimates of its population size and trend have been difficult to obtain (Scott et al. 1986, Foster et al. 2004, Gorresen et al. 2009). Surveys from 1968 to 1973 resulted in a population estimate of 176 $\pm$ 96 birds (U.S. Fish and Wildlife Service 1983), but this is regarded as an underestimate because surveys were conducted primarily on ridge tops, not in the stream valleys preferred by Puaiohi. Subsequent surveys using improved methods led Woodworth et al. (2009) to report an estimate of 300–500 birds, though the data upon which their estimate was based have not been published.

Although formerly distributed island-wide (Burney et al. 2001), the species is now restricted to $<$20 km^2 of wet ($>$6,000 mm annual rainfall) and mesic montane forest above 1,050 m elevation in the remote southern and central Alakai plateau (Scott et al. 1986, Snetsinger et al. 1999). Puaiohi generally nest in cavities or on cliff ledges along deeply incised streams (Figure 1), but may rarely nest in trees (Snetsinger et al. 2005), and have also used artificial nest structures (Pitt et al. 2011). They feed on insects and fruits of native plants (Snetsinger et al. 1999).

Factors thought to be currently threatening the Puaiohi include: introduced predators, particularly the black or ship rat (*Rattus rattus*); diseases carried by introduced mosquitoes, primarily avian malaria (*Plasmodium relictum*) and avian poxvirus (*Poxvirus avium*); habitat loss and degradation; and stochastic events such as hurricanes (U.S. Fish and Wildlife Service 2006). Avian malaria and its mosquito vector are intolerant of cool temperatures, and in Hawaii they are restricted to elevations below 1,500 m. However, there are no areas on Kauai high enough for temperature to prevent the seasonal incursion of malaria (Benning et al. 2002). Puaiohi depend on areas of intact native forest for foraging and nesting, but these forests have been, and continue to be, negatively affected by invasive alien plants and feral ungulates (Foster et al. 2004, Woodworth et al. 2009). Feral ungulates degrade native forest by browsing on foliage, eroding soil, disrupting regeneration, facilitating the spread of invasive alien plants, and creating breeding habitat for mosquitoes (Cabin et al. 2000, Scott et al. 2001, U.S. Fish and Wildlife Service 2006). Although the habit of nesting on steep cliffs may provide some protection for Puaiohi against predators, in some years up to 38% of nests have been depredated by rats (Tweed et al. 2006). Finally, single-island endemics such as the Puaiohi are inherently more vulnerable to extinction than widespread species because of the higher risks posed to a single population by random demographic fluctuations and localized catastrophes such as hurricanes, which struck Kauai in 1983 and 1992 (Wiley and Wunderle 1994).

In an effort to help recover the Puaiohi, a captive breeding program was initiated in 1996–1997, when 15 eggs were taken into a breeding facility run by the Hawaii Endangered Bird Conservation Program (Kuehler et al. 2000). Puaiohi bred well in captivity; the first cohort of captive-bred birds was released back into the wild in 1999, and 222 Puaiohi were released at three sites through 2012 (Switzer et al. 2013). Short-term (28-day) survival was measured for 55% of released birds ($n = 123$) using radio-telemetry, and averaged 66% among years (range: 25–100%; Switzer et al. 2013). Snetsinger et al. (2005) provided limited data on survival of wild Puaiohi from 1997 to 1998, and Tweed et al. (2003, 2006) reported on survival and recruitment of captive-bred Puaiohi released during the first three years of the program, 1999–2001, but longer-term survival estimates of wild and released birds are needed. We estimated survival of wild and captive-bred Puaiohi using mark–resight data from 2005 to 2011 in order to help assess threats to the Puaiohi and to evaluate the contribution of the captive breeding program. We estimated survival during only this period because there was insufficient monitoring effort of wild and released birds in other years. Our objectives were to: 1) estimate survival of wild Puaiohi by sex and age, 2) assess the effect of malaria on survival, 3) estimate survival of captive-bred Puaiohi released at different ages, and 4) evaluate the contribution of the release program to Puaiohi recovery.

METHODS

Study Area and Duration

We studied Puaiohi from 2005 to 2011 at four sites in the Alakai Wilderness Preserve on Kauai: Kawaikoi, Koaie,

FIGURE 1. Puaiohi at nest with nestlings, Kawaikoi, Kauai, Hawaii, USA. Photo credit: E. VanderWerf

Mohihi, and Halepaakai (Figure 2). These sites range in elevation from 1,123 m to 1,303 m. The Koaie, Mohihi, and Halepaakai areas support relatively large numbers of Puaiohi, but Kawaikoi is on the edge of the species' range and supports only a few birds (Snetsinger et al. 1999, Woodworth et al. 2009). Wild Puaiohi were banded and studied previously in the Mohihi area from 1995 to 1998 (Snetsinger et al. 2005), and captive-bred Puaiohi were released at Koaie, Kawaikoi, and Halepaakai from 1999 to 2004 (Tweed et al. 2003, Woodworth et al. 2009), but we did not observe any of the previously marked or released birds at these sites during our study.

The habitat in this region consists of wet and mesic montane forest dominated by ohia (*Metrosideros polymorpha*), koa (*Acacia koa*), olapa (*Cheirodendron trigynum*), lapalapa (*C. platyphyllum*), ohia ha (*Syzygium sandwicensis*), kawau (*Ilex anomala*), and kolea (*Myrsine lessertiana*), with a diverse understory of native plants including ohelo (*Vaccinium calycinum*) and kanawao (*Broussaisia arguta*). Annual rainfall across the area averages 5 m (Giambelluca et al. 2013), but a gradient of decreasing rainfall occurs from northeast to southwest.

Marking and Disease Sampling of Wild Birds

We captured wild Puaiohi adults and fledglings in mist nets and banded them with a unique combination of a U.S. Geological Survey numbered aluminum leg band and three plastic colored leg bands. We occasionally used playbacks of recorded vocalizations to increase capture rates, particularly for males. We banded nestlings in nests that could be accessed without endangering them or staff. Male and female Puaiohi are similar in appearance (Snetsinger et al. 1999), so we determined their sex by the presence of a cloacal protuberance (males) or brood patch (females), by singing behavior (males), or by being paired with a bird of known sex. In a few cases the sex of an adult was not determined ($n = 2$) and we excluded those birds from our analyses. Juvenile Puaiohi have distinctive spots and scalloping on their breast and wing feathers through their second year (Snetsinger et al. 1999), allowing identification of hatch-year (HY) and second-year (SY) birds. We did not know the sex of nestlings unless they were resighted in subsequent years and we were able to determine their sex at that time using the above methods. Our sample contained 87 wild birds, including 19 adult males, 16 adult females, and 61 juveniles or nestlings (of which 9 were resighted and sexed as adults).

We collected a blood sample not exceeding 1% of body weight from the brachial vein of a subset of birds ($n = 16$ adults and 36 nestlings) and used these samples to test for avian malaria. Blood was collected into a heparinized capillary tube and transferred to a tube containing 100 μl of lysis buffer (0.1 M Tris, pH 8.0, 0.1 M EDTA, 2% SDS), stored on wet ice until return to the laboratory, and then frozen at −70°C for long-term storage.

Purified DNA for PCR analysis was extracted from lysed blood cells with Qiagen DNeasy tissue extraction kits (Qiagen, Valencia, California, USA) according to the manufacturer's protocol, but we increased the initial incubation times with Proteinase K to overnight to increase the yield of DNA. DNA was recovered from extraction columns with Tris ethanolamine buffer, measured by spectrophotometry with a Nanodrop spectrophotometer to assess purity and determine DNA concentration, and stored frozen until use in PCR reactions.

We used two sets of published PCR primers for detecting infection with *Plasmodium*. We screened all samples with primers 213F/372R in 25 μl reaction volumes with 100 ng of DNA template following procedures described by Beadell and Fleischer (2005). These primers amplify a short, 160 bp fragment of the mitochondrial cytochrome b gene. When a sample tested positive by PCR with primers 213F/372R, we ran a confirmatory nested PCR reaction using primers developed for parasite ribosomal DNA as described by Jarvi et al. (2002) using nested primers PRNST3 and PRNST5 to amplify a 498 bp product. All PCR reactions were run with a positive control consisting of DNA extracted from a Pekin duckling with an intense experimental infection with *P. relictum* and a negative control that substituted water for DNA.

Releases of Captive-bred Birds

Our sample included 123 captive-bred birds, of which 27 were released at Halepaakai from 2005 to 2006, 87 were

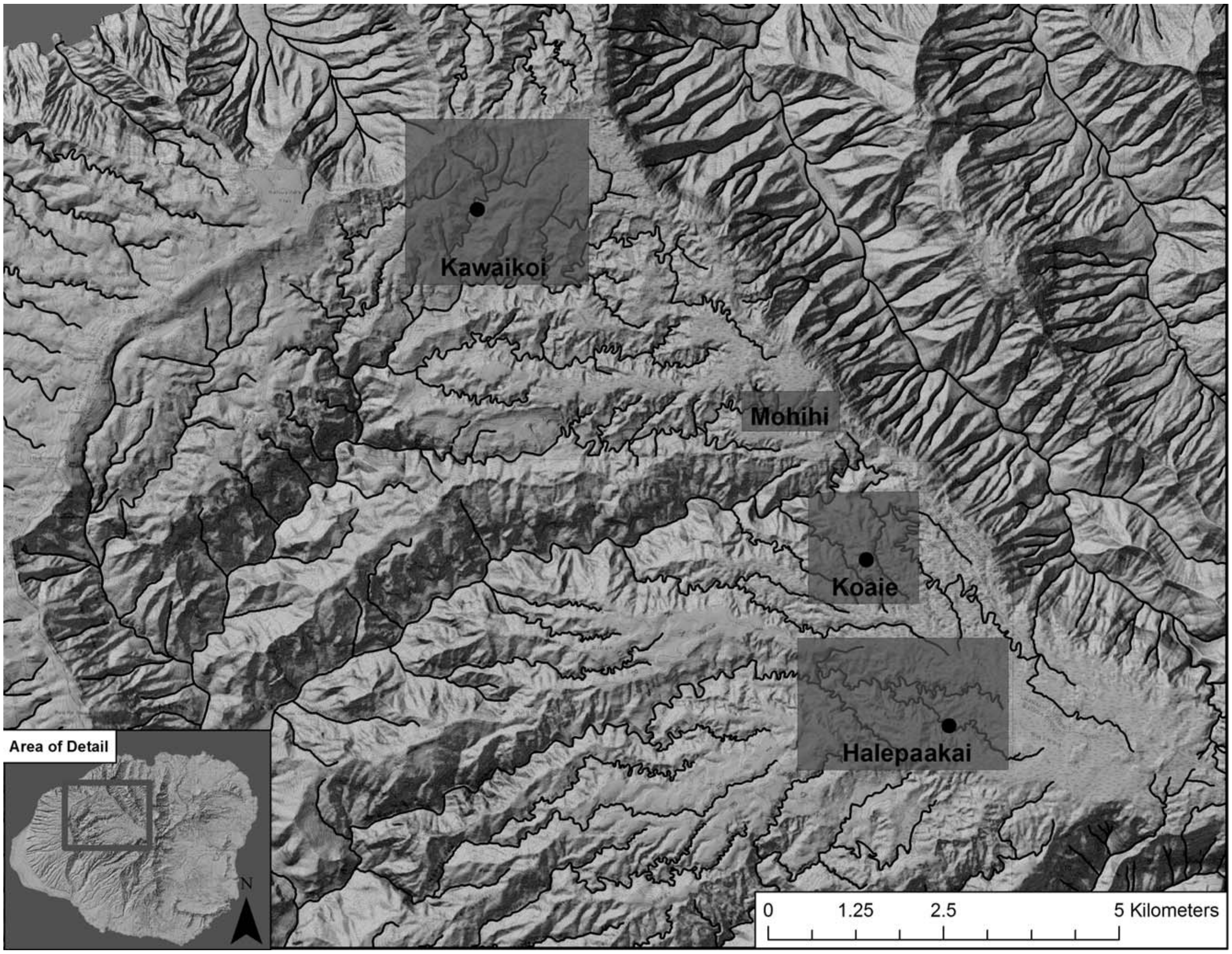

FIGURE 2. Location of Puaiohi study sites in the Alakai Wilderness Preserve on Kauai, Hawaii, USA.

released at Kawaikoi from 2007 to 2010, and 9 were released at Koaie in 2006. The number of birds released varied somewhat among years: 17 in 2005, 19 in 2006, 40 in 2007, 23 in 2008, 12 in 2009, and 12 in 2010. Birds were released at various ages, including 56 juveniles that were <1 yr old and 67 adults that ranged in age from 1 yr to at least 3 yr. We did not include birds released in 1999–2001, which were reported on by Tweed et al. (2003, 2006), or those released in 2002–2004 or 2012, because there was limited postrelease search effort in those years. All captive-bred birds were sexed genetically (Switzer et al. 2013).

Resighting of Released and Wild Birds

We searched for marked birds each year during the breeding season from April to June, and sometimes in other seasons. Each year, almost all birds were resighted during a two- or three-month period from late April to June. Mark–recapture models assume that all individuals have a similar chance of being encountered and therefore that search effort is similar among any groups, time periods, or sites, and that sampling is instantaneous. We measured search effort as the number of person-hours spent searching at each site in each year divided by the number of marked or released birds encountered at a site each year. From 2005 to 2011, we spent 16,823 person-hours at Halepaakai resighting wild and released birds, resulting in an average search effort of 227 hr per marked bird. At Kawaikoi, we spent 2,346 person-hours searching for wild and released birds, for an average effort of 114 hr per marked bird. At Koaie and Mohihi, we spent 216 person-hours with an average effort of 72 hr per marked bird. Search effort was high at all four sites and we believe that it was sufficient to provide a similar chance of encountering birds at each site. The sampling was not instantaneous, thereby violating an assumption of the mark–resight models, but the steep terrain and remote location of the study sites made it impossible to encounter all birds within a short sampling period. Such violations can cause survival estimates to be less accurate, although we have no reason to believe that

TABLE 1. Candidate models used to investigate apparent survival (ϕ) and encounter probability (p) of wild Puaiohi at four sites in the Alakai Wilderness Preserve on Kauai, Hawaii, USA, 2005–2011. Subscripts indicate whether parameters differed among groups (e.g., ϕ_{sex}) or were constant ($\phi_.$). The model with the lowest second-order Akaike's Information Criterion value (AIC_c) was considered to have the best fit. ΔAIC_c is the difference from the best model, which had $AIC_c = 184.58$.

Model	ΔAIC_c	Model likelihood	Number of parameters	Deviance
$\phi_{age}\ p_.$	0.00	1.00	3	47.26
$\phi_{age+sex}\ p_.$	1.26	0.53	5	44.21
$\phi_{age}\ p_{age}$	3.39	0.18	6	44.13
$\phi_{age+sex}\ p_{sex}$	7.05	0.03	8	43.11
$\phi_.\ p_.$	15.77	<0.001	2	65.13

our sampling introduced a systematic bias based on age, sex, or release age.

Data Analysis

We used Cormack-Jolly-Seber models of captures and live resightings in program MARK (version 6.0; White and Burnham 1999) to estimate apparent annual survival (ϕ) and encounter probability (p) of Puaiohi from 2005 to 2011. The values that we report represent apparent survival because the population was open and the fate of birds was unknown. We created an encounter history for each bird using the year of initial capture (or release) and all resightings in subsequent years. We categorized captive-bred released birds by age (juvenile or adult) and sex, resulting in four groups. We categorized wild birds by age (juvenile or adult) and, for adults only, by sex, resulting in three groups. We conducted separate analyses for captive-bred released birds and wild birds because the sex of most wild juveniles was unknown. We used a two-age-class structure to code for juveniles and adults. Because wild juveniles were of unknown sex, they could not graduate into the adult male or adult female groups, and we estimated their survival in subsequent years using a different parameter (HY yr2+). We were not able to examine variation in survival among years or sites because the sample sizes were too small. Our model notation followed Lebreton et al. (1992), in which subscripts indicate whether parameters differed among groups (e.g. ϕ_{sex}) or time periods (ϕ_t) or were constant, indicated by a period ($\phi_.$).

We created a set of candidate models to examine factors of interest (Burham and Anderson 2002). During analyses, we started with the simplest model, in which survival and encounter probability were constant across all groups and time periods, and then forward-selected by adding factors of age, sex, and time. We compared the fit of models with Akaike's Information Criterion corrected for small sample size (AIC_c), as calculated by Program MARK. We considered the model with the lowest AIC_c value to have the best fit, but we also considered models with AIC_c values that differed (ΔAIC_c) by $\leq$2.0 from the best model to have a reasonable fit and to warrant some consideration (Burnham and Anderson 2002). We conducted goodness-of-fit tests on the global models for wild birds and captive-bred released birds using the median $\hat{c}$ approach in MARK to determine whether the global models adequately fit the data and if assumptions underlying analyses were reasonable. For wild birds the value of $\hat{c}$ was 0.99 $\pm$ 0.01, indicating that no adjustment of $\hat{c}$ was necessary. For captive-bred released birds, the value of $\hat{c}$ was 1.79 $\pm$ 0.43, indicating that the data were overdispersed, so we adjusted $\hat{c}$ to the estimated value and used quasi-AIC_c ($QAIC_c$). In addition, because the variance of survival estimates for captive-bred released birds was large, we used a chi-square test to examine whether survival of captive-bred birds was related to age at release, to corroborate the mark–recapture results.

RESULTS

Wild-caught Birds

Addition of an age effect on survival resulted in a large improvement in model fit (ΔAIC_c = 15.77; Table 1), indicating that survival differed between juvenile and adult Puaiohi, with juveniles having lower survival (Table 2). Addition of a sex effect on survival of adults resulted in a small decrease in model fit ($\Delta AIC_c = 1.26$), indicating that there was some evidence that survival differed between the sexes, with males having higher survival than females (Table 2). The small sample size of adults resulted in large standard errors, particularly for females, and likely was responsible for the lack of improvement in model fit with

TABLE 2. Apparent annual survival rates $\pm$ SE (95% CI) and encounter probabilities $\pm$ SE (95% CI) of wild Puaiohi at four sites in the Alakai Wilderness Preserve on Kauai, Hawaii, USA, 2005–2011, by age and sex. HY = juvenile or hatch year; AHY = adult or after hatch year. HY yr2+ indicates subsequent years for birds of unknown sex marked as juveniles.

Age	Sex	Survival	Encounter probability
HY	Both	0.23 $\pm$ 0.06 (0.14–0.37)	0.85 $\pm$ 0.07 (0.67–0.94)
HY yr2+	Both	0.68 $\pm$ 0.11 (0.44–0.85)	0.85 $\pm$ 0.07 (0.67–0.94)
AHY	F	0.46 $\pm$ 0.12 (0.25–0.69)	0.85 $\pm$ 0.07 (0.67–0.94)
AHY	M	0.71 $\pm$ 0.09 (0.51–0.86)	0.85 $\pm$ 0.07 (0.67–0.94)

TABLE 3. Candidate models used to investigate apparent annual survival (ϕ) and encounter probability (p) of captive-bred released Puaiohi at four sites in the Alakai Wilderness Preserve on Kauai, Hawaii, USA, 2005–2011. Subscripts indicate whether parameters differed among groups (e.g. ϕ_{sex}) or were constant ($\phi_.$). The model with the lowest quasi-likelihood Akaike's Information Criterion value ($QAIC_c$) was considered to have the best fit. $\Delta QAIC_c$ is the difference from the best model, which had $QAIC_c = 78.24$.

Model	$\Delta QAIC_c$	Model likelihood	Number of parameters	Deviance
$\phi_{age+HY\ yr2+}\ p_.$	0.00	1.00	4	27.11
$\phi_{age+HY\ yr2+}\ p_{age}$	0.87	0.65	5	25.82
$\phi_{age}\ p_.$	0.88	0.65	3	30.12
$\phi_{age+sex+HY\ yr2+}\ p_.$	0.93	0.63	7	21.44
$\phi_{age+HY\ yr2+}\ p_{HY\ yr2+}$	2.10	0.35	5	27.04
$\phi_.\ p_.$	4.01	0.13	2	35.35

the addition of sex. Survival after the first year of birds marked as juveniles (HY yr2+) was similar to that of adult males (Table 2). Addition of an age effect on encounter probability resulted in a decrease in model fit ($\Delta AIC_c = 3.39$), indicating that encounter probability did not differ between age classes (Table 2). Addition of a sex effect on encounter probability also resulted in worse model fit ($\Delta AIC_c = 7.05 - 1.26 = 5.79$; Table 1), indicating that encounter probability did not differ between males and females.

Effect of Malaria

Three of 36 wild Puaiohi nestlings (8%) tested positive for malaria, and 6 of 16 wild adult Puaiohi (37%) tested positive for malaria. In mark–recapture models, addition of a malaria effect on survival resulted in a small decrease in model support ($\Delta AIC_c = 1.91$), suggesting that the model warranted some consideration. However, survival estimates for wild juveniles and wild adults infected with malaria actually were higher than those of uninfected birds. Two of 3 infected juveniles (67%) were resighted in subsequent years, and 7 of 33 uninfected juveniles were resighted (21%). Among adults, 3 of 6 infected birds were resighted (50%) and 4 of 10 uninfected birds were resighted (40%). Given the small sample sizes and equivocal model support, it is unlikely that malaria had an important effect on survival.

Captive-bred Released Birds

Addition of an age effect on survival improved model fit ($\Delta QAIC_c = 4.01 - 0.88 = 3.13$; Table 3), indicating that survival differed between birds released at different ages. Survival of birds released as juveniles was higher than survival of birds released when they were older (Table 4), but the confidence intervals were very broad. However, the relationship between age at release and survival was corroborated by chi-square analysis, which showed that birds were more likely to be resighted if they were released as juveniles (7 of 56) than if they were released as adults (1 of 66; $\chi^2_1 = 6.08$, $P = 0.01$).

TABLE 4. Apparent annual survival rates ± SE (95% CI) and encounter probabilities ± SE (95% CI) of captive-bred Puaiohi released at four sites in the Alakai Wilderness Preserve on Kauai, Hawaii, USA, 2005–2011, released as juveniles (HY) and adults (AHY). HY yr2+ indicates subsequent years for birds of unknown sex marked as juveniles.

Age	Survival	Encounter probability
HY	0.26 ± 0.21 (0.04–0.75)	0.41 ± 0.34 (0.04–0.92)
HY yr2+	0.75 ± 0.42 (0.04–0.99)	0.13 ± 0.14 (0.01–0.65)
AHY	0.05 ± 0.06 (0.00–0.41)	0.13 ± 0.14 (0.01–0.65)

Addition of a time factor (HY yr2+) in which survival of birds released as juveniles differed between the first year and all subsequent years resulted in improved model fit ($\Delta QAIC_c = 0.88$; Table 3), indicating that survival was higher after the first year (Table 4). Addition of a sex effect on survival of released birds resulted in somewhat worse model fit ($\Delta QAIC_c = 0.93$; Table 3), but also resulted in data for some age–sex groups that were too sparse to allow survival estimation.

Addition of an age effect on encounter probability resulted in a small decrease in model fit ($\Delta QAIC_c = 0.87$; Table 3), indicating that encounter probability differed somewhat in birds released at different ages. However, the confidence intervals were very broad (Table 4). Addition of a time factor in which encounter probability differed between the first year and subsequent years resulted in worse model fit ($\Delta QAIC_c = 2.10$; Table 3), indicating that encounter probability did not vary among years.

DISCUSSION

The previous survival estimates obtained by Snetsinger et al. (2005) for wild adult (0.73 ± 0.13, $n = 11$, sexes combined) and juvenile (0.25 ± 0.07, $n = 36$) Puaiohi are similar to our estimates, despite our larger sample sizes, longer study duration, and use of mark–recapture models. Survival of juvenile Puaiohi was lower than that of adults, which is typical of Hawaiian birds and many other tropical and island bird species sharing a suite of life history characteristics including long lifespan, small clutch size, low fecundity, and extended parental care (VanderWerf 2008, Woodworth and Pratt 2009, Vetter et al. 2012).

We found that annual survival of female Puaiohi was 25% lower than that of males. This pattern has been found in two other Hawaiian passerines, the Oahu Elepaio (*Chasiempis ibidis*) and Maui Parrotbill (*Pseudonestor xanthophrys*), and in these species the lower survival of females was caused by nest predation by alien rats

(VanderWerf and Smith 2002, VanderWerf 2009, VanderWerf et al. 2011, Mounce et al. 2013). Only female Puaiohi incubate eggs and brood young (Snetsinger et al. 2005), which results in greater exposure to nest predators. The differential survival rates between the sexes found in our study and the nest predation documented previously strongly suggest that nest predation by alien rats is a serious threat to the Puaiohi. Snetsinger et al. (2005) found that 10% (10 of 94) of Puaiohi nests were depredated over a three-year period, with at least 48% of predation events attributable to rats and up to 36% of nests depredated by rats in some years, and that breeding females sometimes were taken by predators. Similarly, Tweed et al. (2006) found that predation was the greatest cause of failure in nesting attempts involving captive-bred released Puaiohi, occurring at 38% of active nests, with at least two breeding females killed by rats. Snetsinger et al. (1999) speculated that use of cliff cavities for nesting may be an adaptation by Puaiohi to avoid the heavy rainfall typical of this area, but predation pressure may also explain cavity nesting, although even cliff nest sites are not entirely safe.

In the Oahu Elepaio, rat control not only increased nest success but also increased female survival by 10–27%, whereas male survival was not affected by rat control (VanderWerf and Smith 2002, VanderWerf 2009, VanderWerf et al. 2011). The efficacy of rat control at increasing nest success or female survival has been less clear in Puaiohi. Snetsinger et al. (2005) reported that wild Puaiohi nests at Mohihi protected from rats with poison bait stations experienced zero rat predation, but Tweed et al. (2003) found that control efforts were not effective for captive-bred Puaiohi at Kawaikoi. VanderWerf (2009) and VanderWerf et al. (2011) showed that rat abundance and efficacy of rat control varied among years, and one would expect similar patterns to occur in efforts to protect Puaiohi nests from rats.

An alternative explanation for the lower survival rate of female Puaiohi is that females are more likely to disperse after nest failure than males; distinguishing emigration from mortality is always difficult in mark–recapture studies (e.g., Redmond and Murphy 2012, McKim-Louder et al. 2013). We were unable to include nest success as a covariate in our mark–recapture models because we did not have nest success data for all birds and the resulting dataset would have been inadequate. However, encounter probability was similar for males and females, and all seven female Puaiohi known to have failed in their first nesting attempt remained in the same territory and renested, with 6 of the 7 reusing the same nest site.

The relatively high survival rate of Puaiohi in their second year (HY yr2+) suggests that either these birds had not started breeding yet and thus were not subject to nest predation or that most of them were males. From 2005 to 2012, we have records of 18 second-year birds breeding (12 wild females, 5 captive-bred females, 1 captive-bred male), and Tweed et al. (2006) reported that from 1999 to 2001, 10 second-year females and two second-year males bred, so at least some young birds do breed in this population, although the proportion is unknown. The larger number of females breeding in their second year supports the idea of breeding females being depredated by rats while attending nests, thereby providing more recruitment opportunities for young females.

Avian malaria is a serious threat to many Hawaiian forest birds (van Riper et al. 1986, U.S. Fish and Wildlife Service 2006, Atkinson and LaPointe 2009), but infection with *P. relictum* did not appear to decrease survival of Puaiohi. Since we sampled birds only once, when they were banded, it is possible that birds contracted malaria after they were sampled without our knowledge. However, given that the survival estimates of infected birds actually were higher, it seems safe to conclude that malaria did not decrease Puaiohi survival. Atkinson et al. (2001) found that another species of Hawaiian thrush, the Omao (*Myadestes obscurus*), had high survival and exhibited few pathological effects from acute malarial infection when experimentally infected by mosquito bite. A relatively high percentage of wild Omao (85%, 22/26) and Puaiohi (14%, 1/7) had antibodies to malaria, suggesting that native Hawaiian thrushes are capable of recovering from acute infection in the wild. Prevalence of malaria in wild Puaiohi captured from 2007 to 2013 at Kawaikoi, Mohihi, and Halepaakai was 22% (15/66; Atkinson et al. 2014), indicating that a portion of the population is surviving acute and chronic infection with malaria. Avian lineages that colonized the Hawaiian Islands more recently, such as the Hawaiian thrushes (3.4 million years ago; Price and Clague 2002, Pratt 2009) and monarch flycatchers (*Chasiempis* spp.; 2.3 million years ago; VanderWerf et al. 2010), may be more tolerant of avian malaria than the Hawaiian honeycreepers, which colonized the Hawaiian Islands earlier (5–6 million years ago) and have diverged more from their ancestors (Fleischer and McIntosh 2001, Pratt 2009).

Tweed et al. (2003, 2006) reported that survival of captive-bred Puaiohi released at Kawaikoi was high during the first three years of releases from 1999 to 2001, with 31 of 34 (91%) birds surviving 30 days postrelease and 6 of 14 birds (43%) released in 1999 establishing territories and breeding in the release area the following year. Most of the birds released from 1999 to 2001 were juveniles, and the oldest birds were 14 months old when released (Tweed et al. 2006). Our results show that survival of captive-bred released birds has been lower since the first three years of the release program, for which there are several possible explanations. Most importantly, many birds released in later years were older, and such birds had extremely low survival. Captive Puaiohi released as adults had a very low probability of integrating into the wild population. Only a single bird released as an adult was ever seen again; a female that bred successfully for two years with a wild male. The survival rate in later years of birds released as juveniles (HY yr2+) was similar to that of wild adults, indicating that once they survived the first year, their survival was similar to that of wild birds.

The release site was switched from Kawaikoi to Halepaakai in 2002, and back to Kawaikoi in 2007, with a few ($n = 9$) birds released at Koaie in 2006. Woodworth et al. (2009) suspected that survival was lower and emigration was higher in birds released at Halepaakai, but also noted that a comparison of survival rates between the sites was not appropriate because the release cohorts at Halepaakai included more adults; 35 of 36 birds released at Halepaakai from 2005 to 2006 were adults, only one of which was ever seen postrelease.

Low survival and recruitment rates have been reported in captive breeding and release programs for other species, including the Grey Partridge (*Perdix perdix*; Putaala and Hissa 1998, Parish and Sotherton 2007), Palila (*Loxioides bailleui*; Banko et al. 2009), Hihi or Stitchbird (*Notiomystis cincta*; Low 2010, Ewen et al. 2013), Eastern Bluebird (*Sialis sialia*; Slater et al. 2013), and Key Largo wood-rat (*Neotoma floridiana smalli*; McCleery et al. 2013). Some programs have attempted to overcome the low survival rate by releasing large numbers of individuals to achieve the desired conservation benefit. Considerable effort has been made to raise and release as many Puaiohi as possible (Switzer et al. 2013), but the release cohorts still have been relatively small.

Conclusions and Management Implications

Despite the equivocal success of previous rat control efforts, renewed effort to protect Puaiohi nests from predation by alien rats may be the most effective management tool available to increase survival and reproduction of wild and released birds. The severity of rat predation on Hawaiian forest birds can vary among years, thus rat control efforts can appear to be less effective in some years and several years of data may be required to adequately assess the efficacy of rat control efforts (VanderWerf 2009). The use of improved rat control methods, such as self-resetting pneumatic rat traps and rat-resistant artificial nest boxes, would be beneficial (Pitt et al. 2011).

Releasing captive-bred birds to augment the wild population has been considered an important component of the recovery strategy for Puaiohi (U.S. Fish and Wildlife Service 2006, Woodworth and Pratt 2009). However, the value of captive releases has declined recently compared to the first few years of the program (Tweed et al. 2003, 2006, Switzer et al. 2013). Over the 14 years of the program, only 10% of released birds were ever observed breeding, and most (73%) of these breeding events occurred in the first six years of the program (Switzer et al. 2013). One reason for this diminishing return has been the very low survival of the many adults released in recent years. Releases of adult Puaiohi have contributed very little to the species' recovery. The value of releasing captive-bred Puaiohi into areas that already support a relatively large number of wild Puaiohi, such as Halepaakai, has not been adequately tested because almost all birds released previously into such areas have been adults, which we now know have very low survival. If releases of Puaiohi are to be continued, the program should be reassessed, including the optimal age for release of captive birds and their subsequent reproductive performance since this has not been done since 2001 (Tweed et al. 2006). Other factors that may have contributed to the declining performance of the release program include ongoing habitat degradation and decreased genetic diversity in the captive stock.

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