Wilson Bull., 105(4), 1993, pp. 587–596

SITE TENACITY OF THE ENDANGERED PALILA

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ABSTRACT.—Strong site tenacity might prevent Palila (*Loxioides bailleui*), an endangered Hawaiian honeycreeper, from repopulating favorable habitats in their former range. We used radio telemetry during the nonbreeding and breeding seasons to study movements and dispersal rates of 57 Palila. All Palila remained in the study area, and home range sizes and movement distances were small relative to the potential mobility of the species. Banding and nesting studies revealed that Palila show strong site tenacity. An inverse correlation between movements and elevation was related to an elevational gradient in food supply. Translocations of Palila into presently unoccupied areas in their range might speed the recovery of this endangered species. *Received 7 Dec. 1992, accepted 16 Apr. 1993.*

The Palila (*Loxioides bailleui*) is a finch-billed Hawaiian honeycreeper (Fringillidae, subfamily Drepanidinae) found only in dry woodlands on Mauna Kea on the island of Hawaii (Fig. 1). Historically, Palila occurred in subalpine mamane (*Sophora chrysophylla*)—naio (*Myoporum sandwicense*) forests of Mauna Kea, the northwestern slopes of Mauna Loa, and on the eastern slopes of Hualalai (Fig. 1; U.S. Fish and Wildlife Service 1986) and probably on other islands (Olson and James 1982). Their current 139-km^2 distribution is limited to mamane-naio forests on the southwestern, southern, and eastern slopes of Mauna Kea between approximately 2000 m and 2850 m; highest densities occur near Puu Laau (Scott et al. 1984; Fig. 1). Scott et al. (1986) estimated that Palila currently occupy <5% of their pre-Polynesian range. Population estimates ranged from 1371 to 5354 Palila during 1986–1993 (J. Giffin, unpubl. data).

Overbrowsing of mamane-naio forests by introduced feral ungulates, beginning in the early 1800s, was a major cause of the loss of Palila habitat (Warner 1960, Scowcroft and Giffin 1983). The immature seeds of mamane are the staple food of Palila, who also use mamane trees extensively for nesting and shelter. Recent removal of feral ungulates from Mauna Kea is allowing regeneration of mamane forests, but Palila are absent or occur in only small numbers in many areas of seemingly suitable habitat. Scott et al. (1984) hypothesized that site tenacity may be a factor in the absence of Palila from mamane forests of the Pohakuloa flats. Strong site

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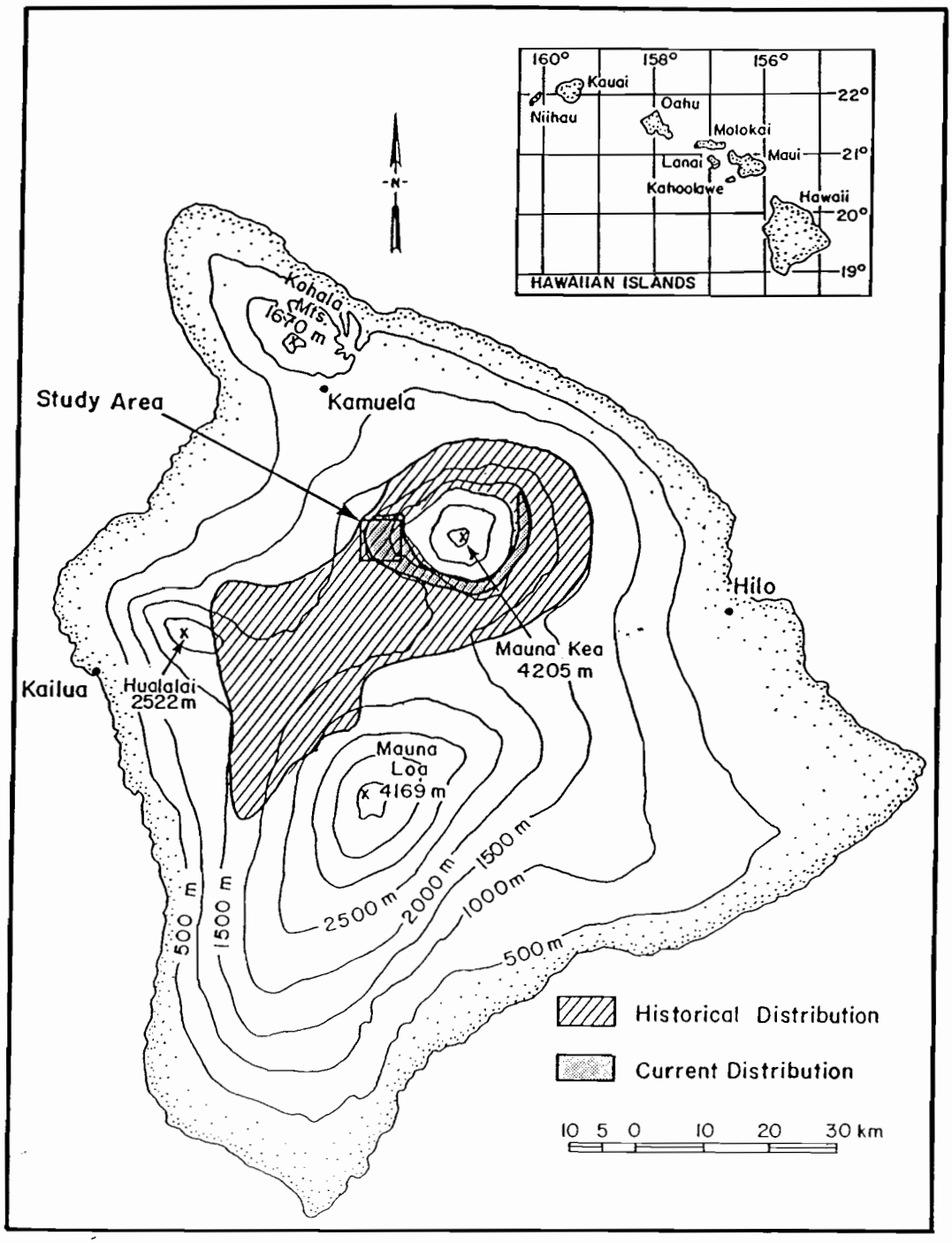

FIG. 1. Distribution of Palila and location of study area on Hawaii.

tenacity might also explain the absence of Palila in regenerating forests on the northern and northeastern slopes of Mauna Kea.

Our primary objective was to determine the extent of Palila movements during the nonbreeding and breeding seasons. The study was part of larger

research on factors limiting Palila population growth. Results will be used to develop management strategies for this endangered population.

METHODS

The 34-km² study area was in native mamane-naio forest with a grass understory near Puu Laau on the southwest slope of Mauna Kea between the 2000–2800 m elevation contours (Fig. 2). Vegetation of the study area was described by van Riper (1980) and Scowcroft and Giffin (1983).

Preliminary studies of captive Omao (*Myadestes obscurus*) and Palila with placebo transmitters indicated no adverse effects on flight, feeding, or interactions with other birds. We attached transmitters weighing 1.6–1.8 g to 37 adult and second-year Palila (mean mass = 36.7 g) during the nonbreeding seasons in 1988 (N = 10; 22 Feb.–20 Mar.) and 1991 (N = 27; 19 Feb.–22 Mar.) and 20 during the breeding season in 1991 (N = 20; 30 May–27 July). Palila were captured in mist nets at the Mauka base camp, the Puu Manao banding stations, and at active nests within 1 km of the Mauka banding station (Fig. 2). We weighed each Palila in a cotton bag with a 100-g Pesola scale and determined sex and age by plumage characteristics (Jeffrey et al. 1993).

To attach a transmitter, we held the bird in one hand and used a thumb and index finger to push the feathers in the interscapular region forward. We then trimmed feathers to a length of 1–2 mm in an area 4–6 mm larger than the base of the transmitter. Trimming rather than removing the feathers prevented regrowth of feathers that would dislodge the transmitter. Skin-Bond cement (Smith-Nephew United, Inc., Largo, Florida) was applied to an oval piece of chiffon and to the trimmed area with a cotton swab, and the chiffon was gently set into place. After allowing the Skin-Bond to dry for 2–3 min, we coated the base of the transmitter with Superglue (or more Skin-Bond in 1988) and used a thumb to hold the transmitter against the chiffon for another 2–3 min to allow it to dry. The feathers that had been pushed forward eventually covered the transmitter, and only the 16-cm antenna protruded posteriorly along the axis of the bird's spine.

We determined locations of Palila by triangulation from three or four permanent sites at Puu Laau, Puu Nanaha, Puu 102, and Puu Manao (Fig. 2) with a null-peak telemetry system (Cochran 1980, White and Garrott 1990). The Puu Nanaha site was not used in 1988. Bearings to each bird were determined 2–3 times daily in 1988 and at 2-h intervals between 08:00 and 17:00 HST in 1991. Roosting locations of Palila also were determined in 1991 from bearings taken after 19:30 h.

Locations were calculated with the program TRIANG (White and Garrott 1990) from bearings taken within 15 min of each other. The mean location error for 10 transmitters placed blind in the study area was 160 m ± 40 m (SE; [range 68–487]). Because of the effect of sample size on reliability of estimates of home range size (Bekoff and Mech 1984, Swihart and Slade 1985), we excluded birds with <30 locations from further analyses.

For each bird, we calculated two measures of site tenacity: the minimum convex polygon (Mohr 1947, Hayne 1949), hereafter referred to as a bird's home range, and the median distance between each location and the bird's center of activity (Hayne 1949), hereafter referred to as the median distance. We used median rather than mean distances to lessen the effect of a few outliers. We used a logarithmic transformation on home range size so that variances were independent of means.

During November and December 1991 and again in November 1992, we systematically searched mamane forests on all slopes of Mauna Kea for color-banded Palila that dispersed from the study area. Teams of two individuals slowly walked through an area, listening and looking for Palila. Observers used binoculars and spotting scopes to determine whether any

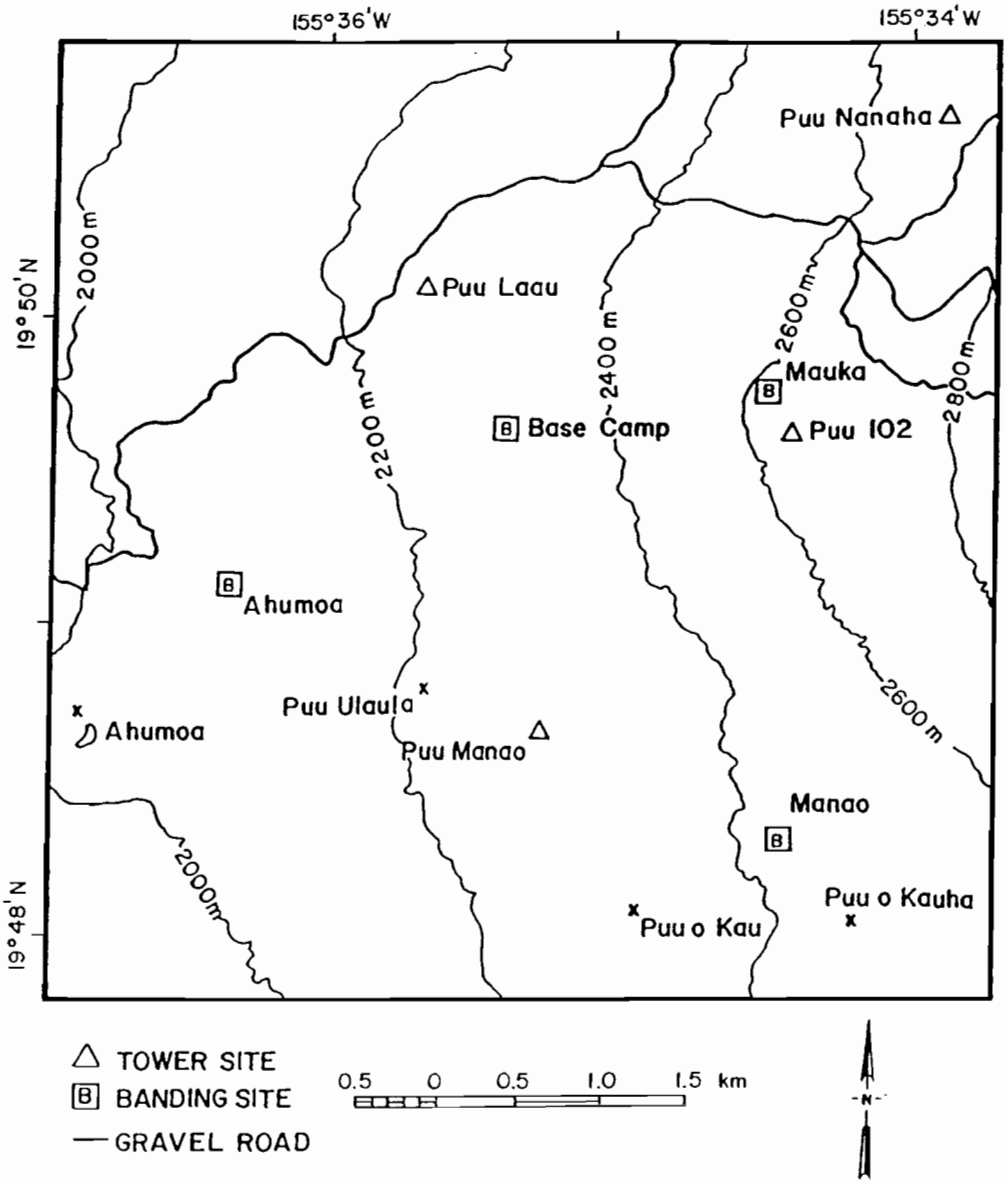

FIG. 2. Banding sites and telemetry towers in the study area on the southwest slope of Mauna Kea volcano, Hawaii, 1988–1991.

Palila that were detected were banded and to identify them from their color-band combinations.

Elevational differences in food supply were measured along three transects (transects 101–103 in Scott et al. 1986:27) between 1972 m and 2859 m elevation on 2 Feb. 1988 and 23 Jan. 1991. The proportion of terminal branchlets with mature green pods was determined for 10 mamane trees >2 m tall in each 150-m segment along transects (N = 960 trees). Mean proportion of pods in each 150-m segment was coded as 0 (<0.5% pods), 1 (0.5–4.9% pods), 2 (5.0–19.9% pods), or 3 (≥20% pods). Density of mamane and naio trees >2 m tall was determined in 150 × 20 m plots along transect 102 on 19 Sept. 1991.

We compared sample means using *t*-tests (SAS 1987) except where noted otherwise. We

used MRPP for grouped data (Multi-response Permutation Procedures; Mielke et al. 1981, Biondini et al. 1988) to test the hypothesis that Palila repeatedly roost in the same portion of their home range. Alpha levels ≤0.05 were considered significant.

RESULTS

We obtained ≥30 locations for 45 of 57 radio-tagged Palila. During the 1991 nonbreeding season, three used transmitters refitted with new batteries failed immediately after releasing the bird, and seven other used transmitters had weak and intermittent signals. Two other transmitters functioned properly but could be received only from one site much of the time because of the topography of the study area; we obtained <30 locations for these transmitters.

All Palila with functioning transmitters remained in the study area throughout each season. We assumed that the three used transmitters failed because one of the Palila was captured two months later with the transmitter still attached, 10 of 12 used transmitters were unreliable, and all Palila with functioning transmitters remained relatively close to their capture site.

One Palila, radio-tagged in February 1988, still carried a transmitter when recaptured seven months later, but most transmitters were lost within 6–8 weeks. Seven transmitters, attached in February 1991, were detached prematurely from the birds approximately three weeks into the study, possibly because of defective adhesive. We noted that the skin in the interscapular region was inflamed, but healing, for two of seven radio-tagged Palila that were recaptured 1–7 months after their initial capture; the other five Palila had replaced the trimmed feathers, and no other problems were noted. The recapture rate for radio-tagged Palila during the 6 months after the 1991 nonbreeding season (4 of 27, 14.8%) was similar to that for Palila captured between February and April 1991 that were not radio-tagged (7 of 55, 12.7%), suggesting that the transmitters had little if any effect on short-term survival. (A similar comparison for the 1988 breeding season was not possible because only two Palila were captured and not radio-tagged).

Two radio-tagged second-year Palila were killed or scavenged by predators during the 1991 nonbreeding season, but whether the transmitter contributed to their death is unclear. The transmitter and a few feathers from one Palila were found 19 days after the bird was radio-tagged. Feral cat (*Felis domesticus*), rat (*Rattus* spp.), and feral pig (*Sus scrofa*) tracks were all found within 20 m of the transmitter. The second transmitter and a few feathers were found inside a rat nest under the pile of boulders 36 days after the Palila was radio-tagged.

Excluding Palila with <30 locations, we found no correlation between

TABLE 1

MOVEMENTS OF 44 PALILA RADIO-TRACKED DURING THE NONBREEDING AND BREEDING SEASONS IN 1988 AND 1991, PUU LAAU, HAWAII

Season	Sex	N[a]	Days tracked	Locations per bird	Distance (m)[b] (Mean ± SE)	Minimum convex polygon (km^2) (Mean ± SE)
	Male	6	10–24	34–92	595 ± 142	3.82 ± 0.91
	Female	2	21–23	43–67	708 ± 102	4.11 ± 1.29
	Unknown	1	20	58	782	2.18
1988 Nonbreeding	Total	9	10–24	34–92	654 ± 100	4.73 ± 1.12
	Male	9	16–33	32–116	382 ± 51	2.61 ± 0.50
	Female	5	16–33	31–121	366 ± 61	2.80 ± 0.99
	Unknown	2	10–21	30–71	472 ± 1	2.56 ± 0.51
1991 Nonbreeding	Total	16	10–33	30–121	388 ± 34	2.66 ± 0.40
	Male	12	15–56	43–156	276 ± 38	2.55 ± 0.55
	Female	8	14–50	45–148	459 ± 196	3.60 ± 1.46
1991 Breeding	Total	20	14–56	43–156	349 ± 81	3.01 ± 0.65

[a] Number of Palila with ≥30 locations.
[b] Median distance between all locations for each bird and its center of activity.

number of locations for each bird and either home range size ($r = 0.15$, $N = 45$, $P = 0.33$) or median distance from the center of activity ($r = -0.11$, $N = 45$, $P = 0.47$). We similarly found no correlation between our two measures of site tenacity and the number of days each Palila was tracked.

During 1991, we found no seasonal difference in home range size ($t = 0.27$, 34 df, $P = 0.79$) or median distance ($t = 0.45$, 25.3 df, $P = 0.66$) when sexes were combined, even when we excluded birds without an active brood patch or cloacal protuberance during the breeding season. Median distances were greater during the 1988 nonbreeding season (mean = 641 m) than during the 1991 nonbreeding season (mean = 388 m, $t = 2.47$, 10 df, $P = 0.03$), but mean home range size in 1988 (3.70 km^2) did not differ from that in 1991 (2.66 km^2).

Within seasons, we found no difference between sexes for home range size or median distance (Table 1). When seasons were combined, we also found no differences between sexes for either home range size ($t = 0.17$, df = 40, $P = 0.87$) or median distance ($t = 0.68$, df = 19, $P = 0.51$). Mean home range sizes and median distances were similar between second-year Palila (both sexes combined) and adults.

Four females were tracked to active nests during the 1991 breeding season. Most locations of two females tracked during the incubation period were within measurement error of the telemetry system to the nest, although one female traveled 851 m from her nest while incubating (Table

TABLE 2

MEDIAN DISTANCE (M) BETWEEN EACH LOCATION AND THE CENTER OF ACTIVITY FOR FOUR FEMALE PALILA AT ACTIVE NESTS DURING JUNE AND JULY, 1991, PUU LAAU, HAWAII[a]

	Incubation period			Brooding period			Fledgling period		
Bird	N	Median	Range	N	Median	Range	N	Median	Range
31	47	73	13–448				44	177	26–1034
41				30	297	82–1859	63	244	46–2646
42	51	172	64–851	53	220	33–808	22	143	35–722
75				13	191	0–610	107	209	21–2054

[a] The nest location was used as the center of activity for the incubation and brooding periods.

2). Median distances for females brooding chicks were similar to those for males and for females after they abandoned the nest or the chicks fledged.

We found inverse correlations between the elevation of each Palila's center of activity and both home range size ($r = -0.37$, N = 45, $P = 0.01$) and median distance ($r = -0.51$, $P = 0.0004$). In January 1991, we also found a correlation between elevation and the proportion of immature pods on mamane trees ($r = 0.45$, $P = 0.0001$). In February 1988, mamane pod production had no elevational trend. The proportion of pods on mamane trees was higher in 1991 than in 1988 (paired t-test, $t = 19.43$, N = 96, $P = 0.0001$). The ratio of mamane to naio trees >2 m tall was correlated with elevation ($r = 0.81$, N = 36, $P = 0.0001$).

Roosting locations of 12 of 34 Palila were more clustered than daytime locations, but for three Palila, the mean distance between daytime locations was less than that for roosting locations (MRPP test, $P < 0.05$). Most locations near the periphery of a bird's home range were recorded during daytime, but Palila did not return to a particular portion of their home range to roost.

Observers detected 100 Palila during 90 h of searching outside of the study area in 1991, and 70 Palila during 43 h of searching in 1992. Only one banded Palila was sighted ≥2 km from its capture site during these surveys. The banded Palila, an adult male, was located ca 10 km from the site where it was captured. No other evidence of dispersal of Palila from the study area was found during searches of mamane stands around Mauna Kea.

DISCUSSION

Our findings support the hypothesis that strong site tenacity, and therefore limited dispersal and colonization potential, might prevent Palila from repopulating favorable areas in their former range. Although radio-

tagged Palila were as far as 8.7 km from their center of activity, none of the radio-tagged Palila left the 34 km^2 study area, and home range sizes were small relative to the potential mobility of this species. Evidence from banding and nesting studies of Palila also support the site tenacity hypothesis. With one exception, all Palila observed during searches of mamane stands outside of the study area on the southern, eastern, and northern slopes of Mauna Kea were either unbanded or within 2 km of their capture site. Twenty-one of the 47 Palila captured in 1991 had been captured previously on 32 occasions ≤34 months earlier, and all previous capture locations were within 2 km of their 1991 capture location. Of 183 Palila captured more than once at a banding station or nest, only 19 were captured at locations ≥2 km apart. The greatest distance between any two locations was <4 km. Females that were found on nests in more than one year nested within one km of their previous nesting location (T. Pratt, unpubl. data).

Most avian species disperse from natal sites as juveniles or subadults and are philopatric once a breeding site has been chosen, especially after successful reproduction (Greenwood 1980). Juvenile Palila do not appear to disperse farther than adults, and it is more likely that dispersal of both juveniles and adults occurs during periods of food shortage as Palila search for concentrations of mamane pods. For example, we banded 178 Palila as nestlings and recaptured or resighted 64 of them on 2–6 occasions, always ≤2 km from their natal nest. Two of these nestlings, both females, subsequently nested as adults; in each case, they nested ≤300 m from their birth site (T. Pratt, unpubl. data). After the breeding season, juvenile Palila often travel with their parents in small feeding flocks as they follow shifts in the distribution of mamane pod concentrations (van Riper 1980, this study). During the summer of 1992, we noted a major shift in the distribution of Palila to lower elevations and an almost complete lack of breeding in response to drought conditions caused by an el niño event. The low availability of green mamane pods during the 1992 breeding season probably explains the greater number of Palila observed outside the study area (and the banded adult male that was observed ≤10 km from its capture site) during our surveys in November 1992.

The inverse relation between elevation and home range size probably is a result of differences in food supply. In 1991, movements were more extensive at lower elevations where mature mamane pods were fewer. The lower availability of mamane pods in 1988 than in 1991 may explain the greater movements of Palila in 1988. More extensive movements in 1988 may also have resulted from greater triangulation errors because we used weak transmitters and less sensitive receivers that year.

Scott et al. (1984) found that the width of mamane-naio woodland was

the most important variable in determining habitat response by Palila. Because of elevational effects on mamane pod production, the greater elevational range of mamane-naio forest and the greater availability of naio berries on the southwestern slope of Mauna Kea might dampen the effects of seasonal and annual changes in the availability of mamane pods, thereby allowing the area to support a higher population of Palila. The elevational range of mamane forest stands on the northern and eastern slopes of Mauna Kea, where Palila are absent or low in numbers, is mostly <500 m, whereas on the southwestern slope the elevational range of the mamane-naio forest is 1040 m. However, the differences between the elevations of the highest and lowest locations of radio-tagged Palila ranged between 81 and 734 m (mean = 322 m ± 141 SD), suggesting that the elevational range of most mamane stands on the northern and eastern slopes of Mauna Kea might be adequate to support Palila populations.

The prime objective of the Palila Recovery Plan (U.S. Fish and Wildlife Service 1986) is to "maintain/restore a self-sustaining population of Palila distributed continuously throughout their range in healthy, regenerating habitat." Currently, the area near Puu Laau supports the bulk of the Palila population, and Palila are absent or very low in numbers in mamane forests elsewhere on Mauna Kea (van Riper 1978; Scott et al. 1984, 1986; unpubl. data). Based on the low dispersal rate of Palila revealed by this study, recovery of the species is expected to be slow in new areas of suitable habitat when they become available. Translocation of Palila from the Puu Laau area to areas in their former range, such as the northern and eastern slopes of Mauna Kea, the Pohakuloa flats, and perhaps mamane forests on Hualalai and Mauna Loa, may accelerate the recovery of this species.

ACKNOWLEDGMENTS

We thank numerous volunteers from the Student Conversation Association program for their assistance with capture and radio-tracking of Palila. We also thank Donna Ball, Paul Banko, Jennifer Crummer, Calvin Harada, Jeff Kelly, Gerald Lindsey, Jim Manolis, Sandra Pletschet, Thane Pratt, Tanya Rubenstein, and Kelly Stapp for field assistance. Paul Banko, Gerald Lindsey, and Thane Pratt allowed us to use unpublished data from their ongoing studies and suggested improvements to the manuscript. Dan Stoneburner, Paul Sykes, and Fred Anderka assisted with transmitter design and attachment. Jeff Kelly supervised field personnel in 1988 and helped with studies of surrogate species. We thank Mark Fuller, Helen James, Cameron Kepler, and an anonymous reviewer for critical reviews of and improvements to the manuscript.

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