

Survival Estimates for Two Hawaiian Honeycreepers¹

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Abstract: Most Hawaiian forest birds are endangered by habitat loss and degradation, predation by introduced mammals, and introduced diseases, but species recovery planning has been hampered by lack of demographic information, such as annual survival rates. To address this knowledge gap, we analyzed mark-recapture data using the program MARK to estimate apparent survival in the endangered Maui parrotbill (*Pseudonestor xanthophrys*) and Maui 'alauahio (*Paroreomyza montana*). Annual survival estimates were high in adult Maui parrotbills (0.84 ± 0.04) and Maui 'alauahio (0.78 ± 0.15). Survival was lower in hatch-year parrotbills (0.76 ± 0.09) and hatch-year 'alauahio (0.64 ± 0.13), and survival of 'alauahio also varied among years (0.51 ± 0.18 to 0.95 ± 0.06 in adults). These results provide important baseline data for two little-known species of honeycreepers and, together with ongoing nest success and productivity studies, will enable assessment of population trends and inform management decisions. Mark-recapture methods are a useful tool for monitoring populations of rare and cryptic species that are difficult to monitor using traditional survey methods.

ISLAND BIRDS are more vulnerable to extinction than many continental species (Steadman 2006), and the Hawaiian avifauna is no exception. Hawai'i has lost more than half of its endemic birds, including nearly two-thirds of all known honeycreeper (Drepanidinae) species (James and Olson 1991, Scott et al. 2001, Pratt 2005). Past and current threats to Hawaiian birds have been well documented and include habitat loss and degradation, introduction of alien predators, and avian diseases (van Riper and Scott 2001, U.S. Fish and Wildlife Service 2006, Pratt et al. 2009). In particular, the introduction of avian poxvirus and avian malaria devastated the Islands'

avifauna and is now the single most important factor limiting distribution, survival, and recovery of most endemic Hawaiian forest birds. The widespread occurrence of these diseases restricts the range of most native bird species to elevations above 1,500 m, where disease prevalence and vector density are lower (Scott et al. 1986, van Riper et al. 1986, Atkinson and LaPointe 2009). Of the 35 Hawaiian forest birds that persisted into the latter half of the last century, 24 are listed under the U.S. Endangered Species Act, 10 of which may be extinct (Pratt et al. 2009). Under International Union for Conservation of Nature (IUCN) criteria, all but two are

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considered at least vulnerable, with five endangered, 14 critically endangered, four extinct, and one extinct in the wild (IUCN 2010).

Most monitoring efforts of Hawaiian bird populations rely on variable circular plot (VCP) surveys, which were initiated in 1976 (Scott et al. 1986) and from which baseline population estimates and densities have been determined (Camp et al. 2009*b*). However, this survey method is relatively ineffective for monitoring population changes in rare and cryptic species, and intensive demographic studies have been recommended as an alternative (Thompson 2002, MacKenzie et al. 2004, U.S. Fish and Wildlife Service 2006). Demographic data can be used to estimate and predict population growth rates and are necessary components of population viability analyses (Armstrong and Ewen 2002, Nicoll et al. 2003, VanderWerf 2009). In long-lived bird species, adult survival is often the most important factor determining population growth (Saether and Bakke 2000, Clark and Martin 2007).

The Maui parrotbill (*Pseudonestor xanthophrys*) and Maui 'alauahio (*Paroreomyza montana*) are long-lived, insectivorous honeycreepers endemic to the Hawaiian island of Maui. They are mostly sympatric, occurring only in high-elevation forests on Haleakalā Volcano (Simon et al. 1997, Baker and Baker 2000). The Maui parrotbill is listed as endangered under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2006) and by the state of Hawai'i, and under IUCN criteria the parrotbill is considered critically endangered. Although the 'alauahio is not listed under the Endangered Species Act, it is considered endangered by the IUCN (IUCN 2010). Population size of the Maui parrotbill was estimated at 502 ± 116 SE birds in 1980 (Scott et al. 1986), with a mean density of 17.2 ± 4.16 SE birds/km² (Camp et al. 2009*a*). Subsequent analysis of VCP data from 1992 to 1996 and 1997 to 2001 resulted in mean density estimates of 17.0 ± 4.24 SE and 11.8 ± 2.55 SE birds/km², respectively (Camp et al. 2009*a*). Population size of the Maui 'alauahio was estimated at $34,839 \pm 2,723$ SE birds in 1980 (Scott et al. 1986), with a mean

density of 731 ± 64 SE birds/km² (Camp et al. 2009*a*). Analysis of VCP data from 1992 to 1996 and 1997 to 2001 resulted in mean density estimates of $1,483 \pm 76$ SE birds/km² and $1,167 \pm 73$ birds/km², respectively. The recent estimates may be indicative of an increasing population (Camp et al. 2009*a*) or could be attributable to differing seasonality during surveys or improved analytical techniques. There is some evidence that ranges of both species have contracted at the lower-elevation boundaries since 1980 (Baker and Baker 2000, Camp et al. 2009*a*). Within Hanawā Natural Area Reserve at the core of their ranges, the density of parrotbills was 40 birds/km² (Scott et al. 1986, Simon et al. 2002), and 'alauahio densities were as high as 1,480 birds/km² (Simon et al. 2002).

The Maui parrotbill lays a single-egg clutch and juveniles are dependent on their parents for as long as 17 months (Simon et al. 1997; Maui Forest Bird Recovery Project, unpubl. data). In contrast, the Maui 'alauahio lives in small family groups of two to six individuals. They are mostly monogamous, produce a two-egg clutch, and the fledglings have a shorter dependent period (2–3 months) but may remain with the family group for up to 20 months (Baker and Baker 2000). Here we provide survival estimates for both species using mark-recapture analysis, and we review these survival estimates in terms of the species' respective life-history strategies.

MATERIALS AND METHODS

Study Area

Our study occurred at four sites in the 3,035 ha Hanawā Natural Area Reserve (20° 45' N, 156° 08' W) (Figure 1). This state reserve, established in 1986, supports some of the most intact native forest remaining in Hawai'i and encompasses the core range of both focal species. Fencing of the upper portion of the reserve (~800 ha) was completed in 1996, and ungulates were eradicated by 1997 (VanderWerf et al. 2003). The study sites (Frisbee Meadows, Po'ouli Camp, State Camp, and Greensword Bog) were located in the ungulate-free area between 1,500 m and 2,100

m elevation (Figure 1) and ranged in size from 48 ha (State Camp) to 74 ha (Frisbee Meadows). The habitat consists primarily of wet montane forest dominated by 'ōhi'a (*Metrosideros polymorpha*), with mesic 'ōhi'a forest, subalpine scrub, and subalpine grassland at higher elevations (Jacobi 1989). Annual rainfall across the area averages 5 m (Giambelluca et al. 1986), but a gradient of decreasing rainfall from northeast to southwest results in variation in canopy height and cover among the sites (Crausbay and Hotchkiss 2010). Po'ouli Camp and Frisbee Meadows also have higher Maui parrotbill densities than State Camp and Greensword Bog (Scott et al. 1986, Pratt et al. 2001).

Study Species

The Maui parrotbill currently is restricted to 50 km² of montane rain forest on windward

(northeastern) East Maui. However, historical observations and subfossils indicate that parrotbills once occurred in koa (*Acacia koa*) and mixed 'ōhi'a-koa forests across the islands of Maui and Moloka'i (James et al. 1987, James and Olson 1991, Simon et al. 1997). Almost all of those habitats have been lost, and the current distribution of the species is likely an artifact of the lack of low-elevation forests with low disease prevalence and vector densities (van Riper et al. 1986, Scott et al. 2001, Atkinson and LaPointe 2009).

Maui parrotbills forage on shrubs and trees for invertebrates, using their large, parrot-like bill to excavate prey. This specialized foraging behavior may partly explain the long juvenile dependency (Lockwood et al. 1994, Simon et al. 1997). Breeding pairs inhabit well-defined all-purpose territories of roughly 9 ha year-round and for successive breeding seasons (Simon et al. 1997). Males defend these

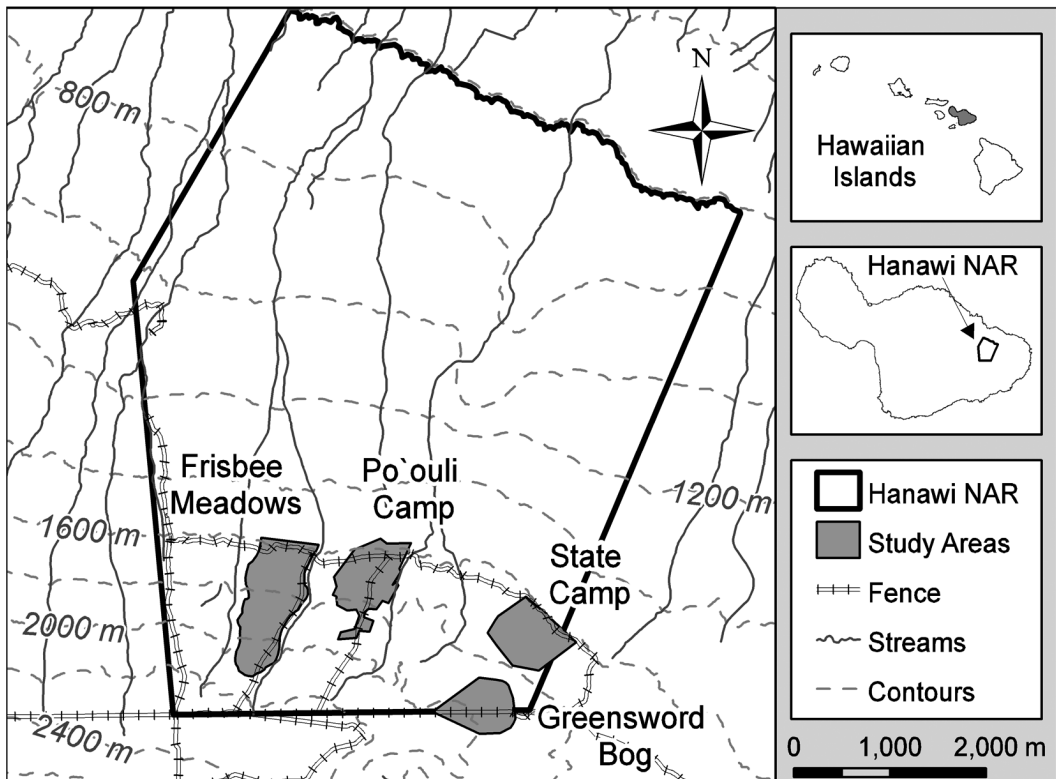


FIGURE 1. Location of four study areas within Hanawā Natural Area Reserve, Maui, Hawai'i.

territories from conspecifics, which leads to low population density, even within suitable habitat. Age at first breeding is unknown, but no second-year birds have been observed nesting nor in breeding condition. Maximum age in the wild is at least 16 yr based on resights of color-banded birds (Maui Forest Bird Recovery Project, unpubl. data).

The Maui 'alauahio is mostly sympatric with the Maui parrotbill, but it occurs over a slightly wider elevational range and in one additional population on the leeward side of East Maui (Baker and Baker 2000, Pratt et al. 2009). Maui 'alauahio primarily glean invertebrates from foliage and may opportunistically forage on substrate recently excavated by parrotbills (Baker and Baker 2000). Maui 'alauahio live in family groups that defend 1- to 2-ha territories from conspecifics, and offspring from previous broods sometimes help to raise siblings (Baker and Baker 2000). Breeding is usually delayed until the third year, and maximum age in the wild is at least 14 yr based on resights of color-banded birds (Maui Forest Bird Recovery Project, unpubl. data).

Data Collection

Mark-recapture studies began in 1994 at Frisbee Meadows and continued until 1997; they were not resumed until 2006 (Berlin et al. 2001, Pratt et al. 2001, Simon et al. 2000, 2002). Similar studies commenced in 1996 at State Camp and Greensword Bog and in 1998 at Po'ouli Camp. Mist-netting and resight effort in those study areas has continued since, with some annual variation in effort within and among sites (see Table 1). Individuals were captured in mist nets and banded with a unique combination of a U.S. Fish and Wildlife Service numbered steel (parrotbills) or aluminum ('alauahio) band and three plastic colored leg bands. Playback was used to increase capture rates, particularly for parrotbills. Parrotbills were sexed and age was determined using plumage and morphometric criteria (Berlin et al. 2001). Juvenile 'alauahio were distinguished from adults by plumage, but determining age for birds after hatch year was difficult because of delayed plumage maturation (Baker and Baker 2000). Definitive

sexing of adult and juvenile Maui 'alauahio was not possible due to incomplete knowledge about age-specific plumage and morphometric differences.

Data Analysis

We used standard Cormack-Jolly-Seber models of captures and subsequent live encounters in program MARK (version 5.1 [White and Burnham 1999]) to estimate apparent annual survival (Φ) and encounter probability (ρ) of Maui parrotbills and Maui 'alauahio based on capture, recapture, and resight data from 1994 to 2007. Populations of both species were open because the fate of birds was unknown, so values reported represent apparent survival. We created an encounter history for each bird using the year of initial capture and all recaptures and resights in subsequent years. This study encompassed a period of 14 yr, but some years had to be excluded for each species due to low effort. For Maui parrotbills, 2001 was excluded because there was insufficient resighting effort, and this interval was set to 2 yr, yielding 13 sampling occasions. For Maui 'alauahio, 1994–1999 were excluded, resulting in eight sampling occasions.

Maui parrotbills were grouped by sex and age (juvenile or adult). Maui 'alauahio were grouped by age only (juvenile or adult) because sex could not be reliably determined in all birds. We used a two age-class structure to code for juveniles (hatch-year birds less than 1 yr old) and adults (second-year birds and older) because second-year birds were difficult to distinguish from adults. 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 dot (φ). For both species, we started with the simplest model in which survival and encounter probability were constant across all groups and time periods, and then added factors of age, sex (for Maui parrotbills), and time.

A goodness-of-fit test using the median \hat{c} approach in MARK was performed on global models for Maui parrotbills and Maui 'alauahio to determine if the model adequately fit

the data and if assumptions underlying analyses were reasonable (Cooch and White 2011). Values of \hat{c} (1.12 ± 0.05 and 1.48 ± 0.03 for Maui parrotbills and Maui alauahio, respectively) indicated that both data sets were slightly overdispersed, so \hat{c} was adjusted to the estimated values. The fit of models was compared with Akaike's Information Criterion corrected for small sample size using the quasi-likelihood adjustment (QAIC_c), as calculated by Program MARK. The model with the lowest QAIC_c value was considered to have the best fit, but models with QAIC_c values that differed (Δ QAIC_c) by ≤ 2 also were considered to have a reasonable fit (Burnham and Anderson 2002). Normalized QAIC_c weights were used as a measure of each model's relative likelihood.

RESULTS

A total of 103 Maui parrotbills (51 males and 52 females) banded in the four study areas from 1994 to 2007 was included in analyses, including seven hatch-year birds. An average of 16 birds was captured, recaptured, or resighted each year, and the number of individuals banded and encountered varied among years (Table 1). Of 209 annual Maui parrotbill encounters, 205 were based on resights and five were based only on recaptures. In the best-fit model, encounter probability differed among years but apparent survival was constant among years (Table 2, Model 1). A

model including an effect of sex on encounter probability (Table 2, Model 2) had only slightly worse fit (Δ QAIC_c = 0.63). Encounter probability of females was 5%–15% higher each year than that of males. A model including an effect of age on survival (Model 3) also had a reasonable fit (Δ QAIC_c = 1.68) and indicated that survival of juveniles (0.76 ± 0.09) was lower than that of adults (0.84 ± 0.04). Addition of other factors resulted in significantly worse fit, indicating that encounter probability was not affected by age (Model 4)

TABLE 1
Numbers of Maui Parrotbills and Maui 'Alauahio Banded/Resighted per Year

Year	Maui Parrotbills	Maui 'Alauahio ^a
1994	9/0	
1995	11/7	
1996	12/12	
1997	12/14	
1998	12/9	
1999	0/13	
2000	2/4	14/2
2001	0/0	11/8
2002	8/4	47/14
2003	11/9	37/43
2004	7/12	29/42
2005	0/6	1/17
2006	3/7	2/19
2007	16/8	27/11
Total	103	179

^a Monitoring of 'alauahio did not begin until 2000, but 11 birds banded in previous years were resighted from 2000 to 2007.

TABLE 2
Models Used to Investigate Survival (Φ) and Encounter Probability (ρ) of Maui Parrotbills

No.	Model	Δ QAIC _c	QAIC _c Weight	No. Parameters	Deviance
1	Φ, ρ_t	—	0.35	13	166.57
2	Φ, ρ_{sex+t}	0.63	0.26	14	164.90
3	Φ_{age}, ρ_t	1.68	0.15	14	165.95
4	Φ, ρ_{age+t}	2.21	0.12	14	166.49
5	Φ_{sex}, ρ_t	2.27	0.11	14	166.54
6	$\Phi_{age+sex+t}, \rho_{age+sex+t}$ *	8.61	<0.01	28	138.06
7	Φ_t, ρ_t	9.80	<0.00	23	152.29
8	Φ, ρ	66.15	<0.00	2	256.52

Note: Subscripts indicate whether parameters differed among groups (e.g., ρ_{sex}) or time periods (ρ_t) or were constant (ρ). Overdispersion or \hat{c} was adjusted to 1.12 based on estimation from the global model (*). Δ QAIC_c is the difference from the best (lowest AIC_c) model. QAIC_c weight is the relative likelihood of each model.

TABLE 3
Models Used to Investigate Survival (Φ) and Encounter Probability (ρ) of Maui 'Alauahio

No.	Model	ΔQAIC_c	QAIC _c Weight	No. Parameters	Deviance
1	$\Phi_t\rho$	—	0.35	8	82.00
2	$\Phi_t\rho_{\text{age}}$	0.03	0.35	9	79.89
3	$\Phi_{\text{age}+t}\rho$	0.90	0.23	9	80.77
4	$\Phi_t\rho_t$	5.60	0.02	13	76.78
5	$\Phi_{\text{age}+t}\rho_{\text{age}+t}$ *	6.11	0.02	15	72.85
6	$\Phi\rho$	8.11	0.01	2	102.59

Note: Overdispersion or \hat{c} was adjusted to 1.48 based on estimation from the global model (*). ΔQAIC_c is the difference from the best (lowest AIC_c) model. QAIC_c weight is the relative likelihood of each model.

and that survival did not differ between the sexes (Model 5). Although survival did not appear to differ among years, small sample sizes in some years may have hindered estimation of annual variation (Table 1).

A total of 179 Maui 'alauahio banded or resighted from 1994 to 2007 was included in analyses, of which 17 were hatch-year birds. An average of 41 birds was captured, recaptured, or resighted each year (Table 1). Of 322 annual Maui 'alauahio encounters, 318 were based on resights and four were based only on recaptures. The top three models had similar fit and included effects of year and age on survival and an effect of age on encounter probability (Table 3). Survival was lower in hatch-year birds (mean $\Phi = 0.64 \pm 0.13$) than in adults (mean $\Phi = 0.78 \pm 0.15$) and also varied among years (Figure 2) (range: 0.51 ± 0.18 to 0.95 ± 0.06 in adults, 0.32 ± 0.07 to 0.89 ± 0.09 in hatch-year birds). Resight probability was higher in hatch-year birds (0.71 ± 0.06) than in adults (0.41 ± 0.20) and was constant among years.

DISCUSSION

Estimates of annual survival in the Maui parrotbill and Maui 'alauahio were high and were consistent with our general knowledge of their life histories. Both species exhibit a life-history pattern typical of tropical, south temperate, and island species, characterized by long life span, low fecundity, and delayed maturation (Martin 1996, Murray 2001). Our estimate of survival in adult Maui parrotbills (0.84) is among the highest recorded in Ha-

waiian forest birds and may compensate for their exceptionally low fecundity. The closest living relative of the Maui parrotbill, the 'akiapōlā'au (*Hemignathus munroi*) from Hawai'i Island, has a similar life-history pattern, a one-egg clutch, and high annual survival (0.71) (Ralph and Fancy 1996). Our Maui 'alauahio survival estimate (0.78) is slightly lower than estimates for the Maui parrotbill, Hawai'i 'elepaio (*Chasiempis sandwichensis*, 0.87 in males, 0.81 in females [VanderWerf 2008]), and O'ahu 'elepaio (*Chasiempis ibidis*, 0.86 in males, 0.82 in females [VanderWerf 2009]) but comparable with other ecologically similar Hawaiian honeycreepers such as the Hawai'i creeper (*Oreomystis mana*, 0.73) and Hawai'i 'ākepa (*Loxops coccineus*, 0.70 [Ralph and Fancy 1994a]) and higher than estimates for other Hawaiian forest birds including 'i'iwi (*Vestiaria coccinea*, 0.55 [Ralph and Fancy 1995]), 'ōma'o (*Myadestes obscurus*, 0.66 [Ralph and Fancy 1994b]), and palila (*Loxioides bailleui*, 0.63 [Lindsey et al. 1995]).

Estimates of juvenile survival in Maui parrotbills and Maui 'alauahio were notably higher than estimates of juvenile survival in other Hawaiian forest birds (0.09 in 'i'iwi, 0.13 in 'apapane, *Himatione sanguinea* [Ralph and Fancy 1995]; 0.36 in palila [Lindsey et al. 1995]; 0.33 in Hawai'i 'elepaio [VanderWerf 2008]), which may be partly due to the small sample sizes in the study reported here. Estimates of juvenile survival reported in this study may also be biased high because survival was monitored from age at banding and thus did not account for mortality between fledging and banding. During concurrent Maui

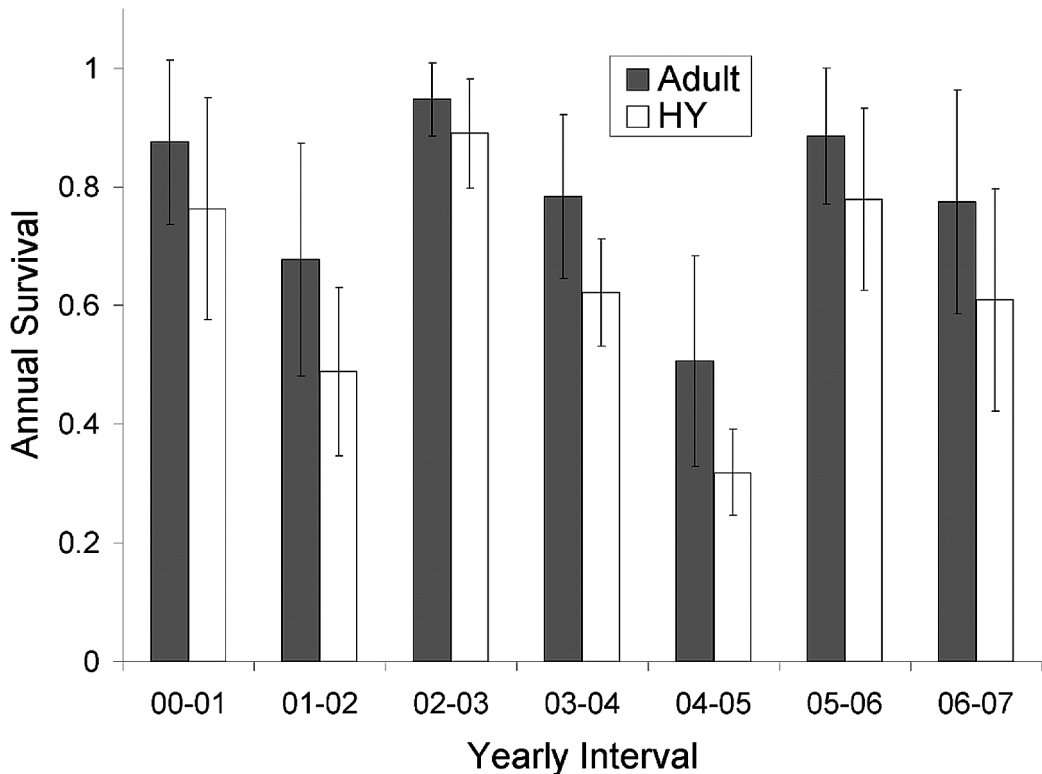


FIGURE 2. Variation in Maui 'alauahio survival estimates with age and year (Table 3, Model 3). Error bars indicate SE.

parrotbill nest studies, several fledglings disappeared at an age considered too young to be independent (and before banding).

The similarity of survival estimates in male and female Maui parrotbills is noteworthy because female birds generally do not survive as long as males due to higher costs of reproduction and higher predation rates while on nests (Bennett and Owens 2002). Survival has been found to be lower in females than males in several species of endangered Hawaiian birds, leading to skewed sex ratios and declining populations (Lindsey et al. 1995, VanderWerf et al. 2001). In the O'ahu 'elepaio, predation of females on nests by alien black rats led to a higher survival rate of males, but survival of females and nest success increased after rats were controlled (VanderWerf and Smith 2002, VanderWerf 2009). Predation on eggs, chicks, and adult Hawaiian forest birds by rats is well known (Atkinson 1977, Baker and

Baker 2000, VanderWerf 2009), but high survival of both male and female parrotbills suggests that nest predation by rats is not a serious threat to this species in Hanawā, perhaps because rats were controlled at some sites during this study (Malcolm et al. 2008). In contrast, Maui 'alauahio nests are generally more accessible than those of Maui parrotbills and could have suffered more frequent rat predation, which might partly account for their slightly higher adult mortality. Improved methods of distinguishing the sexes in Maui 'alauahio are needed to examine sex-specific survival and severity of the threat posed by rat predation.

Encounter probability varied among years in Maui parrotbills, reflecting variable search effort and the difficulty in detecting species like parrotbills that occur at low density. In contrast, encounter probability of Maui 'alauahio was constant among years despite

variation in search effort, perhaps because 'alauahio are much more conspicuous, often approaching observers. The cause of annual variation in survival of Maui 'alauahio is unknown but could be related to fluctuations in climatic factors such as rainfall. It is possible that survival of Maui parrotbills also varied among years but smaller sample sizes and variation in effort hindered estimation of time-dependent models.

Hanawā Natural Area Reserve comprises the core of both species' range and is intensively managed; thus the survival estimates presented here may represent ideal conditions for both species. Measuring demographic rates in other portions of the species' ranges should be a focus of future research. Knowledge of differential survival rates due to varying effects of limiting factors such as avian disease, suboptimal habitat quality, and predation by introduced mammals would be valuable for long-term conservation planning and monitoring effectiveness of current management. Increased banding and resight effort in the study areas would improve sample sizes and help refine survival estimates. These estimates will provide managers with important baseline data that, in conjunction with ongoing nest success and productivity studies, will enable better assessment of population trends and subsequent recovery efforts.

Although labor-intensive, focused demographic research, including mark-recapture analysis, likely is superior to point counts for monitoring population trends in species like the Maui parrotbill that are rare, cryptic, or have variable densities. Demographic analyses also can help identify limiting factors that result in population decline, and mitigation of these threats together with management of demographic bottlenecks has led to the recovery of several critically endangered species (e.g., Bell and Merton 2002, Jones 2004, VanderWerf 2009) and has potential for aiding recovery of Hawai'i's endangered birds.

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