ANNUAL VARIATION IN THE DISTRIBUTION, ABUNDANCE, AND HABITAT RESPONSE OF THE PALILA (*LOXIOIDES BAILLEUI*)

J. Michael Scott,[1] Stephen Mountainspring,[1]
Charles van Riper, III,[2] Cameron B. Kepler,[3] James D. Jacobi,[1]
Timothy A. Burr,[4] and Jon G. Giffin[5]

[1]U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Mauna Loa Field Station,
Hawaii National Park, Hawaii 96718 USA;
[2]Cooperative National Park Resources Study Unit, Department of Zoology and Ecology,
University of California, Davis, California 95616 USA;
[3]U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, 248 Kaweo Place,
Kula, Hawaii 96790 USA;
[4]Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife,
Honolulu, Hawaii 96813 USA; and
[5]Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife,
Kamuela, Hawaii 96743 USA

ABSTRACT.—We studied the distribution, population size, and habitat response of the Palila (*Loxioides bailleui*) during the 1980–1984 nonbreeding seasons to infer factors that limit the population and to develop management strategies. Distribution was fairly constant from year to year. Palila were confined to the subalpine woodland on Mauna Kea on the island of Hawaii, occurred between 2,000 and 2,850 m elevation, and reached highest densities on the southwest slopes. The population showed large annual fluctuations, from 6,400 birds in 1981 to 2,000 in 1984. The width of woodland was the most important variable in determining habitat response. Palila were more common in areas with greater crown cover, taller trees, and a higher proportion of native plants in the understory. Annual variation in Palila density within a habitat reflected variation in levels of their staple food, mamane pods. The main limiting factors of the population appeared to be the availability of good habitat and levels of their staple food. Palila had strongly depressed densities in the Pohakuloa flats area. This low density could not be explained by gross habitat features or food levels. Site tenacity, thermal stress, disturbance, and disease were hypothesized explanations. Our study indicated that the most effective management strategies would be the removal of feral ungulates and certain noxious plants from Palila habitat and the extension of the woodland zone to areas now intensively grazed. *Received 20 May 1983, accepted 9 March 1984.*

DISTRIBUTION, population size, and habitat response of species that may require management to ensure their survival are ecological parameters of special interest. Annual variation in these parameters may offer insight into the factors that limit the present population, yet relatively few workers have attempted to evaluate temporal variation in habitat response. Studies by Raitt and Pimm (1976), Rotenberry and Wiens (1980a, b), and Rice et al. (1981)

demonstrate the potential value of temporal analyses of habitat response in evaluations of factors that limit bird numbers.

In this study we examine annual variations in distribution, population size, and habitat response across the entire range of the Palila (*Loxioides bailleui*), a finch-billed Hawaiian honeycreeper found only in the subalpine woodlands of Mauna Kea on the island of Hawaii (Fig. 1) and one of 30 endangered or threat-
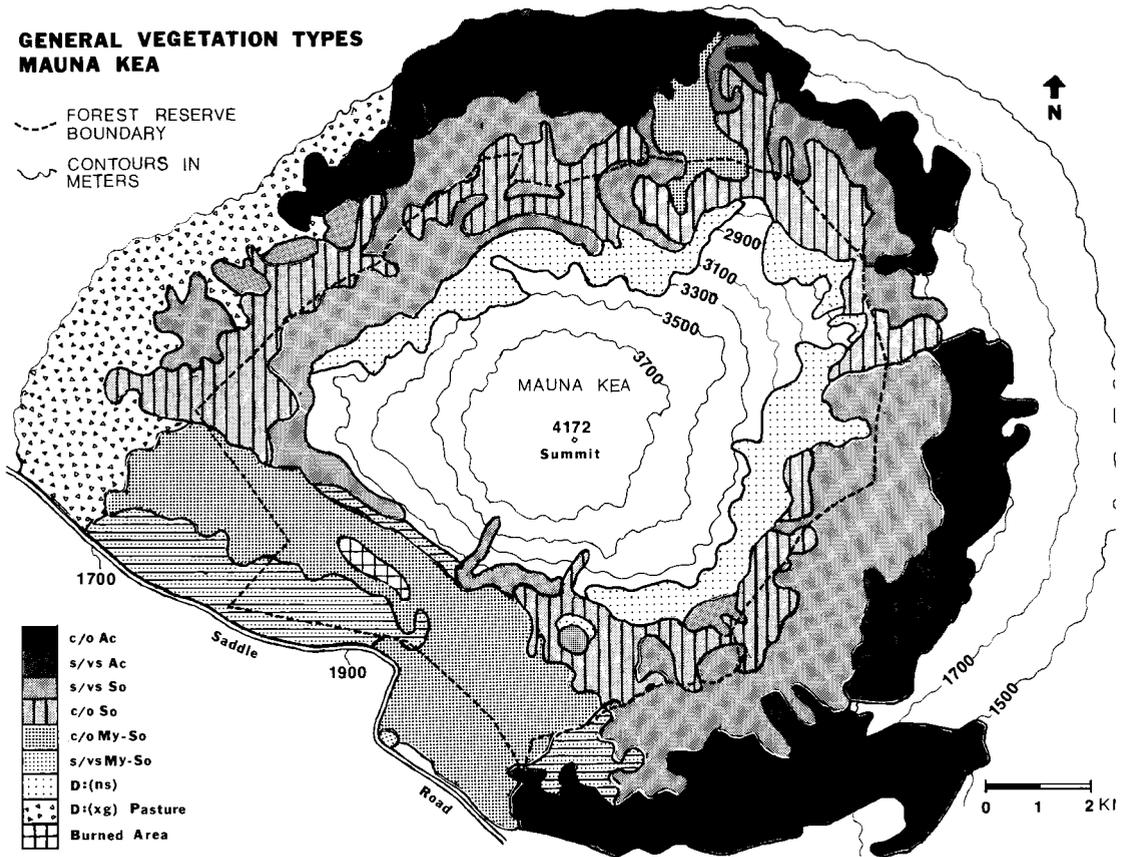
**GENERAL VEGETATION TYPES
MAUNA KEA**

Fig. 1. The dry native forest on Mauna Kea, Hawaii. General vegetation types: c/o Ac = closed to open canopy koa (*Acacia koa*); s/vs Ac = scattered to very scattered koa; s/vs So = scattered to very scattered mamane forest; c/o So = closed to open canopy mamane; c/o My-So = closed to open canopy mamane-naio; s/vs My-So = scattered to very scattered mamane-naio; D:(ns) = dry native shrub; D:(xg) = dry exotic grass pasture; Burned Area = site of 1979 fire.

ened birds in Hawaii (U.S. Fish and Wildlife Service 1983). The population size of the Palila was estimated at 1,600 birds in the 1975 nonbreeding season (van Riper et al. 1978).

The behavior and ecology of the Palila were intensively studied by Berger (1970) and van Riper (1978, 1980a). Palila are adapted for feeding on green seed pods of the mamane tree (*Sophora chrysophylla*), although mamane flowers, naio (*Myoporum sandwicense*) fruit, and insects are also eaten, particularly when pods are scarce. The breeding season extends from April to September and coincides with maximum production of mamane pods. During the nonbreeding season, local and some long-distance movement occurs in response to food levels. We studied the species toward the end of the

nonbreeding season, when population levels were lowest in the annual cycle, food was most likely to be limiting, and bird distribution was most likely to reflect local variation in food levels.

The objectives of this study were to (1) examine annual variation in distribution, population size, and habitat response during the nonbreeding season across the range of the Palila; (2) evaluate some of the factors that may limit present distribution and numbers; and (3) development management strategies to ensure the survival of the species.

STUDY SITES AND METHODS

Study sites.—The entire range of the Palila lies within the subalpine mamane and mamane-naio
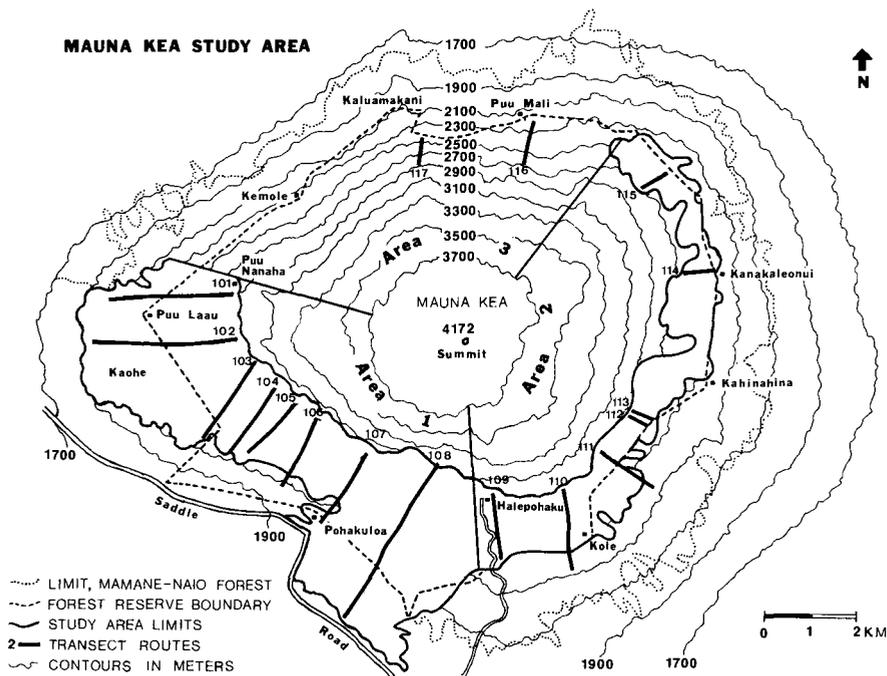
Fig. 2.   Location of study area and transects on Mauna Kea, Hawaii.

woodland on Mauna Kea (Fig. 1). Our sampling universe was the present range of Palila, a 139 km² area (Fig. 2). We also sampled the north slopes of Mauna Kea, where Palila no longer occur (transects 116 and 117 in area 3), in order to document repopulation of the area. Data from this area were not included in our analysis.

The woodland on Mauna Kea ranges from 1,800 to 3,000 m elevation. The trees are generally short (3–10 m), and canopy cover varies from very scattered (<5%) to partly closed (60%). Rainfall averages 35–75 cm annually.

Mamane occurs around the entire mountain, but naio is mainly restricted to the southwest slopes. A detailed description of the vegetation is given in Hartt and Neal (1940).

Sampling design.—Information from the 1975 survey (van Riper et al. 1978) was used to stratify the subalpine woodland according to Palila density into three areas: a high-density area (area 1), a low-density area (area 2), and a supplemental area (area 3), where Palila once occurred historically (Fig. 2).

Transects were randomly placed a minimum of 500 m apart and approximately perpendicular to elevational contours in areas 1 and 2. Stations were placed 150 m apart from approximately 75 m below treeline to the lower woodland boundary. In area 3 we placed 24 stations along two transects randomly located in the best remaining woodland only to verify the bird's

absence and to detect recolonization. The stations were the sample points for monitoring plant phenology, counting birds, and verifying the vegetation map.

Annual surveys were conducted in the nonbreeding season during 7–21 February 1980, 20–29 January 1981, 22 February–4 March 1982, 25 February–4 March 1983, and 6–9 February 1984. We used the variable circular-plot method with a 6-min sampling period (Reynolds et al. 1980). This period was determined to be long enough to hear or see Palila near the station, yet short enough to minimize the chances of counting the same bird twice or of birds moving into the count area (Scott and Ramsey 1981). During this period, observers recorded each Palila heard or seen except for birds flying high overhead (Reynolds et al. 1980). The counts were conducted from approximately 0730 to 1300, the period of greatest Palila activity (van Riper 1978). Observers were assigned to transects by random draw within a sampling area, and no counts were conducted when precipitation or winds greater than 4 on the Beaufort Scale (>29 km/ h) occurred. Transects 102 and 103, the area of highest density, were each sampled twice and a mean density was computed for those stations.

The 20 observers that participated in the survey were trained in identifying Palila and estimating detection distances (Kepler and Scott 1981). All but two observers met hearing standards suggested by Emlen

and DeJong (1981), and one of these did not partici-
pate after 1980.

Density estimates.—Using the methods of Ramsey
and Scott (1981), we calculated density estimates for
Palila. Using values pooled over 4 yr, we derived
correction factors for each observer and vegetation
type as sample sizes allowed. The effective area sur-
veyed at a station varied from 0.69 to 1.48 ha.

Populations were estimated for each area from the
Palila densities at the individual stations. To estimate
the total population in the Palila universe, we
weighted the populations and variances in areas 1
and 2 by the size of the area and pooled the results.

Densities were plotted by means of 5-point mov-
ing averages. Interpolation of densities was done
subjectively, with consideration given to vegetation
types and elevation. We assumed that density varied
in a continuous manner from one point to another.

Habitat description.—Vegetation structure and com-
position were recorded at each station by observers
who had been intensively trained in estimating
vegetation variables. The observers estimated the av-
erage crown or foliage coverage of trees, shrubs,
herbs, and grasses and the coverage fraction and av-
erage height of mamane and naio trees in the canopy
within a 50-m-diameter circle centered on station.
The percentage of branches that had yellow mamane
flowers, fully expanded green mamane pods with lit-
tle or no brown on them, or white naio fruits was
estimated in order to index densities of items in the
Palila diet (van Riper 1978).

Station locations were plotted on high-resolution
aerial photographs and U.S. Geological Survey 7.5'
topographic maps. Tree coverages estimated in the
field were compared with photointerpretative esti-
mates. This procedure ensured standardization of ob-
servers and gave more accurate estimates for very
patchy woodlands.

Vegetation maps of the study area were prepared
at a 1:24,000 scale. Vegetation types were initially
interpreted on aerial photographs at a 1:45,000 scale
with a mirror stereoscope of 3× and 6× magnifica-
tion. These preliminary map units were verified on
the ground, and a helicopter was used to resolve in-
terpretation problems in some areas. The final map-
unit boundaries were compiled by means of a Kern
PG-2 plotter.

Habitat response.—We derived 14 independent vari-
ables from the habitat data and graphically examined
univariate distributions and Palila response to each
variable to determine necessary standardizations and
transformations. The independent variables in the
analysis were:

Elevation (m)—from the USGS 1:24,000 topographic
    map;
Elevation squared—to represent potential ditonic re-
    sponse;
Crown (%);

Canopy height (m);
Mamane biomass—mamane cover (%) times mamane
    height (m);
Naio biomass—naio cover (%) times naio height (m);
Total tree biomass—the sum of mamane and naio
    biomass;
Shrub cover (%);
Grass cover (%)—cover of grasses and herbs;
Mamane flower biomas—the average precentage of
    mamane branches in flower on the 10 trees sam-
    pled at station multiplied by mamane biomass;
Mamame fruit biomass—same as for mamane flower;
Naio fruit biomass—same as for mamane flower;
Pohakuloa flats—a binary variable to indicate the Po-
    hakuloa flats area and the immediately adjacent
    slopes (bottom of transects 106, 107, and 108), 0 =
    absent, 1 = present;
Woodland width (km)—the width of mamane and
    mamane-naio woodland, measured perpendicular
    to the contour along the transect line, but exclud-
    ing as unsuitable habitat areas of scattered to very
    scattered trees and the areas in Pohakuloa flats.

Data analysis.—A logarithmic transformation, $x' =
\log_{10}(x + 1)$, was applied to stabilize the variance and
correct for excessively straggling tails in Palila den-
sity and in the biomass of mamane flower, mamane
fruit, and naio fruit.

To quantify the habitat response of the Palila and
the annual variation in that response, we computed
the Pearson correlation coefficient, r, between Palila
density and the 14 habitat variables for each year.
The five correlations of a single Palila/habitat vari-
able pair were tested for homogeneity by means of
the χ^2 summation of Z-transformed correlations (Steel
and Torrie 1980: 280). Correlations were calculated
between Palila densities in different years to quan-
tify the tendency for birds to occur on the same sites.

Multiple regression was performed on the data of
each year to identify the strongest variables affecting
Palila response, given the relations among other
variables (Draper and Smith 1981). Crown cover, can-
opy height, and total tree biomass were excluded be-
cause of their high correlation with mamane and naio
biomass. We used a structured stepwise procedure
that worked down through a series of hierarchical
levels, adding significant ($P < 0.05$) variables to the
regression equation and deleting variables that be-
came insignificant. Variables were organized into hi-
erarchical levels to reflect increasingly detailed hab-
itat features (see Scott et al. in press). Variables were
considered for inclusion in this order: (1) elevation,
(2) [elevation]², (3) mamane and naio biomass, (4)
shrub and grass cover, (5) flower and fruit variables,
and (6) Pohakuloa flats and woodland width. The last
two variables are nonlocal and extensive; we placed
them last to avoid confounding them with localized
responses.

To compare years further, we grouped stations by
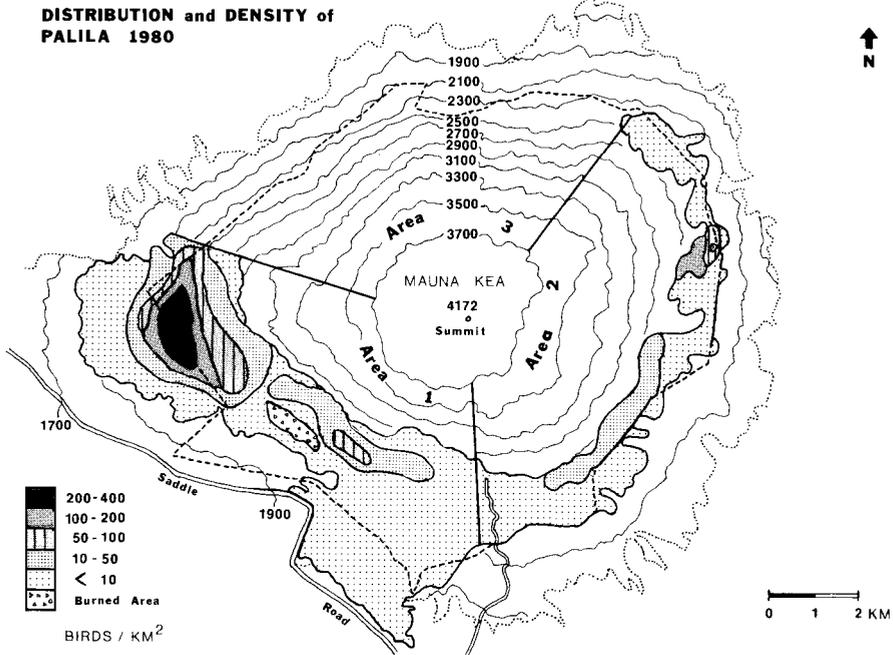
**DISTRIBUTION and DENSITY of
PALILA 1980**

Fig. 3. Distribution and abundance of Palila in 1980.

the vegetation units used in mapping. The Palila densities at the stations in each group were compared by means of Fisher's protected least significant difference (lsd) test for multiple comparisons (Steel and Torrie 1980: 173). This is a two-part test: first, we computed one-way analyses of variance to test whether or not there was significant variation between years; when this test was significant, we constructed the lsd test from s, the square root of the pooled error variance, as $lsd = 1.98s\sqrt{2/n}$, where n is the number of stations sampled each year. Means differing by more than the lsd were significant at the 5% level.

The counts taken on consecutive days on transects 102 and 103 were compared to assess daily variation due to Palila movement. To determine whether daily variation was more prominent between or within vegetation units, an analysis of variance was performed on stations grouped by vegetation units.

The adequacy of the sample size for a quantification of habitat response was checked by computing correlations and regression equations from randomly constructed subsamples of 25% and 50% of the full data set. Results from the 50% subsamples were substantially identical to those from the full data set. Deviations among the 25% subsamples suggested that 100–150 stations were needed to allow us to make statements about habitat response in the sampling universe.

Because summary statistics characterize general

patterns, variation at finer scales is glossed over, and nonlinear interactions may be overlooked entirely (James and Wamer 1982). To display some of the multidimensional variation in response, we constructed contour graphs of Palila response to independent variables by plotting each station, smoothing over cells of 2–5% of the total graph area, and drawing contours by eye. The independent variables used for axes were chosen for their predictive power and management interest.

RESULTS

Distribution.—Distributional patterns of the Palila were rather constant during our 5-yr study (Figs. 3–7) and quite similar to those found in 1975 (van Riper et al. 1978).

The highest densities (>200 birds/km²) were always centered around the 2,300 m elevational contour near Puu Laau on transect 102 in area 1. This area lies immediately above an ecotone between the mamane and mamane-naio woodlands. A second much smaller high-density cell was found 5 km southeast on transect 107; it was especially prominent in 1981. Areas with a density of more than 200 birds/km² never exceeded 7% of the Palila's range, and areas with fewer than 10 birds/km² accounted for
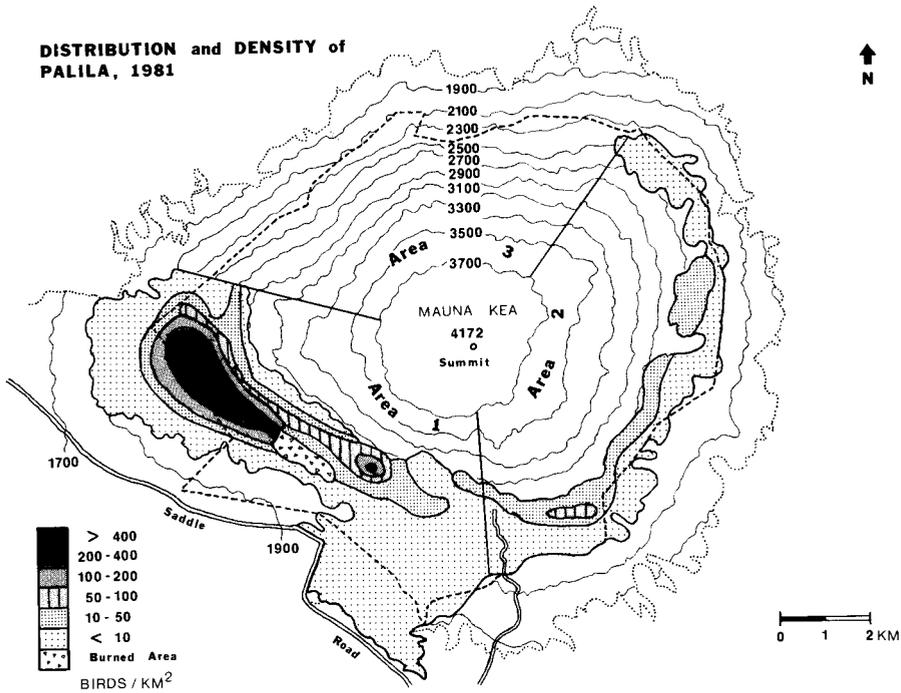
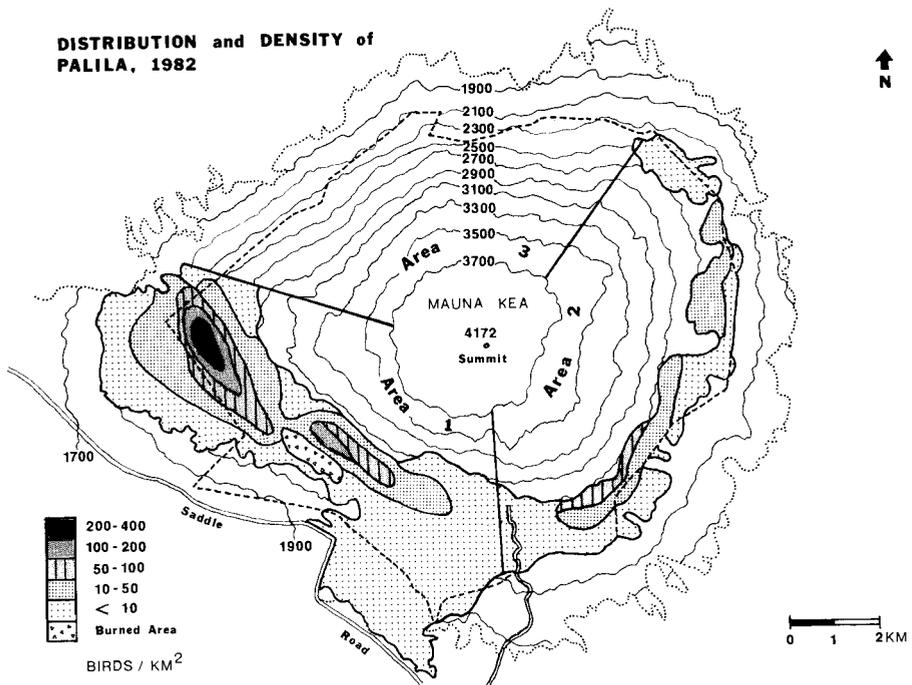Fig. 4. Distribution and abundance of Palila in 1981.

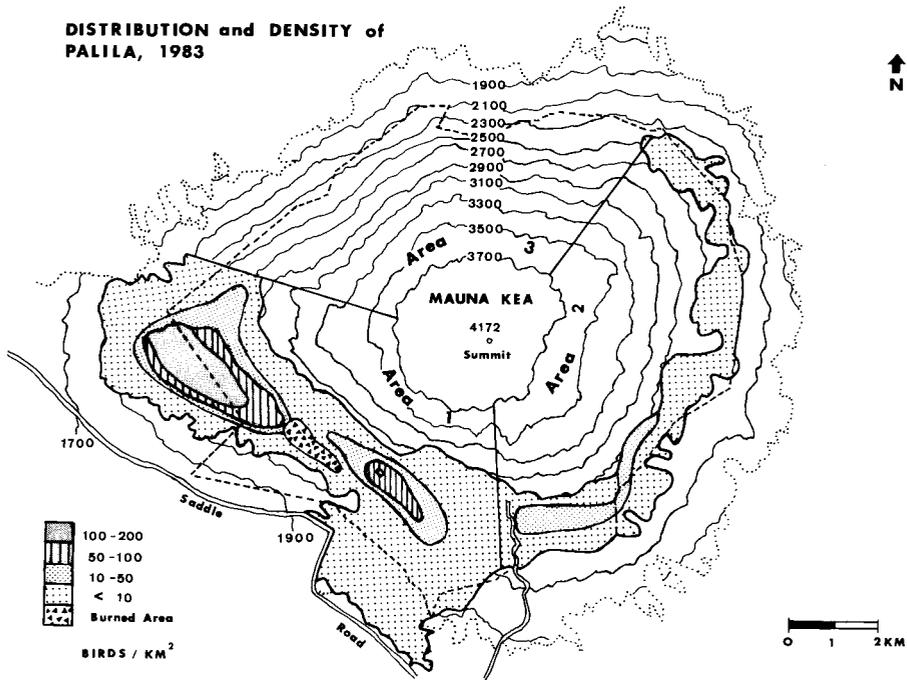Fig. 5. Distribution and abundance of Palila in 1982.

DISTRIBUTION and DENSITY of
PALILA, 1983

Fig. 6. Distribution and abundance of Palila in 1983.

more than 65% of the range every year (Figs. 3–7). In 1983, a small shift in the Puu Laau density cell corresponded to higher resource levels in mamane-naio woodland, as compared with those in pure mamane woodland.

The upper elevational limit of Palila generally coincided with treeline at about 2,850 m in both areas 1 and 2. In area 1 the lower elevational limit of the Palila was approximately 2,000 m and generally marked a transition to scrub forest or grassland. In area 2 the lower limit was approximately 2,500 m at the boundary of the Mauna Kea Forest Reserve and was characterized by scattered to very scattered trees in heavily grazed pastures. These range limits are much higher than those found in the 1890's (Perkins 1903).

Population size.—The estimated Palila population varied from 6,400 birds in 1981 to 2,000 in 1984 (Table 1). The differences in population size were significant ($P < 0.05$) between 1981 and the other years, but not among 1980, 1982, 1983, and 1984. In 1975, the Palila population was estimated at 1,614 (95% CI = 1,057–2,171) during the nonbreeding season (van Riper et al. 1978). This value is significantly below the 1980, 1981, and 1982 estimates. In the 1975–1981 period, therefore, Palila populations appear to have increased nearly fourfold, but by 1984 the population lost 68% of its 1981 numbers.

From 1980 to 1981 the population apparently increased 91%, only to return in 1982 to the 1980 level. This points to a high potential for large annual fluctuations in numbers, perhaps resulting from optimal weather and high food stocks during the May–September 1980 breeding season, followed by high mortality (of young birds?) due to poor weather or depleted food stocks later during 1981.

Rainfall records from Puu Laau indicate that 1980 had the greatest rainfall of all years from 1973 to 1983, whereas 1981 and 1983 had the least rainfall of that period (R. Bachman unpubl. data). Van Riper (1980b) found that mamane fruiting responded strongly to precipitation; thus, there may have been a large mamane pod crop in 1980 that supported the boom observed in 1981, followed by a crop failure in 1981 that led to the population "bust" in the 1982 survey. The low population in 1984 also seems to reflect adverse weather. Our data
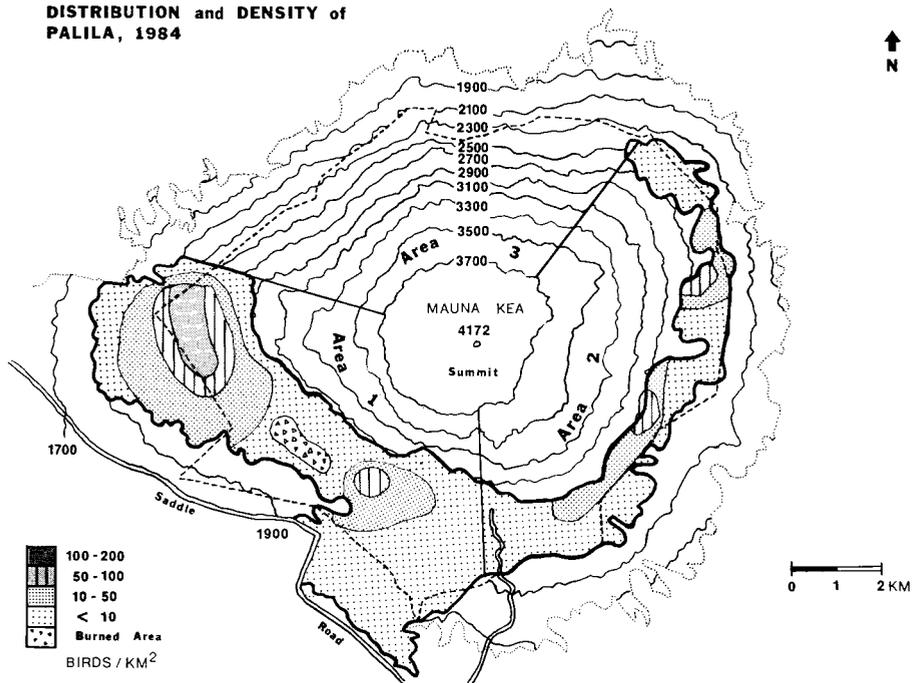
DISTRIBUTION and DENSITY of PALILA, 1984

Fig. 7. Distribution and abundance of Palila in 1984.

are inadequate to determine the causes of annual population fluctuations, because we recorded resource levels for only a short interval of time and not the whole year. Apparent doubling or halving of insular passerine populations from one year to the next is not unusual. J. L. Sincock (unpubl. data) has documented wide fluctuations in the numbers of Laysan Finches (*Telespyza cantans*) and Nihoa Millerbirds (*Acrocephalus familiaris kingi*) on the leeward islands of Hawaii.

In area 1, populations differed significantly between 1981 and the other years. The ratio of the highest (1981) to the lowest (1984) population was 3.4. Densities in area 1 averaged 2.4 times as high as in area 2, and, owing to the greater size of area 1, from 79% to 90% of the total Palila population occurred there.

In area 2, populations did not differ significantly between years. This was partly due to the more scattered occurrence of Palila and lower sampling intensity, resulting in higher coefficients of variation, but the ratio of highest (1980) to lowest (1984) population, 2.2, is lower than in area 1 and suggests a more stable population.

Annual and daily correlation in occurrence.—The correlations between years for Palila densities at the same station (Table 2) varied from $r = 0.16$ to 0.51 and were all significant. This indicates that Palila tended to occur at the same sites that they have in the past, although substantial variation also occurred.

Two transects in the areas of greatest Palila density were replicated on consecutive days to quantify the extent of daily movement of the population. The correlations for consecutive day counts were low, with a mean r of 0.36 (0.08 SE) and a range of -0.17 to 0.81 for the 10 correlations. When the sample points were stratified by vegetation unit, correlations improved to a mean r of 0.74 (0.08 SE), with a range of 0.24 to 0.99. All 10 correlations computed from vegetation units were higher than those computed from stations, suggesting either that Palila movement between vegetation units was less than movement between stations or that daily Palila movement tended to result in the same relative numbers in each vegetation unit.

Habitat correlates and habitat response models.— The correlations between Palila density and

TABLE 1. Summary of population estimates for the Palila.

	Area 1	Area 2	Palila universe
Area (km²)	97	42	139
Number of stations	237	88	325
Population estimate			
1980	2,650	701	3,350
1981	5,795	615	6,410
1982	2,612	693	3,305
1983	1,882	386	2,268
1984	1,701	321	2,022
Population, 95% CI			
1980	1,635–3,665	207–1,195	2,240–4,480
1981	4,120–7,470	221–1,009	4,690–8,131
1982	1,703–3,521	321–1,065	2,323–4,287
1983	1,283–2,480	58–714	1,584–2,951
1984	1,121–2,281	115–527	1,407–2,637
Number Palila counted			
1980	136	17	153
1981	229	14	243
1982	131	18	149
1983	117	10	127
1984	87	9	96
Frequency (%)			
1980	19%	10%	17%
1981	27%	12%	23%
1982	22%	16%	20%
1983	19%	7%	16%
1984	16%	10%	15%

habitat variables provide an overview of Palila habitat response and its annual variation (Table 3). Every year, the width of subalpine woodland had the strongest correlation with Palila density. Palila also consistently responded strongly to total tree biomass, crown cover, and canopy height. Significant annual variation occurred in the correlations with mamane biomass, naio biomass, and naio fruit. These differences seemed mainly due to phenological variation and resource shifting, as discussed below. A negative response to the Pohakuloa flats area occurred each year, and only two Palila were found on the 42 stations in the flats over the 5-yr period.

A multivariate perspective on response to habitat was given by the regression equations (Table 4). From 17% to 36% of the variance was accounted for, these somewhat low values reflecting the patchy distribution of Palila over even short distances. The most important variable in every case was the width of mamane-naio woodland. Pohakuloa flats had a negative term in four of the models. Ground cover, usu-ally exotic grasses and herbs indicative of a long history of heavy disturbance, was negatively associated with Palila in three models, but in the 1983 model shrub cover was entered instead. Shrub cover was indicative of lighter disturbance and was negatively correlated with ground cover ($r = -0.58$, $P < 10^{-40}$). These models may therefore be interpreted as representing avoidance of heavily disturbed vegetation. Multiple regression was thus helpful in identifying important variables that would be overlooked in a bivariate analysis. The correlations of Palila with shrub and ground cover were modest until zone width, phenology, and

TABLE 2. Correlations of Palila density between years at the same stations. All correlations are significant, $P < 0.01$.

	1980	1981	1982	1983
1981	0.36			
1982	0.51	0.37		
1983	0.23	0.51	0.27	
1984	0.42	0.27	0.35	0.16

TABLE 3. Correlations between Palila density and habitat variables. An asterisk after the variable name indicates significant variation between years, $P < 0.01$. Significance values for the correlations are $|r| = 0.11$, $P = 0.05$; $|r| = 0.18$, $P = 0.001$.

Variable	1980	1981	1982	1983	1984
Elevation	−0.01	0.04	0.02	−0.10	−0.08
Total tree biomass	0.24	0.27	0.13	0.25	0.23
Crown cover	0.16	0.20	0.11	0.27	0.11
Canopy height	0.20	0.20	0.09	0.12	0.22
Mamane biomass*	0.27	0.09	0.11	0.03	0.31
Naio biomass*	0.07	0.30	0.08	0.34	0.00
Shrub cover	−0.17	−0.03	−0.11	−0.07	−0.26
Grass cover	−0.07	−0.20	−0.04	−0.03	0.08
Mamane flower	0.20	0.08	0.21	0.03	0.03
Mamane fruit	0.24	0.26	0.07	0.21	0.14
Naio fruit*	−0.05	−0.03	0.06	0.28	−0.03
Pohakuloa effect	−0.17	−0.16	−0.17	−0.16	−0.12
Woodland width	0.37	0.36	0.33	0.37	0.35

other factors were taken into consideration, when it became apparent that Palila discriminated against heavily disturbed areas. Naio habitat components varied widely among the years and are discussed below. In the 1981 model, the two naio variables were entered with opposite signs, indicating that Palila were using areas of mamane-naio woodland that had relatively low naio fruiting intensity.

Variation in density among habitat types.—Palila densities showed striking variation among habitat types (Table 5). The variation among habitat types and across years generally paralleled the patterns in the previous analysis.

The habitats fell into two general series: pure mamane woodland units and mixed mamane-naio woodland units. In each series, units ranged from taller, more forested to shorter, more open habitat. Additional contrasts were made between native and exotic understories and between points lying within and outside Pohakuloa flats.

Palila densities were highest in tall, more forested habitat in both the mamane and mamane-naio series, the maximum density of 206 birds/km² occurring in 1981 in tall, partly closed, mamane-naio woodland with a native understory (Table 5). Tall, partly closed, mamane-naio woodland had significantly higher Palila density (based on the 5-yr pooled values) than did otherwise identical open woodland ($t = 4.2$, $P < 10^{-4}$).

TABLE 4. Habitat response models constructed by stepwise multiple regression. All equations are highly significant ($P \ll 0.001$). Entries for variables are t-statistics. All variables entered are significant at $P < 0.05$; * indicates $P < 0.001$.

Variable	1980	1981	1982	1983	1984
R² (variance accounted for)	0.236	0.361	0.171	0.300	0.178
Elevation	—	—	—	—	—
(Elevation)²	—	—	—	—	—
Mamane biomass	4.3*	—	—	—	4.6*
Naio biomass	—	8.1*	—	3.0	—
Shrub cover	—	—	—	2.4	—
Grass cover	−3.4*	−4.8*	−2.7	—	—
Mamane flower	—	—	2.9	—	—
Mamane fruit	2.1	—	—	—	—
Naio fruit	—	−5.0*	—	2.7	—
Pohakuloa flats	−2.0	−2.4	−3.2	−6.2*	—
Woodland width	5.7*	8.3*	5.7*	6.5*	5.6*

TABLE 5.   Annual variation in Palila density by habitat type. Height: tall 5–10 m, short 2–5 m. Crown cover: partly closed 50–60%, open 20–40%, scattered 5–20%, very scattered 0–5%. u/s = understory. Superscripts distinguish significantly different years according to the protected lsd test.

Habitat type (height, cover, understory)		Stations sampled	Palila densities (birds/km²)					
			1980	1981	1982	1983	1984	Pooled
Pure mamane woodland								
Tall, open, native u/s	$\bar{x}$	36	87[b]	69[b]	72[b]	13[a]	41[a,b]	57
	SE		26	21	22	5	10	8
Tall, open, exotic u/s	$\bar{x}$	21	36	14	21	0	53	25
	SE		14	8	15	0	19	6
Short, open, native u/s	$\bar{x}$	53	8	16	14	16	0	11
	SE		5	7	5	6	0	2
Short, scattered, mixed u/s	$\bar{x}$	35	13	21	25	1	14	15
	SE		6	7	8	1	7	3
Short, very scattered, mixed u/s	$\bar{x}$	14	0	0	0	0	0	0
	SE		0	0	0	0	0	0
Mixed mamane-naio woodland								
Tall, partly closed, native u/s	$\bar{x}$	35	50[a]	206[b]	37[a]	73[a]	23[a]	78
	SE		15	38	9	15	7	9
Tall, open, native u/s (outside Pohakuloa flats)	$\bar{x}$	42	23[a]	79[b]	34[a]	18[a]	13[a]	34
	SE		7	20	13	6	6	5
Tall, open, native u/s (in Pohakuloa flats)	$\bar{x}$	32	0	2	0	0	2	1
	SE		0	2	0	0	2	1
Tall, open, exotic u/s	$\bar{x}$	22	5	4	16	26	12	12
	SE		4	4	6	10	6	3
Short, open, native u/s	$\bar{x}$	13	12	0	0	6	6	5
	SE		12	0	0	6	6	3
Short, scattered, mixed u/s	$\bar{x}$	22	0	4	5	0	0	2
	SE		0	4	4	0	0	1

Tall open woodlands with native understories had significantly higher Palila densities than did those with exotic understories ($t = 3.2$, $P < 0.01$ for mamane and $t = 3.5$, $P < 0.001$ for mamane-naio). This probably reflected greater food resources in native understory from mamane and naio trees less than 2 m tall and from *Osteomeles*. Exotic understories, which were comprised almost entirely of grasses and certain rank herbs, may also provide less shelter.

A glaring exception to the strong response of Palila to tall, open woodland with native understory occurred within Pohakuloa flats, where densities were significantly ($t = 6.2$, $P < 10^{-8}$) below densities in virtually identical habitat with comparable phenology at about the same elevation.

Next, we compared tall and short open woodlands with native understories. In both habitat series tall woodlands had significantly higher densities: about 5.3 times as high in

mamane ($t = 5.4$, $P < 10^{-7}$), 7.2 times in mamane-naio ($t = 4.8$, $P < 10^{-6}$). Short scattered woodlands with native or exotic understories generate about the same level of Palila response as short open woodlands ($P > 0.30$). Short very scattered mamane "woodlands" had no Palila, significantly fewer than short scattered mamane woodlands ($t = 5.4$, $P < 10^{-7}$).

Although highest Palila densities occurred in partly closed, mamane-naio woodland, pure mamane woodland supported higher densities than structurally similar mamane-naio woodland. In tall open woodland with native understory, Palila densities were 1.7 times higher in mamane than in mamane-naio ($t = 2.3$, $P < 0.05$); in tall open woodland with exotic understory, 2.0 times higher ($t = 1.9$, $P < 0.07$); in short open woodland, 2.3 times higher ($t = 1.6$, $P < 0.12$); and in short scattered woodland, 7.8 times higher ($t = 4.4$, $P < 10^{-5}$). Overall, Palila densities were higher in mamane than in struc-

SCOTT ET AL.

TABLE 6. Annual variation in flowering and fruiting intensity in habitats with significant annual variation in Palila density. Superscripts distinguish significantly different years according to the protected lsd test.

Habitat type (height, cover, understory)	Phenology intensity (% branches in flower/fruit)				
	1980	1981	1982	1983	1984
Pure mamane woodland					
Tall, open, native understory					
Mamane flowers	13[b]	5[a]	23[c]	3[a]	11[b]
Mamane fruit	4[a]	12[b]	28[c]	2[a]	30[c]
Mixed mamane-naio woodland					
Tall, partly closed, native understory					
Mamane flowers	27[c]	20[b,c]	55[d]	15[a,b]	8[a]
Mamane fruit	9[a,b]	13[b]	4[a]	14[b]	8[a,b]
Naio fruit	7[a,b]	15[b,c]	9[a,b]	19[c]	3[a]
Tall, open, native understory (outside Pohakuloa flats)					
Mamane flowers	15[a]	9[a]	35[b]	9[a]	9[a]
Mamane fruit	2[a]	25[b]	5[a]	5[a]	3[a]
Naio fruit	10[b]	10[b]	5[a,b]	18[c]	2[a]

turally similar mamane-naio ($\chi^2 = 38.6$, df = 8, $P < 10^{-5}$).

In general, Palila thus preferred (1) greater crown cover, (2) greater canopy height, (3) native instead of exotic understory, (4) locations outside Pohakuloa flats, and (5) pure mamane woodland over structurally comparable mixed mamane-naio woodland.

Annual variation in habitat response.—Annual variation in Palila densities was significantly greater than would be expected if the variation were random in three habitat types: tall open mamane woodland with native understory ($F = 2.6$, $P = 0.05$); tall, partly closed mamane-naio with native understory ($F = 13.4$, $P < 10^{-40}$); and tall, open mamane-naio with native understory ($F = 5.1$, $P < 0.001$). This annual variation may be plausibly attributed to variation in food-resource levels, particularly mamane pods, the staple of the Palila diet.

In tall open mamane with native understory, Palila densities in 1983 were significantly lower than in 1980–1982 (Table 5), and both mamane pods and mamane flowers were at their lowest level in 1983 (Table 6). Hence, in 1983 Palila may have experienced severe food shortage in this habitat and emigrated, whereas in the low pod year of 1980, pods were twice as abundant as in 1983, and mamane flowers were also more abundant and may have been an alternative food.

Extremely high Palila densities in 1981 in tall,

partly closed mamane-naio with native understory coincided with high mamane flower, mamane pod, and naio fruit levels. Phenology values were also high in 1983. At first glance, the 1983 density value (73 birds/km²) does not seem to corroborate the pattern of high density/high phenology, but the Palila population was very low that year, and 73 birds/km² was by far the highest Palila density in the 11 habitat types in 1983. Compared with the mean density, densities in tall partly closed mamane-naio were 2.1 times the annual mean in 1980, 4.5 in 1981, 1.6 in 1982, 4.5 in 1983, and 1.6 in 1984, suggesting similar high responses in 1981 and 1983.

Finally, in tall open mamane-naio with native understory, both Palila densities and mamane pods were at significantly higher levels in 1981 than in other years. In the 1981 habitat-response model (Table 4), the combination of positive naio biomass and negative naio fruit terms may indicate that Palila were keying in on the mamane pods in this habitat and ignoring naio fruit in other areas. Mamane flowers were significantly more abundant in 1982 than in other years, and this may have led to slightly higher Palila densities in 1982 than in 1980, 1983, or 1984 for that habitat.

Contour graphs.—To give an impression of annual variation in habitat response, we constructed contour graphs (Fig. 8) of Palila density as a function of two important variables—woodland width and total tree biomass. The
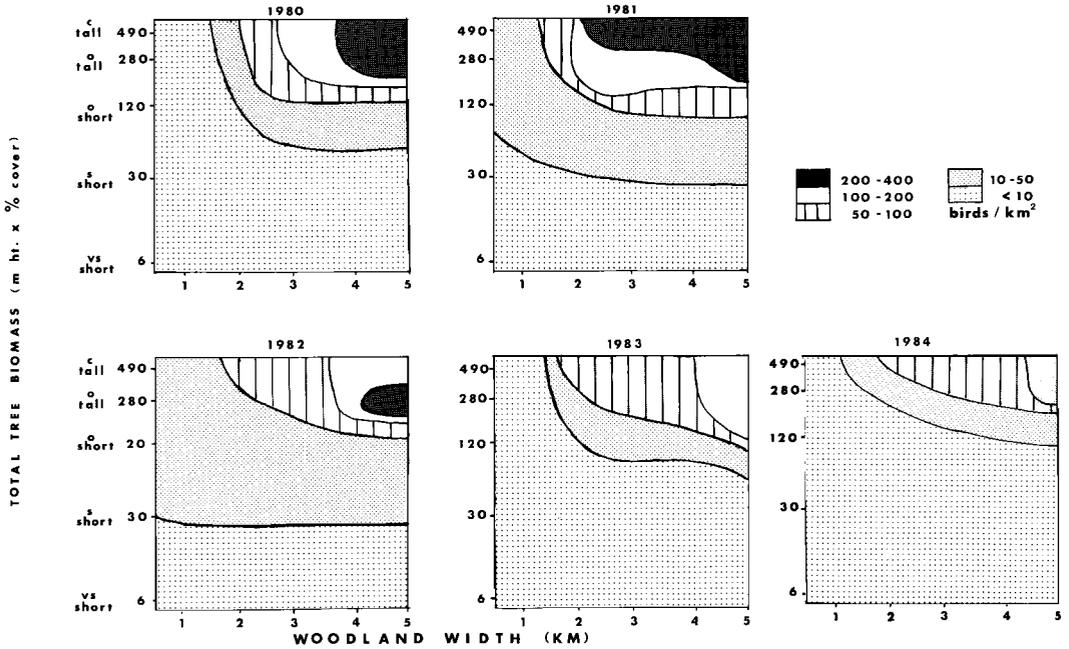
Fig. 8. Habitat response of Palila with respect to woodland width and total tree biomass.

latter variable was logarithmically scaled to index general forest development.

The graphic responses more or less paralleled the correlations of Palila with these two variables (Table 3). The dependence of Palila on wider woodlands and structurally more complex habitat appeared in each graph, but annual variation was also apparent. Palila were especially associated with wide woodlands in 1980, 1982, 1983, and 1984, the years of reduced abundance, but in 1981 the Palila ranged frequently into narrower woodlands. Similarly for total tree biomass, the broadest range of occurrence was in 1981.

The graphs also indicate that Palila apparently tolerated very narrow woodlands more readily than very sparse habitat. This may represent the occasional use of small, somewhat isolated patches of suitable habitat and the general avoidance of scattered trees (no matter how much good habitat is nearby) and, hence, illustrates a degree of active habitat selection.

These results thus fit Diamond's (1975) "hot spot" model of a species expanding out from and contracting in to the best remaining habitat as the population fluctuates. The Palila pattern is also similar to that of the Kirtland's Warbler (*Dendroica kirtlandii*) during its recent population decline (Mayfield 1972, Byelich et al. 1976).

DISCUSSION

Comparability of methods with 1975 survey.—Because our method of determining range and density differed from that of van Riper et al. (1978), we should consider the possibilities that may account for the differences in population size. The Emlen transect method that van Riper et al. (1978) used has been directly compared with the variable circular-plot method in several studies (Edwards et al. 1981, Anderson and Ohmart 1981). The two methods provide comparable numbers when sample sizes exceed 30. In addition, densities derived from variable circular-plot estimates and mapped plots are very similar (DeSante 1981). Thus, we believe that the variable circular-plot method provides density estimates comparable to those obtained with the Emlen line transect.

Van Riper et al. (1978) defined range as that area bounded by a line connecting the outermost sightings. This is a conservative measure of range, which includes less area with low bird

densities than does a range based on incidental records, elevation, and presence of suitable habitat. The density values are thus higher in the more conservative definition of range, but the population estimates derived from the two methods should be comparable.

Area of historic range occupied.—Van Riper et al. (1978) estimated that in 1975 the Palila occupied only 10% of its historical range, defined as equivalent to the range of mamane forests on Hawaii. We now have a more accurate estimate of the area of mamane forests, 545 km², than was available during 1975. We found the Palila in 139 km², or 25.6%, of the 545 km² of extant mamane woodlands.

The present distributional pattern suggests a relict population. Indeed, as a result of habitat degradation and avian diseases at lower elevations, Palila may now be restricted to areas that historically were less than optimal habitat but that are the best remaining.

Historical patterns of distribution and abundance.—Considering the present distribution and abundance of the Palila in a historical context gives perspective on the factors that presently limit the population. Before the first Polynesians arrived about A.D. 400, the lowlands of the main islands supported extensive dryland forests that included mamane. Fossil evidence (Olson and James 1982) indicates that Palila apparently occurred down to sea level in these forests on Oahu and probably on other islands as well. The Polynesians converted dry lowland forests to grasslands by burning (Kirch 1982). By the time of Western contact (1778), Palila, along with several other finch-billed honeycreepers (*Rhodacanthis flaviceps, R. palmeri,* and *Chloridops kona*), were evidently restricted to the mid- and high elevation dry forests of Kona and Mauna Kea. Scott et al. (in press) estimated that Palila occupy less than 5% of their pre-Polynesian range.

In 1891, Palmer (in Rothschild 1900) found Palila abundant in Kona from 1,200 to 1,800 m elevation. Perkins (1893) also found them quite common in Kona in 1892, but in 1894 and in 1896 he found only two birds (Munro 1944, Banko 1979). Munro (1944) visited Perkins' Kona sites in 1936 and failed to find Palila, as did Richards and Baldwin (1953) in 1946. Palila were found in Kona neither during the 1978 Hawaii Forest Bird Survey (Scott et al. in press) nor during recent searches by other workers (C. van Riper, III, J. G. Giffin pers. observ.; R.

Bachman, P. Banko, W. Banko, D. Jenkins, H. Sakai, R. Walker pers. comm.).

Palila were extirpated from Kona between 1896 and 1936, we believe most probably around 1900–1910, contemporaneous with the extinction of the three other finch-billed honeycreepers. Ranching activities in the late 19th century (e.g. water impoundment, forest clearing) most likely accelerated the mosquito invasion of higher elevations by creating high-elevation breeding sites. The rapid disappearance of the four species in Kona may have been due to their lack of immunity to avian malaria or pox, as Warner (1968) and van Riper et al. (1982) suggested. In addition, Kona is subject to strong winter winds from the south and west that blow mosquitos up to the higher elevations. Water troughs at 1,500 m elevation in Kona held large populations of mosquito larvae in the summer of 1978 (J. M. Scott pers. observ.).

Role of feral ungulates in mamane-naio woodlands.—Feral ungulates have had a severe impact on Palila habitat on Mauna Kea and appear to be the major factor that indirectly limits the present distribution of the Palila. Ungulates generally prefer mamane, *Osteomeles*, and native grasses over naio and exotic herbs and grasses (Giffin 1976, 1982; van Riper 1980b).

In 1823, immense feral cattle (*Bos taurus*) herds were reported on Mauna Kea, and by 1904 an estimated 10,000 feral cattle were on Mauna Kea (Ellis 1917). By 1931 feral cattle had been eliminated from the upper elevations of Mauna Kea (Tomich 1969). Damage to mamane forests by feral cattle is incompletely documented, but Rock (1913) and Warner (1960) describe some effects.

Feral sheep (*Ovis aries*) did not become abundant until after the decline of cattle, although sheep carcasses were found near the summit of Mauna Kea in 1822 (Ellis 1917), and Bishop (1852) estimated 3,000 feral sheep on Hawaii in 1851. Feral sheep numbers were limited for many years by feral dogs (*Canis familiaris*) (Judd 1936), but the dogs were eliminated from Mauna Kea around 1920 by poisoning (Tomich 1969). By 1937, an estimated 40,000 sheep occurred on Mauna Kea (Bryan 1937), and control measures were initiated to protect the habitat. Only 200 sheep remained (Giffin 1976) in 1950, when management of Mauna Kea changed to sustained yield hunting. Sheep gradually increased in numbers, fluctuating between 1,000 and 4,000, from 1955 to 1975 (Giffin 1976), but

the subalpine woodland steadily deteriorated with as few as 1,500 sheep on the mountain (Warner 1960, Scowcroft and Giffin 1983). Berger (1981) estimated that treeline had receded 200 m in elevation since the 1850's due to sheep activity. Following a legal ruling under Section 9 of the Endangered Species Act, virtually all feral sheep were removed from Mauna Kea by July 1982. Small numbers of sheep still immigrate from adjacent lands, however.

Mouflon (*Ovis musimon*) were released in 1963 on the east flank of Mauna Kea (Tomich 1969) and are potentially as destructive as feral sheep to the subalpine woodland (Giffin 1982). The continued presence of sizable populations of mouflon in areas 2 and 3 portends further habitat degradation there.

We have noted a vigorous resurgence of native understory vegetation in area 1, from which feral sheep have been removed. A similar regeneration of the understory and mamane trees in area 2 would be expected if mouflon were eliminated from the mountain. Several sightings of mouflon in area 1 since 1981 (J. G. Giffin unpubl. data) further indicate the need to remove mouflon.

Feral goats (*Capra hircus*) figure prominently in the vegetation destruction on Mauna Loa and Maui and apparently occurred on Mauna Kea in some numbers in the 1930's, although they were not as destructive as sheep (Judd 1936). Goats persisted on Mauna Kea until their virtual extirpation during the 1982 sheep removal.

The degradation and fragmentation of the subalpine woodland by feral ungulates has contributed greatly to the reduction in range and population size of the Palila. The negative impact of feral ungulates on Palila habitat is also made clear by the negative response of Palila to grass cover and their positive response to less heavily browsed shrub understories. It is expected that the numbers of Palila will increase with the removal of feral ungulates (Berger et al. 1977), although the response will be delayed until mamane trees reach suitable sizes.

Present limiting factors.—Because mamane pods are the chief food of Palila, seasonal variation in pod abundance and distribution affects Palila abundance and distribution. Van Riper (1980b) found that mamane phenology varied with elevation and exposure, so that edible pods were available on the mountain at all times of the year. Areas with the greatest elevational range of good mamane forest thus provide the best opportunities for Palila to exploit shifts in abundance of mamane pods and flowers. This is reflected by the strong correlation we found between Palila density and woodland width. Relatively low densities of Palila on the southeast slopes of Mauna Kea (transects 109–113) may be due to the narrow width (1–2 km) of the mamane woodland in that area. Allowing the heavily grazed pasture that lies below the forest reserve fences to return to mamane woodland offers a good opportunity for increasing Palila and re-establishing populations in these areas. Planting trees may be necessary in some areas.

Branch size potentially affects Palila density, because Palila are fairly heavy birds (40 g) and are unable to obtain pods hanging from smaller twigs (van Riper 1978). Trees with multiple small trunks and correspondingly smaller branches occur in some areas as a result of heavy browsing pressure, and elsewhere small trees indicate recent release from past browsing activity. A combination of small trees and narrow elevational width of subalpine woodland may explain the absence of Palila on the north and northwest slopes of Mauna Kea. These areas are isolated from populations on the southwest and southeast slopes by large gaps in suitable habitat and by very narrow habitat corridors on the east slopes, which makes colonization difficult.

Pohakuloa flats.—The stations lying in Pohakuloa flats exhibited an extraordinary depression in Palila density compared with stations outside that area in similar habitat (Table 5). Reports from R. L. Walker and E. R. Kosaka, who lived in the flats for a period of years in the 1950's and 1970's, indicate that Palila have been absent from the flats for at least the past 30 yr. Although the absence of Palila in the flats remains unexplained at this point, the most plausible hypotheses are site tenacity, thermal stress, and disease, several other hypotheses being less probable.

The absence of Palila in the flats may be caused by some unspecified factor that operated once, say, in the past 50 or 100 yr, such as the destruction of vegetation by sheep 50 yr ago. According to this hypothesis, Palila could now inhabit the flats, but because of strong site tenacity there are virtually no potential colonizers. Site tenacity might also work in conjunction with a factor that operates intermit-

tently every several years, such as infrequent incursions of malaria-infected mosquitoes.

Palila are relatively intolerant of heat compared with other passerines, and their upper critical temperature is only 31°C (Weathers and van Riper 1982). Temperature records at the Pohakuloa Endangered Species Captive Propagation Facility indicated monthly highs in excess of 33°C for over half the months during 1978-1982 (R. Bachman unpubl. data). At a nearby airfield weather station, highs above 29°C were recorded for 3 months of the year, and a high of 31°C for 1 month, during 1979-1980 (Bradshaw Airfield, unpubl. data). At Puu Laau, center of Palila distribution, the highest temperature during 1973-1975 was 29°C (van Riper 1980a). Thus, temperatures in the flats may rise to levels that are unsuitable for Palila on sunny calm days.

The occasional presence of disease in Pohakuloa flats may kill Palila. This hypothesis is plausible, because: (1) Palila are very susceptible to avian malaria (van Riper et al. 1982) and in all probability are susceptible to avian pox; (2) night-biting mosquitoes, the vector for malaria, occasionally occur in the flats and breed in water impoundments in that area; (3) large populations of exotic birds, especially gallinaceous gamebirds, House Sparrows (*Passer domesticus*), House Finches (*Carpodacus mexicanus*), Red-billed Leiothrix (*Leiothrix lutea*), and Common Mynas (*Acridotheres tristis*), are established around sites of human activity in the flats, and may serve as reservoirs for pathogenic organisms; and (4) avian disease is believed to be responsible for a large portion of the extinctions and range contractions of the native Hawaiian forest birds that have occurred in the past century (Warner 1968, van Riper et al. 1982, Scott et al. in press). Because human activities and some exotic passerine populations (House Sparrows, Common Mynas) are restricted to the flats, the disease-affected area would be fairly small and constitute the flats and immediately adjacent slopes, exactly where Palila are inexplicably absent.

Many other potential explanations can be hypothesized for the absence of Palila in the flats. Disturbance from military activities—artillery practice, troop movements—may be high at times. Predation from feral house cats (*Felis domesticus*), roof rats (*Rattus rattus*), or the small Indian mongoose (*Herpestes auropunctatus*) may be excessive in the flats, although van Riper

(1978) found all three predators present at Puu Laau, where highest densities of Palila, Elepaio (*Chasiempis sandwichensis*), and Common Amakihi (*Hemignathus virens*) occurred. The absence may be due to stochastic population fluctuations that resulted in local extinction, but the habitat, and presumably the population, was continuous with the high-density areas. In as much as the flats would support 800 Palila, assuming 35 birds/km², stochastic fluctuation to extinction seems improbable. Studies with caged and radio-tagged birds should prove useful in testing hypotheses.

Management strategies.—Our study suggests several management strategies to increase Palila numbers and improve the survival prospects. The most urgent need is control, or preferably elimination, of mouflon on Mauna Kea to prevent further degradation of mamane-naio woodland and to encourage forest regeneration, particularly near timberline. Substantial tree and understory regeneration has already occurred in area 1 following the removal of sheep in 1982.

Even with feral ungulates removed, the subalpine woodland is threatened by exotic plants and fire. In 1979 a fire consumed 200 ha of mamane-naio woodland adjacent to the high-density area. Fountain grass (*Pennisetum setaceum*), an aggressive, fire-adapted African tussock grass that has recently established colonies on the south slopes of Mauna Kea, could fuel future fires. Another potential problem is German ivy (*Senecio mikanioides*), a choking, climbing liana that has recently been discovered as a sporadic infestation over about 500 ha near Puu Laau. Effective control measures for these noxious introductions are needed before they expand beyond their tenacious toeholds.

An appropriate long-term management strategy is to restore the very scattered mamane woodlands that lie below transects 110-114 on the southeast slopes of Mauna Kea by removing cattle and possibly planting seedlings. The importance of woodland width in ensuring a good stock of mamane pods year round indicates high potential for dramatic response in Palila density as these areas return to woodland. Cattle grazing should also be barred on the northwest and north slopes of Mauna Kea to re-establish Palila in area 3.

Finally, if disease proves to be responsible for the absence of Palila on Pohakuloa flats, then strict measures are needed to control mos-

quito breeding sites and exotic passerine populations, particularly House Sparrows and Common Mynas.

LITERATURE CITED

ANDERSON, B. W., & R. D. OHMART. 1981. Comparisons of avian census results using variable distance transect and variable circular plot techniques. Pp. 186–192 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. 6.

BANKO, W. E. 1979. Avian history report 2. History of endemic Hawaiian bird specimens in museum collections. Honolulu, Hawaii, Coop. Natl. Park Res. Stud. Unit, Univ. Hawaii.

BERGER, A. J. 1970. The eggs and young of the Palila, an endangered species. Condor 72: 238–240.

———. 1981. Hawaiian birdlife, second ed. Honolulu, Hawaii, Univ. Press Hawaii.

———, E. KOSAKA, E. KRIDLER, J. M. SCOTT, P. SCOWCROFT, C. WAKIDA, D. WOODSIDE, & C. VAN RIPER, III. 1977. Palila recovery plan. Portland, Oregon, U.S. Fish Wildl. Serv.

BISHOP, C. R. 1852. Rept. Trans. Royal Hawaiian Agric. Soc. 1 (3): 91.

BRYAN, L. W. 1937. Wild sheep in Hawaii. Paradise Pacific 49 (3): 19, 31.

BYELICH, J., W. IRVINE, N. JOHNSON, W. JAMES, H. MAYFIELD, R. RADTKE, & W. SHAKE. 1976. Kirtland's Warbler recovery plan. Washington, D.C., U.S. Fish Wildl. Serv.

DESANTE, D. F. 1981. A field test of the variable circular-plot censusing technique in a California coastal scrub breeding community. Pp. 177–185 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. 6.

DIAMOND, J. M. 1975. Assembly of species communities. Pp. 342–444 *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, Eds.). Cambridge, Massachusetts, Belknap Press.

DRAPER, N. R., & H. SMITH. 1981. Applied regression analysis, second ed. New York, J. Wiley.

EDWARDS, D. K., G. L. DORSEY, & J. A. CRAWFORD. 1981. A comparison of three avian census methods. Pp. 170–176 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. 6.

ELLIS, W. 1917. A narrative of a tour through Hawaii, etc. (reprint of 1827 edition). Honolulu, Hawaii, Hawaiian Gazette.

EMLEN, J. T., & M. J. DEJONG. 1981. The application of song detection threshold distance to census operations. Pp. 346–352 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. 6.

GIFFIN, J. G. 1976. Ecology of the feral sheep on Mauna Kea. Pittman-Robertson Proj. W-15-5, Study XI. Honolulu, Hawaii, Hawaii Dept. Land Nat. Resources.

———. 1982. Ecology of the mouflon sheep on Mauna Kea. Pittman-Robertson Proj. W-17-R, Study R-III. Honolulu, Hawaii, Hawaii Dept. Land Nat. Resources.

HARTT, C. E., & M. C. NEAL. 1940. The plant ecology of Mauna Kea, Hawaii. Ecology 21: 237–266.

JAMES, F. C., & N. O. WAMER. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63: 159–171.

JUDD, C. S. 1936. Hawaii's forests winning their battle with wild animals. Honolulu Star-Bulletin, March 21, 3rd Sec., pp. 1, 7.

KEPLER, C. B., & J. M. SCOTT. 1981. Reducing count variability by training observers. Pp. 366–371 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. 6.

KIRCH, P. V. 1982. The impact of the prehistoric Polynesians on the Hawaiian ecosystem. Pacific Sci. 36: 1–14.

MAYFIELD, H. F. 1972. Third decennial census of Kirtland's Warbler. Auk 89: 263–268.

MUNRO, G. C. 1944. Birds of Hawaii. Honolulu, Hawaii, Tongg Press.

OLSON, S. L., & H. F. JAMES. 1982. Prodromus of the fossil avifauna of the Hawaiian Islands. Smithsonian Contrib. Zool. 365.

PERKINS, R. C. L. 1893. Notes on collecting in Kona, Hawaii. Ibis Ser. 6, 5: 101–114.

———. 1903. Vertebrata. Pp. 365–466 *in* Fauna Hawaiiensis, vol. 1, part 4 (D. Sharp, Ed.). Cambridge, England, Univ. Press.

RAITT, R. J., & S. L. PIMM. 1976. Dynamics of bird communities in the Chihuahuan Desert, New Mexico. Condor 78: 427–442.

RAMSEY, F. L., & J. M. SCOTT. 1981. Analysis of bird survey data using a modification of Emlen's method. Pp. 483–487 *in* Estimating numbers of

terrestrial birds (C. J. Ralph and J. M. Scott, Eds.). Stud. Avian Biol. 6.

REYNOLDS, R. T., J. M. SCOTT, & R. A. NUSSBAUM. 1980. A variable circular-plot method for estimating bird numbers. Condor 82: 309–313.

RICE, J., R. D. OHMART, & B. W. ANDERSON. 1981. Bird community use of riparian habitats: the importance of temporal scale in interpreting discriminant analysis. Pp. 186–194 in The use of multivariate statistics in studies of wildlife habitat (D. E. Capen, Ed.). Fort Collins, Colorado, U.S. For. Serv., Gen. Tech. Rept. RM-87.

RICHARDS, L. P., & P. H. BALDWIN. 1953. Recent records of some Hawaiian honeycreepers. Condor 55: 221–222.

VAN RIPER, III, C. 1978. The breeding ecology of the Amakihi (Loxops virens) and Palila (Psittirostra baileui) on Mauna Kea, Hawaii. Unpublished Ph.D. dissertation. Honolulu, Hawaii, Univ. Hawaii.

———. 1980a. Observations on the breeding of the Palila Psittirostra baileui of Hawaii. Ibis 122: 462–475.

———. 1980b. The phenology of the dryland forest of Mauna Kea, Hawaii, and the impact of recent environmental perturbations. Biotropica 1034 12: 282–291.

———, J. M. SCOTT, & D. M. WOODSIDE. 1978. Distribution and abundance patterns of the Palila on Mauna Kea, Hawaii. Auk 95: 518–527.

———, S. G. VAN RIPER, M. L. GOFF, & M. LAIRD. 1982. The impact of malaria on birds in Hawaii Volcanoes National Park. Tech. Rept. 47. Honolulu, Hawaii, Coop. Natl. Park Res. Stud. Unit, Univ. Hawaii.

ROCK, J. F. 1913. The indigenous trees of the Hawaiian Islands. Honolulu, Hawaii, privately printed.

ROTENBERRY, J. T., & J. A. WIENS. 1980a. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228–1250.

———, & ———. 1980b. Temporal variation in habitat structure and shrubsteppe bird dynamics. Oecologia 47: 1–9.

ROTHSCHILD, W. 1900. The avifauna of Laysan and the neighbouring islands, vol. 3. London, R. L. Porter.

SCOTT, J. M., & F. L. RAMSEY. 1981. Length of count period as a possible source of bias in estimating bird numbers. Pp. 409–413 in Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, (Eds.). Stud. Avian Biol. 6.

———, S. MOUNTAINSPRING, F. L. RAMSEY, & C. B. KEPLER. In press. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Stud. Avian Biol.

SCOWCROFT, P. G., & J. G. GIFFIN. 1983. Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. J. Range Mgmt. 36: 638–645.

STEEL, R. G. D., & J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach, second ed. New York, McGraw-Hill.

TOMICH, P. Q. 1969. Mammals in Hawaii: a synopsis and notational bibliography. Spec. Pub. 57. Honolulu, Hawaii, Bernice P. Bishop Mus.

UNITED STATES FISH AND WILDLIFE SERVICE. 1983. Republication of the lists of endangered and threatened species. Fed. Reg. 48: 34182–34196.

WARNER, R. E. 1960. A forest dies on Mauna Kea. Pacific Discovery 13: 6–14.

———. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 65: 3–23.

WEATHERS, W. W., & C. VAN RIPER, III. 1982. Temperature regulation in two endangered Hawaiian honeycreepers: the Palila (Psittirostra baileui) and the Laysan Finch (Psittirostra cantans). Auk 99: 667–674.