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POPULATION STRUCTURE AND SURVIVAL OF PALILA[1]

G. D. LINDSEY, S. G. FANCY, M. H. REYNOLDS, T. K. PRATT,
K. A. WILSON, P. C. BANKO AND J. D. JACOBI
*National Biological Service, Pacific Islands Science Center, Hawaii Field Station,
P.O. Box 44, Hawaii National Park, HI 96718*

Abstract. Annual survival, age, and sex ratios of the endangered Palila (*Loxioides bailleui*) on Mauna Kea, Hawaii, were determined from multiple captures and resightings of 984 individuals during 1987–1993. The proportion of Second Year (SY) Palila in the population was relatively constant among years, whereas the proportion of Hatching Year (HY) birds ranged from 3.1 to 22.6% over three years. Sex ratios of nestling and SY Palila did not differ from unity, but the sex ratio of HY and ASY Palila was male-biased. Mean proportion of adult males was 63.7% ± 1.8 SE, and males outnumbered females in all six years of the study. Mean annual survival of HY Palila (0.36 ± 0.08) was lower than that of After Hatching Year (AHY) birds (0.63 ± 0.05), but annual survival of AHY males (0.65 ± 0.07) did not differ from that of AHY females (0.62 ± 0.06). Survival was negatively correlated with annual changes in the availability of green mamane (*Sophora chrysophylla*) pods, the primary food of Palila. The skewed adult sex ratio may result from greater emigration or mortality of HY females, or from greater mortality of breeding females due to increased exposure to predation.

Keywords: Palila; Loxioides bailleui; *demography; survival; population; conservation; Hawaii.*

INTRODUCTION

The Palila (*Loxioides bailleui*) is an endangered Hawaiian finch belonging to the family Fringillidae, subfamily Drepanidinae. This subfamily apparently evolved from a single founding species of cardueline finch (Freed et al. 1987) that successfully colonized the Hawaiian Islands. Presently, the Palila occupies <5% of its historic range and is confined to mamane (*Sophora chrysophylla*) and mixed mamane and naio (*Myoporum sandwicense*) forests above 1,950 m elevation on Mauna Kea, Hawaii (Scott et al. 1986). Mamane forests exist outside its current range, but strong site tenacity (Fancy et al. 1993), disease, or predation may be preventing Palila from recolonizing these areas. Because it feeds principally on unripened mamane seeds and nests almost exclusively in mamane trees, the Palila is dependent upon the mamane ecosystem for its existence.

Although the Palila has been well-studied compared with other Hawaiian forest birds (Berger 1970; van Riper et al. 1978; van Riper 1980a; Scott et al. 1984, 1986; Pletschet and Kelly 1990; Amarasekare 1993; Fancy et al. 1993), little is known about its demography. In 1987, we began a study of Palila demography, and here report on the age and sex structure, and annual survival of the only remaining Palila population.

STUDY AREA AND METHODS

Between June 1987 and September 1993, we operated mist nets near Puu Laau (19°50′N, 155°35′W) on the western slope of Mauna Kea, Hawaii. Vegetation in the study area was described by van Riper (1980b) and Scowcroft and Giffin (1983). We established four fixed banding stations that ranged in elevation from 2,100 to 2,600 m (Fig. 1). Birds were captured with 12-m long, 4-shelf mist nets of 36-mm black nylon mesh. We operated 10 nets, separated by ≥20 m within an area of approximately 2–4 ha, at each banding station. Nets were usually opened between 07:30–17:30 hr and checked at ≤30 minute intervals on 1–4 days each week at one of the four banding stations. We closed nets during periods of rain or high winds (>32 kph) to avoid injury to birds.

Banding effort varied among years; mist nets were operated for three months (June–August) in 1987, six months (February, August–December) in 1988, eight months (January, March–June, October–December) in 1989, five months (February–March, October–December) in 1990, 11 months (January–November) in 1991, 12 months

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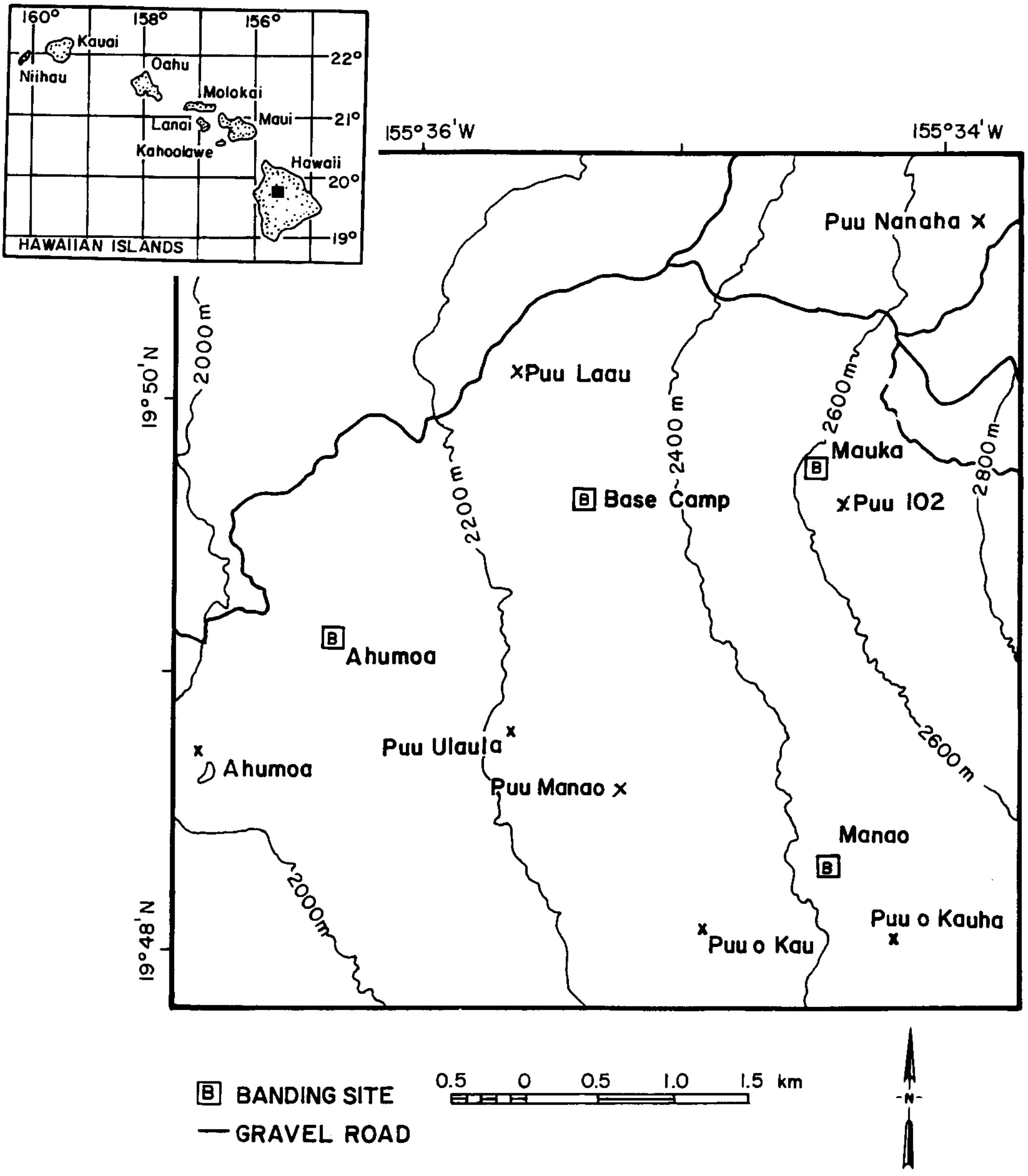

FIGURE 1. Location of study area and fixed banding stations at Puu Laau, Mauna Kea, Hawaii.

in 1992, and six months (April–September) in 1993. After operating nets for several days at a banding station, we waited at least 18 days (and usually ≥25 days) before again opening nets at that station. This strategy minimized the development of net shyness (Lovejoy 1975) and increased the capture rate.

In addition to station netting, we also netted annually at nests to capture breeding Palila. Nets were placed at the nest tree when the nestlings were ≥14 days old so as to capture adults while minimizing interference with nest success. Nestlings were banded at approximately 12 days of age.

At first capture, we marked each Palila with a unique combination of three plastic colored bands and a U.S. Fish and Wildlife Service numbered aluminum band. We measured and examined each bird to determine its sex, age, and molt and reproductive status (as in Jeffrey et al. 1993), before it was released at the banding station. Age of birds was based on the calendar year as used by the Bird Banding Laboratory and classified as Hatching Year (HY), Second Year (SY), After Hatching Year (AHY), or After Second Year (ASY). At irregular intervals throughout the six-year study, we conducted resight trips by walking throughout the study area to locate and identify individuals.

We used the number of Palila in each age class during April–September, 1991–1993, as an index of the age structure of the population because capture effort during these months was relatively consistent among years. To compute sex ratios, we used only birds initially aged as nestlings, HY or SY Palila that were subsequently captured and sexed after attaining adult plumage. Although this resulted in smaller sample sizes, we know of no method for sexing nestlings and HY Palila from measurements or plumage, and the appearance of the napeline is not totally reliable for sexing SY Palila (Jeffrey et al. 1993). We assumed that the sex ratio at hatching was even (Breitwisch 1989).

We calculated annual survival for Palila using Jolly-Seber models (Pollock et al. 1990) and data from 1,999 captures and resightings of 984 Palila first captured either as nestlings (n = 197), HY birds (n = 122), or AHY birds (n = 665). We used Model A2X of program JOLLYAGE (Pollock et al. 1990), which computes time-specific capture and survival probabilities and incorporates data from resightings. The complement of annual survival that we report here includes both mortality and permanent emigration. We selected a four-month sampling period each year from June through September, 1987–1993, based on goodness-of-fit tests from preliminary runs, and did not include a bird in the analysis until it was captured during this four-month interval. Birds captured or resighted during the eight-month period from October through May were coded as resightings in the analysis (Pollock et al. 1990). We excluded all data for 35 Palila that were translocated in March 1993 to Kanakeleonui, on the eastern slope of Mauna Kea.

The effect of food availability on annual survival was tested by correlating survival rates of HY and AHY Palila each year between 1989 and 1993 (n = 4) with the proportion of 105 mamane trees that were barren of green mamane pods in April (i.e., the beginning of the Palila breeding season, when the availability of mamane pods is near its peak) and September (i.e., the end of the breeding season, when pod availability is at a minimum).

RESULTS

During the six years of study, we captured 984 Palila 1,357 times at nests or fixed banding stations and identified free-ranging individuals from their color bands on an additional 642 occasions. Capture rates were calculated from 745 captures of 521 Palila at the four fixed banding stations (n = 27,091 net hr), and varied among stations and months (Fig. 2). Mean monthly capture rate (number of Palila captured per 100 net hr) for the four fixed banding stations was 2.72 ± 0.31 SE (n = 121, Range = 0–16.54). Monthly capture rates were consistently lower at the Ahumoa banding station (Fig. 2), which was located at the lower elevational limit of the Palila range.

AGE AND SEX RATIOS

The age structure of the Palila population varied considerably among years as a result of differences in production of young. The proportion of SY Palila in the population was relatively constant among years, whereas the proportion of HY birds captured ranged from 3.1% in 1992 to 22.6% in 1993 (Table 1). The sex ratio of nestling and SY Palila that were recaptured as adults did not differ from unity, but the sex ratio for HY Palila was male biased (Table 2). For all six years of study, we also found male bias among ASY Palila (χ^2 = 0.79, n = 6, P = 0.022; Table 3). Mean proportion of ASY males was 63.7% ± 1.8 SE.

ANNUAL SURVIVAL

The number of Palila captured or resighted each year during the June–September sampling period ranged from 5 to 73 for HY birds and 18 to 122 for AHY Palila (Table 4). When data for both sexes were combined, mean survival of HY Palila (0.36 ± 0.08) was lower (χ^2 = 17.0, df = 6, P = 0.009) than that of AHY birds (0.63 ± 0.05). The probability of capturing or resighting an individual in a given year if that individual was alive and in the study area was 0.16 ± 0.03.

We conducted separate analyses for each sex using the same four-month sampling interval, but after excluding data for 1987 because no HY females were captured in that year. Because we were unable to sex nestlings and HY Palila, HY

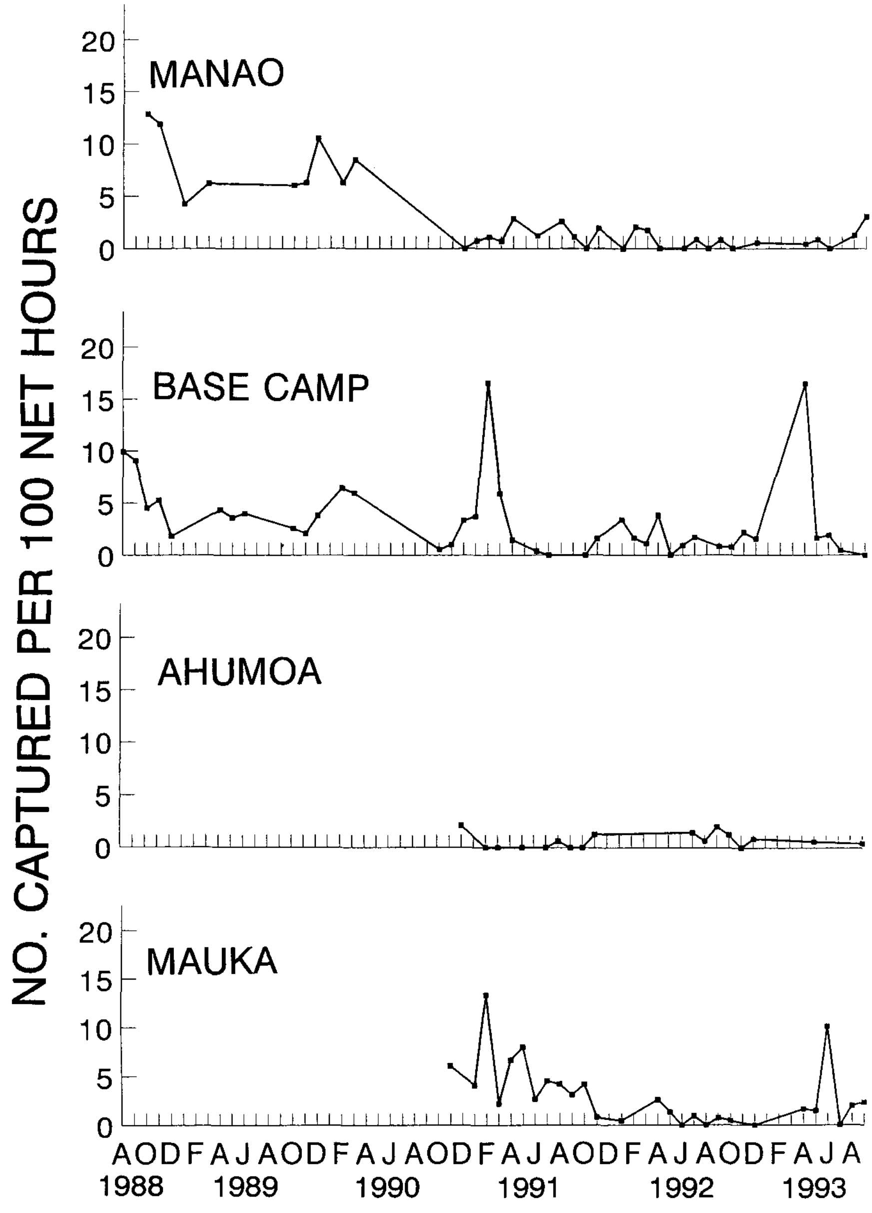

FIGURE 2. Mean monthly capture rates of Palila at four fixed banding stations, Puu Laau, Hawaii, 1988–1993.

birds were only included if they were later captured and sexed as an adult. Consequently, survival was overestimated for HY Palila in these separate analyses. Mean survival was 0.88 ± 0.13 for HY male Palila and 0.54 ± 0.19 for HY female Palila. Mean survival was 0.65 ± 0.07 for AHY males and 0.62 ± 0.06 for AHY females (paired *t*-test, $t = 0.52$, $n = 4$, $P = 0.64$). The probability of capturing or resighting an individual that was present on the study area during the June–September interval was 0.16 ± 0.04 for males and 0.16 ± 0.05 for females.

Annual survival of AHY Palila was negatively correlated with the proportion of mamane trees that were barren of green pods at the beginning of the breeding season in each of the four years

TABLE 1. Number (%) of Palila in each age class captured at Puu Laau, Hawaii, April–September 1991–1993. Palila were aged as Hatching Year (HY), Second Year (SY), and After Second Year (ASY) birds.

Year	Age			Total
	HY	SY	ASY	
1991	6 (10.5)	5 (8.8)	46 (80.7)	57
1992	1 (3.1)	4 (12.5)	27 (84.4)	32
1993	14 (22.6)	6 (9.7)	42 (67.7)	62

TABLE 3. Annual sex ratios of After Second Year Palila.

Year	Male	Female	% Males
1988	35	23	60.3
1989	77	57	57.5
1990	57	30	65.5
1991	97	47	67.3
1992	31	19	62.0
1993	84	37	69.4

between 1989 and 1993 ($r = -0.99$, $P = 0.01$). Considering that we only had corresponding survival and mamane pod availability data for four years, this result indicates a strong link between annual survival and food supply. The availability of mamane pods in September, when they are usually at their lowest level, was also negatively correlated with annual survival ($r = -0.98$, $P = 0.02$). Survival of HY Palila was not correlated with mamane pod availability in either month ($r = -0.31$, $P = 0.69$, April; $r = -0.33$, $P = 0.67$, September), nor was it correlated with survival of AHY Palila ($r = 0.43$, $P = 0.57$).

DISCUSSION

Grant and Grant (1992) found that the age structure of breeding populations of two species of Darwin's finches, *Geospiza scandens* and *G. fortis,* was unstable because of episodic reproduction and variable survival under fluctuating environmental conditions. The number of nesting attempts by Palila appeared to be influenced by annual differences in precipitation and differences in the availability of immature mamane pods prior to and during the Palila breeding season (van Riper 1980b; P. Banko, unpubl. data). For example, we located 71 Palila nests in our study area during 1991, a year of relatively high mamane pod production, compared to 52 nests during the previous year when mamane pods were moderately available (T. Pratt, unpubl. data). In 1992, when a drought caused an almost complete failure in the mamane crop, we located only five Palila nests. Adult Palila had higher survival in years when mamane production was relatively high. Surprisingly, survival of HY Palila was not correlated with annual changes in mamane pod production, nor was it correlated with adult survival.

TABLE 2. Sex ratios of nestlings, Hatching Year, and Second Year Palila that were subsequently captured and sexed after attaining adult plumage.

Age	Male	Female	χ^2	P[a]
Nestling	5	3	0.50	0.48
Hatching Year	10	2	5.33	0.02
Second Year	10	14	0.67	0.41

[a] Chi-square test to determine if sex ratio within each age class differs from unity.

Sex ratios of monogamous, biparental birds are generally at unity for nestlings but are male-biased among adults (Breitwisch 1989). Breitwisch (1989) listed three hypotheses regarding the origin of male-biased adult sex ratios—differential mortality of females (1) as juveniles, (2) as adults from nonreproductive causes, or (3) as adults from parental investment. Typically, skewing of the sex ratio occurs after the termination of parental care. For example, Schreeve (1980) reported even numbers of male and female nestlings of the Aleutian Gray-crowned Rosy Finch (*Leucosticte tephrocotis griseonucha*), a cardueline finch, but found that the population became male-biased by the time birds reached sexual maturity.

Ten of the 12 Palila that we banded as HY birds and later recaptured as adults were males.

TABLE 4. Number of Palila captured or resighted during June–September each year, 1987–1993.

Year	Number caught[a]		Number caught and seen later		Number not caught and seen later	Annual survival	
	AHY	HY	AHY	HY		HY	AHY
1987	18	5	6	1	0	0.3214	0.5357
1988	36	17	19	6	5	0.3371	0.5041
1989	108	73	60	28	11	0.5625	0.8262
1990	61	44	27	10	59	0.2406	0.6447
1991	62	42	30	11	57	0.3143	0.6607
1992	35	7	17	3	62		
1993	122	34	14	4	6		

[a] Includes birds resighted during June–September as well as birds captured in mist nets.

Considering the high mortality of HY Palila, the skewed adult sex ratio could result from greater mortality or emigration of HY females. Most avian species disperse from natal sites as juveniles or subadults, and females are more likely to disperse than males (Greenwood 1980). A higher emigration rate for HY females, possibly coupled with higher mortality since they are emigrating from the most optimal habitat (Scott et al. 1986), may explain the skewed adult sex ratio for Palila. We have found little evidence of emigration from our banding and radio-telemetry work with Palila (Fancy et al. 1993), but we have not radio-marked HY birds.

Breitwisch's (1989) second and third hypotheses deal with higher mortality of females as adults, either from nonreproductive causes or parental investment. Breitwisch concluded that insufficient evidence exists to support the hypothesis that females in monogamous bird species expend greater parental investment than males. However, because female Palila construct the nest and do all of the incubating and brooding (van Riper 1980a, Pletschet and Kelly 1990), they may suffer higher mortality due to increased exposure to predation on the ground and at the nest.

Predation by black rats (*Rattus rattus*), feral cats (*Felis catus*), mongooses (*Herpestes auropunctatus*) and the Hawaiian Short-eared Owl or Pueo (*Asio flammeus sandwichensis*) is thought to be an important cause of mortality among endemic Hawaiian forest birds (Atkinson 1977, Scott et al. 1986, Snetsinger et al. 1994). Pletschet and Kelly (1990) attributed 5% of Palila nest mortality to egg depredation and 35% to nestling depredation by feral cats and black rats, and suggested that predation on adult birds could have contributed to the high rate of nest abandonment they observed. Van Riper (1980a) observed a feral cat eating a brooding Palila female at a nest, and because he trapped around each active nest, felt that predation may be more important than his data indicated. Snetsinger et al. (1994) found that 68% of cat scats collected near Puu Laau contained bird remains, and thought that feral cats were an important predator on Hawaiian forest birds. In our study, several nest failures in 1993 were attributed to predation of nestlings by feral cats (T. Pratt, unpubl. data). Amarasekare (1993) concluded that predation had little effect on the Palila, but her study focused primarily on black rat predation either in the core Palila nesting area, where few black rats occur, or in naio-dominated forests, where few Palila attempt to nest. It is noteworthy that, at Puu Laau, van Riper (1995) found an even adult sex ratio for Elepaio (*Chasiempis sandwichensis*), a species where both sexes construct the nest, incubate, and brood their young, whereas he found a male-biased sex ratio for Common Amakihi (*Hemignathus virens*; van Riper 1987), a species with sexual roles similar to those of Palila.

Annual survival rates for HY and AHY Palila are comparable to those found for other Hawaiian forest birds. Annual survival of HY (0.40 ± 0.09) and AHY (0.66 ± 0.08) Omao (*Myadestes obscurus*; Ralph and Fancy 1994a) was similar to our survival rates for Palila. Ralph and Fancy (1994b) reported adult survival rates of 0.73 ± 0.12 for Hawaii Creeper (*Oreomystis mana*) and 0.70 ± 0.27 for Hawaii Akepa (*Loxops coccinea*). Adult survival was 0.72 ± 0.11 for Apapane (*Himatione sanguinea*) and 0.55 ± 0.12 for Iiwi (*Vestiaria coccinea*; C. J. Ralph and S. G. Fancy, unpubl. data). Survival rates of Hawaiian species are comparable to those calculated by Karr et al. (1990) for 35 species of birds in temperate and tropical forests.

MANAGEMENT IMPLICATIONS

The recovery plan for Palila (USFWS 1986) specifies that to downlist the species to threatened status, the Palila population must be distributed throughout its 139-km^2 critical range at a density of ≥ 25 birds/km^2. Currently, most of the Palila population is concentrated on the southwest slope of Mauna Kea near Puu Laau, and little successful nesting occurs elsewhere (T. Pratt, unpubl. data). The elevational range of the mamane forest is greatest in the area where most Palila occur, presumably because of a phenological gradient that results in a more stable supply of immature mamane pods within a relatively short distance (Scott et al. 1984, 1986; Fancy et al. 1993). This study and previous work have found that the Palila population shows considerable annual variation in numbers and population structure, primarily as a result of variation in reproductive attempts.

Palila show strong site tenacity (Fancy et al. 1993), and it appears that Palila may disperse from the core nesting area near Puu Laau only during times of food shortage. Banded females usually nest within 500 m of their previous nests (T. Pratt, unpubl. data). Amarasekare (1993) found that black rats are associated primarily with naio trees and occur only in low densities in the core Palila nesting area where mamane predominates. Thus, it is likely that higher rates of predation outside of the core nesting area, coupled with the Palila's high nest site fidelity and low dispersal potential, could explain why few Palila nest successfully outside of the Puu Laau area.

We believe that control of black rats and feral cats in the naio-dominated forests south and southeast of the core Palila nesting area, in combination with translocation of HY Palila to these areas, would result in an expanded core nesting area for Palila and speed recovery of this species. An experimental translocation of adult Palila in 1993 (S. Fancy, unpubl. data) showed that adult Palila will remain and breed in a new area, but the close proximity of the naio-dominated forests to the core nesting area makes it more probable that translocated adults would return to their capture site. We advocate translocation of young Palila since juveniles of most passerines are more likely to disperse (Greenwood 1980) and, therefore, have a higher probability of remaining at the release site. Habitat restoration efforts that promote mamane growth, such as removing cattle and controlling fires, would also speed recovery of the Palila population.

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