Long-Term Population Variability in the Palila, An Endangered Hawaiian Honeycreeper[1]

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ABSTRACT: Annual surveys of the entire range of the endangered Palila (*Loxioides bailleui* Oustalet) on Mauna Kea, Hawai'i, were conducted during 1980–1995. The majority of the Palila population was found on the southwestern slope of Mauna Kea near Pu'u Lā'au, and the range of Palila has not changed since 1975. The Palila population was highly variable. Mean population size during 1980–1995 was 3390 ± 333 SE, but the population ranged from 1584 ± 324 in 1985 to 5685 ± 535 in 1981. Population size outside the population center near Pu'u Lā'au has decreased significantly since 1980.

THE PALILA (*Loxioides bailleui* Oustalet) is an endangered Hawaiian honeycreeper (Fringillidae, Drepanidinae) currently found only in subalpine woodlands of Mauna Kea on the island of Hawai'i (Figure 1). The species is highly dependent upon the māmane (*Sophora chrysophylla* [Salisb.] Seem.) tree, from which it obtains the unripe seeds that are its primary food (van Riper et al. 1978, van Riper 1980*a*, Scott et al. 1984). Essentially all nesting occurs in māmane, even in areas where naio (*Myoporum sandwicense* A. Gray) is the dominant tree species. Scott et al. (1986) estimated that Palila now occupy <5% of the range they inhabited before the arrival of the Polynesians, and their current range may always have been marginal habitat (Scott et al. 1984).

Habitat loss and modification, and annual variation in food supply in their high-elevation habitat are thought to be the primary reasons for the current small range and population size of the Palila. Avian malaria and avian pox have had devastating effects on Hawaiian forest birds and may prevent Palila from recolonizing portions of their former range below 1800 m elevation (Scott et al. 1984, van Riper et al. 1986). Degradation and fragmentation of the māmane woodland by introduced feral sheep (*Ovis aries*) and mouflon (*Ovis musimon*) led to two lawsuits in the 1980s to halt browsing of māmane (Scowcroft and Giffin 1983). Most of the feral ungulates have now been removed from Mauna Kea, and the forest is showing increased regeneration of māmane and other plant species.

In this study, we present results of 16 annual surveys of the entire range of Palila. We sampled the same locations established by the Hawaiian Forest Bird Surveys (Scott et al. 1986) to document long-term changes in population size and range of Palila.

MATERIALS AND METHODS

The 250-km² study area encompassed the entire māmane and māmane-naio woodland on Mauna Kea volcano on the island of Hawai'i. This subalpine forest extends from 1800 to 3000 m elevation and is dominated by short-stature (3–10 m) trees (Scowcroft and Giffin 1983, Scott et al. 1984). Māmane occurs around the entire mountain, but naio is mainly restricted to the southern and southwestern slopes. Rainfall averages 35–75 cm annually.
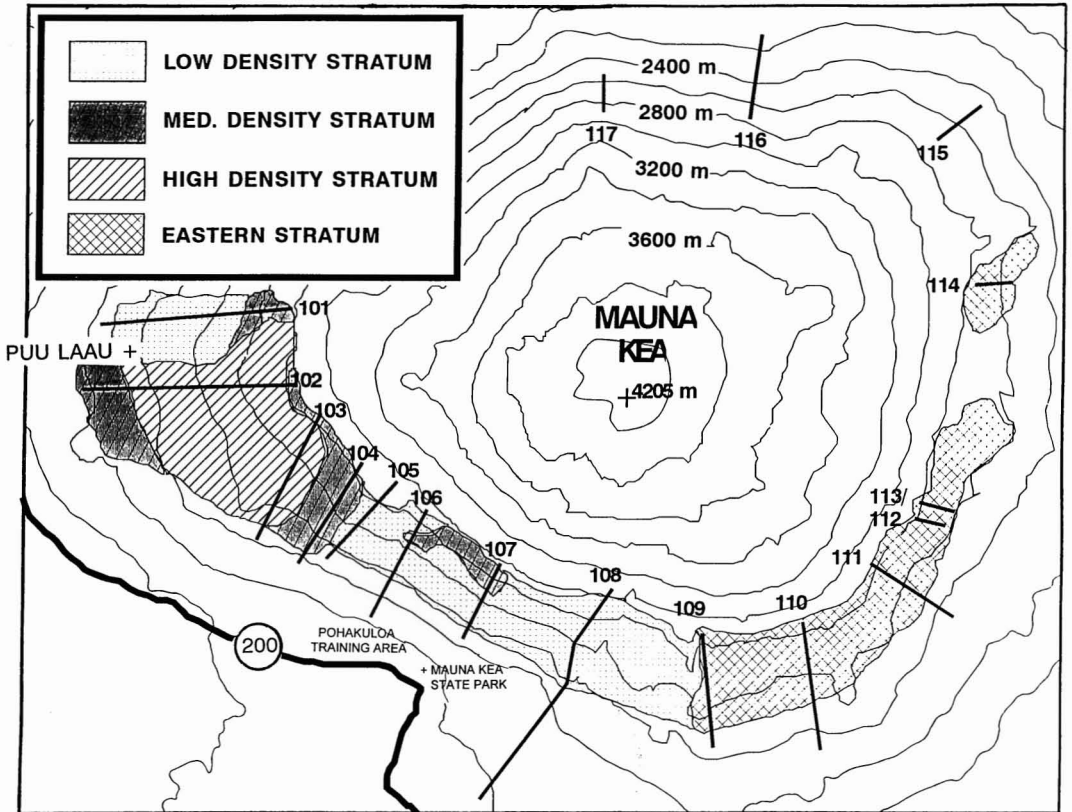
FIGURE 1. Location of 17 transects and four density strata used to determine population size and range of Palila on Mauna Kea, Hawai'i, 1980–1995.

We used the variable circular-plot method (Reynolds et al. 1980) with 6-min counts to record the occurrence of Palila. The same sampling stations along 17 randomly placed transects (Figure 1) were surveyed each year during January or February, 1980–1995, following methods described by Scott et al. (1984). Counts were not conducted when wind speed exceeded 30 km/hr. The 48 observers that participated in the annual surveys were trained to identify Palila by sight and from vocalizations and to estimate distances in Palila habitat. Beginning in 1991, we sampled each station only once each year, but before 1991, ca. 60 stations on transects 101–103 (Figure 1) were sampled twice during each survey. Stations counted twice were sampled by different observers on different days and were treated as independent samples. No Palila were detected on transects 115–117 during the 16 annual surveys, and we excluded stations on those transects from analyses of Palila density.

We assigned each station to one of four density strata based on the total number of Palila detected at the station during the 16 yr of study (Figure 1). Stratum boundaries were drawn on vegetation maps of the study area (Jacobi 1989) by S.G.F. in consultation with three other biologists who had conducted intensive research on Palila since 1990 (P. Banko, T. Pratt, and G. Lindsey). Vegetation boundaries and elevational contours were followed to delineate stratum boundaries between transects. The high-density stratum included areas above 2130 m near transects 102 and 103, where most of the successful breeding by Palila occurs. The medium-density

stratum included several areas on the southwestern slope of Mauna Kea adjacent to the high-density stratum, plus an area dominated by naio on the southern slope of Mauna Kea near transect 107 (Figure 1). Most of the Palila range east of transect 105 was placed in the low-density or eastern strata. The total number of Palila detected at stations in the low-density and eastern strata was similar, but we assigned stations on transects 109–114 to the eastern stratum so that we could determine the size and trend of the Palila population on the eastern slope of Mauna Kea separately.

The density of Palila in each stratum was calculated by a modification of Ramsey et al.'s (1987) method where the logarithm of effective area surveyed is used as a link to covariates that affect detectability of birds (Fancy 1997). To determine the effect of different observers, wind speed, and time of day on detection distances, we transformed distances to areas and used multiple linear regression to fit the model:

$$\ln(Area) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots \beta_n X_n$$

where $X_1 \ldots X_n$ are covariates such as observer and time of day and $\beta_0 \ldots \beta_n$ are regression coefficients that explain the effect of each covariate on detection distances. All detection distances for Palila were adjusted as if they were all recorded by the same observer under average conditions, and the effective area surveyed under these standard conditions was calculated by the program DISTANCE (Laake et al. 1994). We selected J.D.J. as the reference observer because he participated in more surveys than most observers and his effective area was in the midrange of effective areas for different observers. Detection distances for observers with ≤25 Palila detections were combined with J.D.J.'s distances to establish the reference condition. The combined data set for the reference observer (J.D.J. + 25 others) included 357 (19% of the 1846 distances) detection distances for Palila. We used 0900 hours as the reference time and Beaufort scale 1 as the reference wind speed.

The effective detection radius for Palila

under standardized conditions was 64.04 m, with a coefficient of variation of 1.47%. Wind speed did not affect effective area surveyed ($P = 0.35$) and was dropped from the regression model. Effective area decreased as time of day increased ($\beta_{TIME} = -0.16$, $P = 0.0001$), and adjustments were therefore made for different observers and time of day when a station was sampled. The best model from the DISTANCE program was obtained by fitting a Fourier function to the 2203 detection distances ($\chi^2 = 4.69$, df = 7, $P = 0.70$) after grouping distances into 17-m intervals (Buckland et al. 1993:111). Density at each station was calculated as the number of Palila detected divided by effective area surveyed, and stratum means were calculated from densities of all stations within each stratum. Variation in effective area surveyed was included by sampling from a random normal distribution centered on the mean effective area, and confidence intervals were calculated from 5000 bootstrap samples using the computer program VCPADJ (Fancy 1997).

RESULTS

The majority of the Palila population was found on the southwestern slope of Mauna Kea near Pu'u Lā'au. Palila density was highest in the vicinity of transect 102 (Figure 1). Elevational range of the species was 1975–2930 m. No change in the extent of the Palila's range has been detected since 1975.

Annual estimates of the Palila population (mean ± SEM) ranged from 1584 ± 324 in 1985 to 5685 ± 535 in 1981 (Figure 2, Table 1). The population showed considerable annual variation (39% CV), with periods of decreasing population size during 1981–1985 and 1987–1992. Although our mean densities were similar to those reported by Scott et al. (1984), we were able to calculate smaller confidence intervals because of larger sample sizes and post-stratification of survey data.

We regressed population estimates for each stratum on year to determine population trends for each stratum. We found no trend for the medium- ($F = 0.70$, $P = 0.80$) or
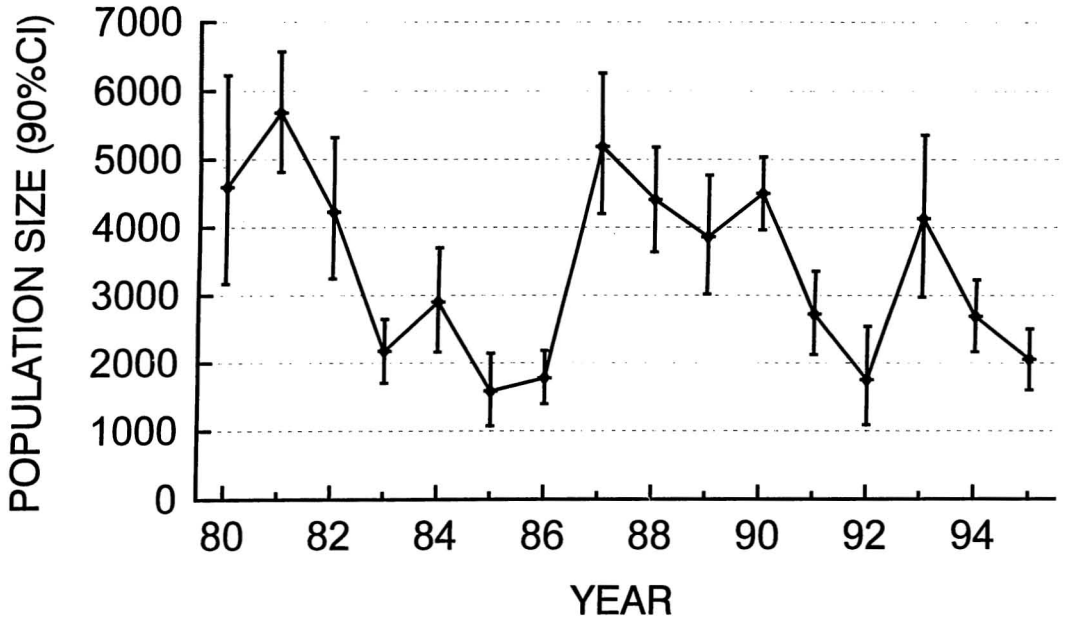
FIGURE 2. Population size (mean ± 90% confidence interval) of Palila on Mauna Kea, Hawai'i, 1980–1995.

TABLE 1

POPULATION SIZE OF PALILA ON MAUNA KEA, HAWAI'I, 1980–1995

| | | | POPULATION SIZE | | |
YEAR	STATIONS SAMPLED	NO. PALILA DETECTED	MEAN	SEM	90% CONFIDENCE INTERVAL
1980	270	153	4,592	922	3,171–6,225
1981	267	239	5,685	535	4,814–6,570
1982	244	132	4,224	626	3,246–5,320
1983	257	96	2,177	288	1,707–2,648
1984	267	93	2,903	465	2,164–3,699
1985	268	69	1,584	324	1,076–2,142
1986	270	108	1,778	238	1,396–2,182
1987	270	164	5,186	621	4,197–6,258
1988	270	219	4,405	467	3,635–5,177
1989	269	159	3,859	530	3,017–4,766
1990	267	274	4,498	324	3,961–5,037
1991	209	101	2,724	378	2,125–3,355
1992	209	43	1,753	448	1,090–2,543
1993	208	118	4,130	731	2,974–5,360
1994	208	116	2,691	320	2,166–3,228
1995	208	113	2,056	274	1,603–2,503

high- ($F = 0.02$, $P = 0.90$) density strata, but decreasing trends were found for both the low-density ($F = 12.87$, $P = 0.003$) and eastern ($F = 10.23$, $P = 0.006$) strata (Figure 3). This indicates that although the Palila population in the best habitat near Pu'u Lā'au has not declined during 1980–1995, the population in areas with lowest densities con-
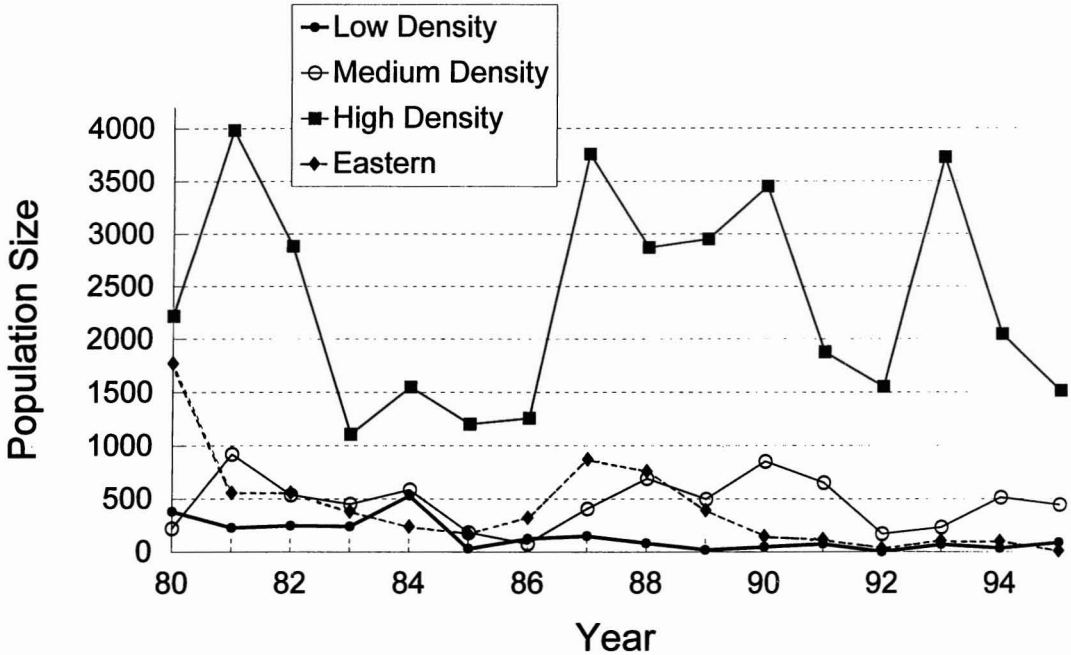
FIGURE 3. Mean population size of Palila within each of four strata on Mauna Kea, Hawai'i, 1980–1995.

tinues to decline. The largest decrease has been in the eastern stratum, where the mean population decline was 61 Palila per year.

DISCUSSION

Most passerine bird populations vary markedly from year to year in response to variations in resource abundance, weather, predation, and other factors (e.g., Wiens 1989, Hogstad 1993, Blake et al. 1994). In addition to the actual variability in population size among counts, there may also be variability due to inexactness of the counts (Link et al. 1994). In most studies, it is impossible to know whether annual changes at a site are caused simply by movements of birds to other areas or to changes in recruitment or mortality. In this study, we sampled the entire range of the Palila for 16 yr in a structurally simple, open habitat. Although sampling errors contributed an unknown but potentially large amount of variation to our annual population estimates, we know that

differences among years reflect population processes in response to environmental factors rather than changes in the range of the population (Fancy et al. 1993).

We found that Palila occurred at highest density near Pu'u Lā'au, where the elevational extent of māmane forest was greatest. Māmane phenology varies with elevation and exposure (van Riper 1980b), and a greater elevational range of māmane forest provides Palila with more opportunity to exploit shifts in abundance of māmane pods and flowers (Scott et al. 1984, Fancy et al. 1993). Palila range has changed little in 20 yr; the areas that currently support the highest and lowest densities of Palila are the same as those reported by van Riper et al. (1978) in 1975 and by Scott et al. (1984) in 1980–1984. We have seen noticeable regeneration of māmane in the past few years following reduction of feral ungulate numbers on Mauna Kea, but the trees are still too small to expect changes in Palila range or numbers in response to this new growth. Scowcroft and Conrad (1988) thought that the expected in-

crease in tree size and crown cover would not measurably benefit Palila until the early part of the twenty-first century.

Several factors are known to affect the population dynamics of Palila. Annual changes in māmane pod production (van Riper 1980b; P. Banko, unpubl. data), which presumably are the result of the vagaries of weather in this high-elevation, dry forest ecosystem, affect both recruitment and survival of Palila. Although nesting success does not differ greatly among years (T. Pratt, unpubl. data), the number of nesting attempts and the length of the nesting season are greater in years of relatively good māmane pod production (T. Pratt, unpubl. data). Direct mortality of chicks because of storms has also been documented (T. Pratt, unpubl. data). Lindsey et al. (1995) reported that adult survival was correlated with annual availability of green māmane pods.

Predation is thought to be an important factor affecting the range and limited nesting range of Palila. Black rats (*Rattus rattus*), feral cats (*Felis catus*), and Pueo (*Asio flammeus sandwichensis*) take Palila eggs, nestlings, and adults (van Riper 1980a, Pletschet and Kelly 1990, Amarasekare 1993, 1994, Fancy et al. 1993, Snetsinger et al. 1994; T. Pratt, unpubl. data). Within the Palila's range, rats are more abundant and more often found in areas where naio is present (Amarasekare 1993, 1994). Predation may be the most important factor limiting successful nesting of Palila outside the current "core" nesting area near Pu'u Lā'au (Lindsey et al. 1995). Control of introduced predators has been proposed as a means of increasing the nesting range of Palila (Lindsey et al. 1995). Strong site tenacity (Fancy et al. 1993) and social behavior among individuals also appear to influence the range of Palila.

The lowest population estimates in 1985 and 1992 occurred during droughts caused by El Niño events (Trenberth 1991), which caused most Palila to forego breeding (T. Pratt, unpubl. data). It is possible that the low estimates in those years were a result of lower detectability of Palila (e.g., less singing or flying) rather than an actual decrease in Palila numbers. Nevertheless, the annual estimates show two 4- to 5-yr periods of population decline ending with a doubling of the Palila population following El Niño years. A doubling of the population in 1 yr is possible, because of the Palila's ability to raise more than one clutch of young during periods of good māmane production (T. Pratt, unpubl. data). Arcese et al. (1992) documented annual fluctuations of 10-fold or more in an insular population of Song Sparrows (*Melospiza melodia*), and high annual variability has been documented for many passerine populations (e.g., Loiselle 1988, Droege and Sauer 1990, Virkkala 1991). It is unclear whether the breeding pause that occurred in El Niño years was a factor in the rapid rebound in the Palila population following the drought, or whether the population increases could be explained by changes in resource availability.

Although the Palila population has averaged more than 3000 birds during the past 16 yr, the species is still prone to extinction because of its limited range and high annual variation in numbers. Approximately 92% of the population occurs west of transect 105 (Scott et al. 1986:27) in an area that is at high risk to fire. Decreasing population size in the low-density and eastern strata is of great concern because the risk of extinction to a population from fire or some other catastrophe is greater when the population is concentrated in a small area. The eastern stratum, although classified as critical habitat, is unable to sustain Palila over the long term because the māmane forest there occurs in a narrow elevational band with little difference in phenology among trees. Mosquitoes, the vector for avian malaria and pox, have been found in cattle stock ponds and discarded tires in the grazing lands below transect 14, and avian disease may also be responsible for decreasing Palila populations in the eastern stratum. Removal of cattle and stock ponds, and replanting of māmane trees in the pastures downslope from the forest reserve on eastern Mauna Kea is needed for long-term management and survival of the Palila. The establishment of a separate

breeding population, perhaps within the Palila's former range on Mauna Loa or Hualālai volcanos, would be an important step toward ensuring the long-term survival of this species.

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