

OBSERVATIONS ON THE BREEDING OF THE PALILA *PSITTIROSTRA BAILLEUI* OF HAWAII

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The Palila *Psittirostra bailleui*, one of six species of its genus (Amadon 1950), was first collected in the Kona District of Hawaii by Bailleu in 1876 (Oustalet 1877). Historically the Palila was confined to the mamane *Sophora chrysophylla* and mamane-naio *Myoporum sandwicense* forests at high elevations on the mountains of Mauna Kea, Hualalai and Mauna Loa (Wilson & Evans 1890–1899, Perkins 1893, Rothschild 1893–1900). This range has been greatly reduced since the turn of the century. The bird is now found only on c. 5560 ha of Mauna Kea, occupying merely 10% of its former range. The present population is estimated to be 1500–1700 individuals at densities of approximately 37 birds per 100 ha (van Riper, Scott & Woodside 1978).

Habitat degradation has been extensive in Hawaii, yet little work has been carried out concerning the effects of habitat alteration on the endemic organisms. The Palila is specialized in its feeding habits, being totally reliant upon the mamane ecosystem, which is rapidly diminishing (Warner 1960). This study was undertaken to define the basic breeding parameters of the remaining population on Mauna Kea, and to identify reasons why the bird is today so rare.

METHODS

The study extended from 1970 through 1975, with 757 days spent in the field. During the last three years data were collected in every month. Study sites were at 1980, 2130 and 2290 m in the Kaohe and Mauna Kea Game Management areas at Puu Laau on the southwestern slope of Mauna Kea, Hawaii (Fig. 1). Adult birds were captured in mist-nets and marked with U.S. Fish and Wildlife Service metal rings in combination with coloured plastic rings. Moults were determined from mist-netted birds and museum skins. Seven nestlings from four nests were weighed each day and photographed. Nest measurements were taken on 26 nests. The long and short axes of eight eggs were measured using vernier calipers accurate to the nearest 0.1 mm, and an Egg Shape Index = lesser egg diameter/greater egg diameter \times 100, was calculated. Egg weights were taken with Pesola scales accurate to 0.1 g. Observations at nests (over 400 h) were made with binoculars.

Annual productivity (P) is represented by the equation: Productivity = CBS/N where C = clutch size, B = length of breeding season, S = breeding success (proportion of eggs laid that fledged young) and N = length of nest cycle, i.e., $N = b + e + y + n + f$, where b = nest building interval (in days), e = number of days for egg laying, y = incubation period (in days), n = nestling period (in days) and f = fledgling period (in days). In order to determine the number of young produced per unit area of forest, the following equation was used: $T = PD$, where P = annual productivity and D = density of breeding birds. Density was divided in half to account for pairs and modified according to the approximate percentage of nonbreeding birds in the population with the equation: $D = dz/2$, where d = observed population density and z = percentage of resident breeders. By comparing non-breeders to the number of known breeding individuals in a section of the site, it was estimated that 20% of the population was composed of nonbreeding individuals.

RESULTS

BREEDING SEASON

Active nests ($n = 26$) were recorded from March through September with young fledging from May to September. The most intensive breeding occurred from June to August; this peak corresponded to the period of greatest mamane pod production (Fig. 2). Moulting occurred from late May until early December, with a large degree of

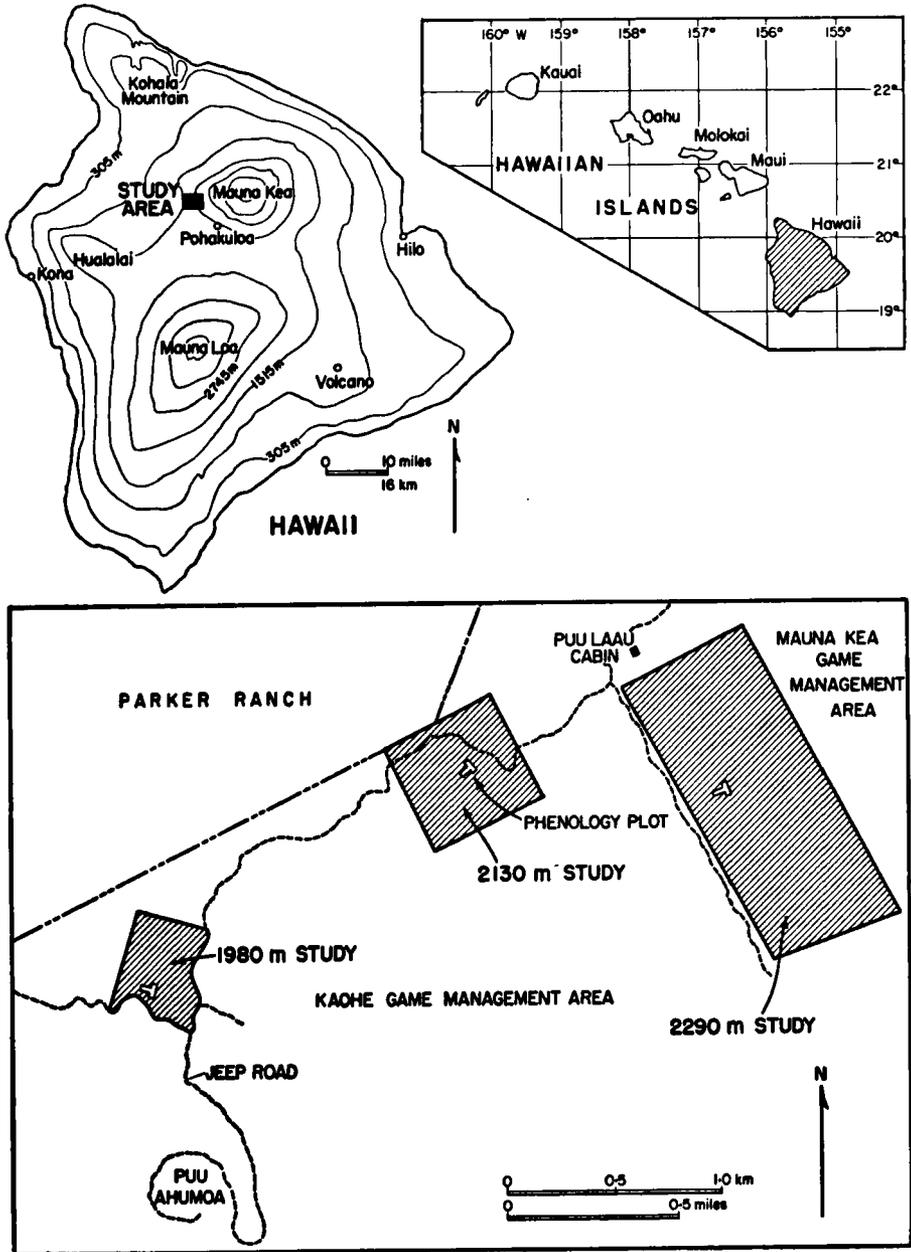


FIGURE 1. The island of Hawaii showing study sites on Mauna Kea.

breeding-moult overlap. Between breeding efforts birds flocked and followed shifts in mamane pod concentrations; one bird was observed 2.5 km from where it had bred.

COURTSHIP

Low advertizing flights (a slow fluttering of wings followed by a short glide) were given by males during courtship, and sexual chasing (either a low, rapid, straight-line chase or high, rapid flight) occurred primarily during the early breeding season. Males frequently courtship-fed females, especially during incubation (Table 1). The females would vocalize and wing-quiver prior to receiving food. From late incubation to the end of the nesting cycle courtship-feeding decreased and was replaced by mutual billing, during which the birds touched bills from side-to-side but no food was exchanged.

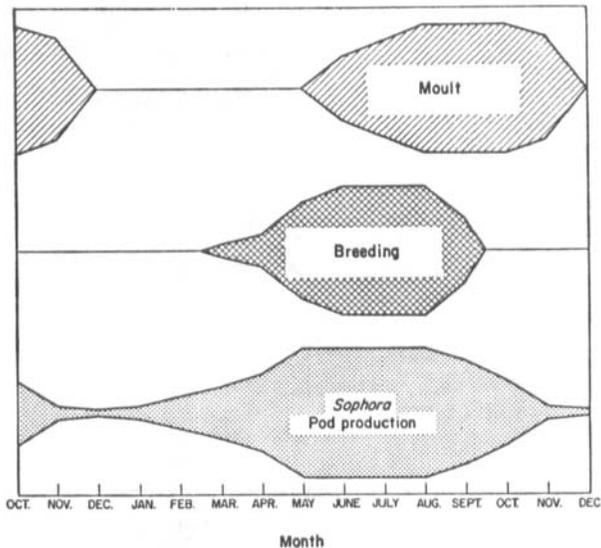


FIGURE 2. Comparison of the Palila breeding season with moult and mamane (*Sophora*) pod production.

TERRITORY

Early in the breeding cycle, territory was a 'mate-defended area' (Conder 1949), with the male excluding all conspecifics from the vicinity of the female, usually by song and direct chase. As incubation began, defence centred more on the nest, with females infrequently chasing other birds. Two territories were measured; the area bounded by the outermost points of aggressive encounter included 3900 m² and 600 m², respectively. Territories were abandoned when the young fledged. The birds then joined small feeding flocks. Individuals would return to the same area to nest the following year (one ringed female returned for three consecutive seasons).

THE NEST

The first and, prior to this study, only other active nest was found by Berger (1970). Twenty-three of 26 nests were in mamane trees. Larger trees were preferred; the average tree height (6.9 m) and circumference at breast height (CBH) (83.4 cm) were both near the maxima for trees in the forest (van Riper 1980). Nest placement averaged 5.2 m above the ground and was positively correlated ($r = 0.76$) with the height of the nest tree (Fig. 3). Nests were placed on horizontal branches (15 nests), terminal forks (four nests) or in

lateral forks (seven nests). Often three branches formed an upright cup on to which the nest was placed. Mean distance of the nest from the trunk was 2.7 m and from the end of the branch, 1.05 m.

Nest sites were selected by females. The duration of nest building varied considerably, ranging from 7 to 20 days. Most nest construction occurred during the morning hours, and both sexes participated, albeit the male helped incorporate material only during very early nest building. The birds would often pile up material in many short trips, and the female would then remain on the nest for an extended period of time moulding and reweaving grasses into the structure.

TABLE 1
Palila courtship feeding rates

Days of cycle	Total hours observed	Total no. of courtship feedings	No. of courtship feedings h ⁻¹
<i>Incubation period</i>			
(Clutch completed)			
0-3	13.5	24	1.78
4-7	13.5	9	0.67
8-11	25.0	19	0.76
12-15	18.5	9	0.49
<i>Nestling period</i>			
(Hatching)			
16-19	56.8	40	0.70
20-23	28.5	6	0.21
24-27	29.4	7	0.24
28-31	28.2	2	0.07
32-35	14.8	0	0
36-39	11.0	0	0
(Fledging)			

The nest base usually consisted of large dead twigs broken off and collected from the nest tree. The bowl was composed of interwoven grasses (sometimes sheep wool; van Riper 1977) and lined with either lichens *Usnea* sp. or fine grasses and rootlets. Width of 26 nests averaged 14.7 cm (range = 9.6-18.8 cm) and total height 7.7 cm (range = 4.6-9.6 cm). The bowl depth (av. = 3.9 cm, range = 2.5-5.3 cm) and bowl width (av. = 7.4 cm, range = 5.8-8.9 cm) were similar throughout the population. Rim thickness was the most variable measurement, ranging from 1.5 to 6.9 cm. Six nests had a mean weight of 74.1 g, but individual weights ranged from 41 to 105 g.

THE EGGS AND CLUTCH SIZE

Eggs were laid early in the morning (before 0800 h), and in all cases ($n = 12$), one per day. The time lapse between nest completion and laying was quite variable (range = 15 days). Eggs were characterized by a whitish ground colour with superimposed reddish-brown markings, usually forming a dense cap around the larger end. Eight eggs averaged 25.0 mm in length and 16.8 mm in width, yielding an Egg Shape Index of 67.1%. Four eggs weighed on average 2.8 g (range = 2.6-3.0 g), and two shells averaged 0.2 g. Clutch size of 11 nests was two eggs; at one nest only one egg was laid. Palila are apparently determinate layers; I removed the second egg of one clutch on the morning of laying, and no other eggs were subsequently laid.

INCUBATION

Nest attendance increased with the laying of the first egg, and birds were present at the nest approximately 50% of the time on day 0 ($n = 2$ nests, Fig. 4). Whether or not heat is applied to the first egg of a clutch is unknown. Females incubated the eggs, but in at least one case on day 0 a male also attended. Eggs were covered over 75% of daylight hours during the remainder of incubation, and turned on average 1.6 times per hour. They were evidently also incubated throughout the night; probes in the nest lining revealed constant heat from the nest. Incubation periods at two nests were 16 d 6 h and 15 d 22 h, and at a third was between 15 and 16 days.

PARENTAL CARE OF THE YOUNG

The first egg started hatching either late at night or early in the morning, and the second not before the middle of that day. After the hatch, the female removed eggshells

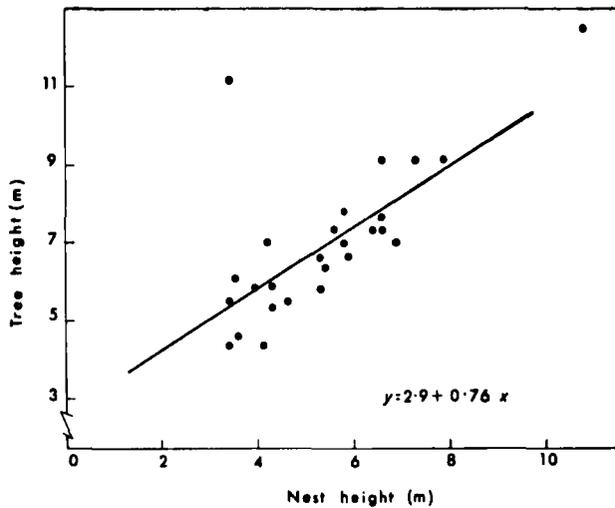


FIGURE 3. The relationship between Palila nest heights and heights of mamane (*Sophora*) and naio (*Myoporum*) nest-trees on Mauna Kea, Hawaii; sample of 26 nests.

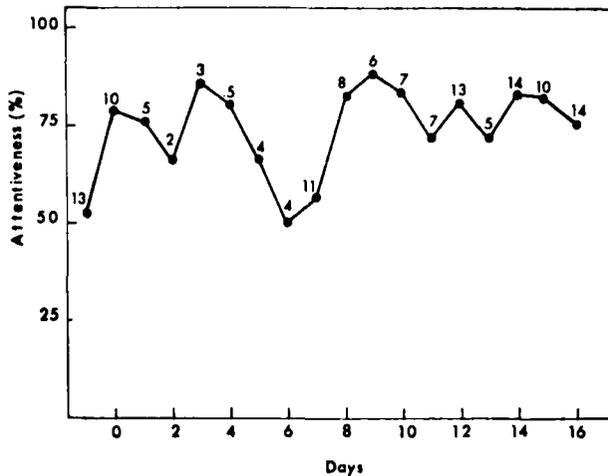


FIGURE 4. Attentiveness of Palila during incubation, measured at six nests during 141 h observation. Numbers denote hours of observation.

from the nest. It may be that the stimulus of sharp edges triggers eggshell disposal; in one nest the shell was soft and pliable and was not removed but eventually worked into the bottom of the nest.

Only the female brooded, and time on the nest declined steadily throughout the nestling period until day 15 when brooding effectively stopped (Fig. 5). If a heavy rain occurred during brooding, the female stayed on the nest. At night the nest was covered until at least day 18.

Nestling feeding rates, as measured by the number of trips to the nest by adults, showed that females fed the young more than males (Fig. 6). The number of feedings decreased slightly over the nestling period (regression: $y = 2.57 - 0.034x$). At nest 4-74, on day 16 of the nestling period, a feral cat ate the brooding female. Over the next 10

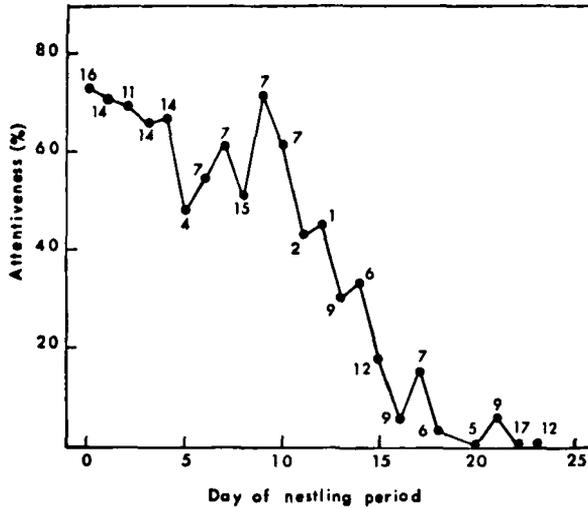


FIGURE 5. Brooding rate of Palila, measured at four nests during 211 h observation. Numbers denote hours of observation.

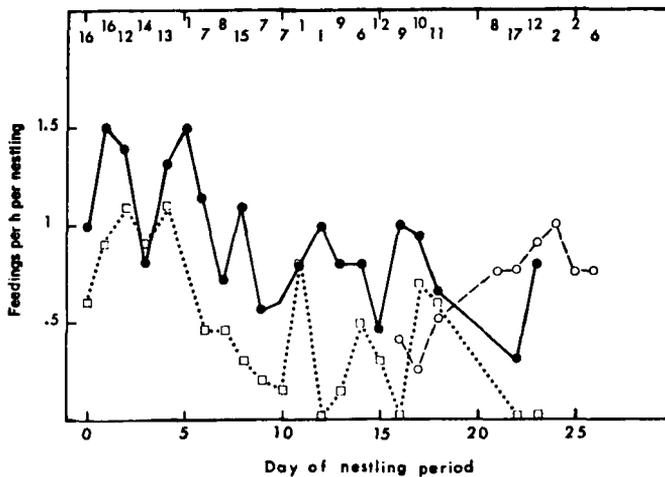


FIGURE 6. The number of hourly feeding sessions at a nest for each nestling by male and female Palila, measured during 222 h of observation at four nests. Numbers denote hours of observation. ●, Female; □, male; ○, male, nest 4-74.

days the male increased his feeding rate, presumably to compensate for the absence of his mate (Fig. 6). This was the only nest I observed that had helpers in the sense of Skutch (1961). At least two helpers made five trips to the nest with food from days 16 to 26. The feedings by the helpers were quite irregular, and when they occurred often followed shortly after a feeding by the parent male.

Although young were not sacrificed for crop analysis, some information was gathered on the food they were fed from the colour and shape of items discerned through the skin of the neck. In early nest life (days 0–2) young were fed finely masticated items. At nest 1–73, on the day of hatching, I observed a female repeatedly nip off flower and leaf buds

TABLE 2

Types of food Palila were observed eating during 152 days of observation on Mauna Kea, Hawaii

Observation period	No. of days observed	Times ¹ recorded feeding	Percent of food type taken per month					
			<i>Sophora</i>			<i>Myoporum</i>	Insects	Other
pods	flowers	leaves	fruit					
1974								
March	13	29	14	28	0	52	3	3
April	9	15	7	64	0	29	0	0
May	14	31	52	22	0	26	0	0
June	12	69	70	9	0	3	17	1
July	24	22	32	50	0	0	18	0
December	9	12	58	9	8	0	17	8
1975								
March	6	21	67	33	0	0	0	0
April	12	49	39	55	0	2	0	4
May	11	24	38	33	0	29	0	0
June	11	72	42	8	0	10	40	0
July	11	34	50	6	0	6	38	0
August	14	72	85	6	0	2	7	0
September	6	31	100	0	0	0	0	0

Note: ¹ Each recorded feeding represents the food type being eaten by a bird when first seen.

from a mamane tree, and after numerous regurgitations feed them to the young. I was unable to prove conclusively that insects were fed during the first few days of the nestling period. Data from Table 2, however, show that adults take more insects during the breeding season than during the rest of the year, suggesting that insects were fed to the young (see also Perkins 1903). On day 2 (one case) and 3 (three cases), mamane seeds were present in the crop of the young; the seeds were not whole but broken into small pieces. From this time onward seeds appeared to be the major food item, although a viscous white milky substance was also regurgitated to the young.

The most striking feature of a used nest was an accumulation of faecal material. Both parents removed faecal sacs, and the nest remained clean until day 4. At day 5 sacs started accumulating on the nest rim, and by day 8 were abundant. The rate of faecal sac removal increased from 0.2 h⁻¹ at day 2 to a peak removal rate of 4.6 h⁻¹ at day 8. After day 10 removal decreased rapidly until day 13, when it occurred only at infrequent intervals. From day 7 the female and male removed only sacs from the bowl and ignored, for the most part, those on the rim. By day 22 the nest, limbs of the tree, and ground below were covered with dried faecal material.

NESTLING DEVELOPMENT

At hatching, young were completely helpless. They were pinkish-orange in colour with small areas of black nestling down in the pterylae. Eye slits, grasping reflex, fear response, ability to stand, beak colour, preening and flapping of wings all appeared at different times and developed gradually (Table 3). Feather development was slow, with pin feathers beginning to open about day 12-14 (Table 4). Nestlings gained weight at a fairly steady rate throughout the nestling period, but because young left the nest prematurely if disturbed, I did not take weights after day 20 (Fig. 7). The young fledged at weights perhaps slightly less than those of adults.

TABLE 3
Developmental patterns in young Palila

Developmental pattern	Day of nestling period																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Opening of eyes					slits opening				fully open																
Grasping	not able to grasp										grasping developed														
Fear response						gape readily					covering in nest														
Ability to stand	unable to stand								standing well																
Colour of beak	yellow						orange						black												
Preening	none							some							vigorous										
Flapping of wings	no flapping of wings																		flapping						

FLEDGING OF YOUNG

Before fledging, young repeatedly left the nest, moving to nearby branches and returning. Apparently fledging in the Palila constitutes leaving the nest tree and not just departure from the nest. When asynchronous fledging occurred, one parent accompanied the fledgling while the mate remained at the nest site. Fledglings could fly well, and at nest 4-74 both young flew to a tree over 20 m from the nest when they fledged. Nestling periods ranged from 21 to 27 days at four nests. I never observed young return to the nest after they had fledged.

The young were quite sedentary during the first week of the fledgling period. They would remain in a single tree, sometimes for a two-day period, and adults would forage out from that point returning to the tree only for feedings. I observed feeding of fledglings for three days and found the rate to be much the same as in the last days of the nestling period. After leaving the nest area, the young remained with the parents for an extended

TABLE 4
Development of feather tracts in Palila nestlings¹

Feather tracts	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Spinal										
Alar									
Ventral																										
Caudal																										
Capital																										
Humeral																										

Note: ¹ = pin feathers; - - - = unsheathing of feathers; — = feathers completely un-sheathed.

period, moving in small post-breeding flocks. I have observed ringed young with their parents over 30 days after fledging, about 100 m from the nest site.

REPRODUCTIVE SUCCESS

During 1972–1975, reproductive success (number of eggs laid that fledged young) was 52.2%. Individual years were quite variable, probably due to the low number of nests under observation. Hatching success was 65.2% and nestling success 80%. Causes of mortality included failure of eggs to hatch due either to embryonic death or to infertility (17% of all eggs incubated to term), desertion, unexplained nestling death, weather or poor nest construction. Predation was observed at only one nest, but I feel that it is

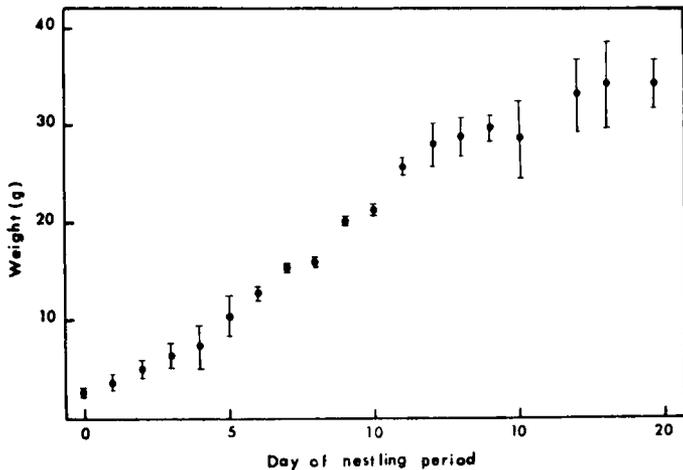


FIGURE 7. Daily nestling weights of young Palila from seven nestlings at four nests. Circles denote means and bars +95% confidence limits.

probably a greater factor at Puu Laau than these data indicate. Because my sample size was small, and extensive mammal trapping was done concurrently with the most intensive periods of study (van Riper 1978), predation was most likely reduced at the nests I observed.

DISCUSSION

In studying the Palila one must confront the question of why it is rare and today maintains such a precarious existence. In the population at Puu Laau the ecological rôle of the species, timing and length of the breeding effort, slow nestling development, potential mortality from predation, and reduced genetic fitness all gave evidence of regulating population levels. No single mechanism was alone responsible, but all acted together in a cumulative manner to depress numbers.

Probably of greatest importance was the ecological rôle of the species. The Palila has evolved into a rather specialized niche, becoming totally reliant upon the mamane ecosystem. This has had a pervading influence upon many aspects of the bird's biology. Mamane is the major tree chosen for nest sites and also provides its principal source of food. Pianka (1974: 188) argued that highly specialized organisms usually have narrow tolerance limits along one or more of their niche dimensions. Often these specialists have very specific habitat requirements and, as a result, are not very abundant. Cody (1974: 117), in his analysis of generalists and specialists in eight North American study areas, showed that generalism seemed to assure success—there were few rare generalists but an abundance of rare specialists. Thus we see that the Palila's ecological niche in a way predetermined low numbers.

Problems, therefore, did not begin for the bird until man and feral mammals had significantly altered the habitat. Since that time (*c.* 1850) there has been a steady decline in mamane forests on Hawaii (Warner 1960). With the reduction of this habitat has come a parallel diminution of Palila numbers. The bird presently occupies only 10% of its former range (van Riper *et al.* 1978), and Giffin (1976) showed that this area is diminishing rapidly. Furthermore, as large mamane trees are preferred for nesting and feeding, what appears at first glance to be acceptable habitat might not be so to the birds (see discussion by Whitmore 1977). Thus, the already small realized niche has become even more restricted.

TIMING AND LENGTH OF BREEDING

The Palila breeding season was protracted, lasting 6–8 months, but most birds bred within a 2–3 month seasonal span. It is still uncertain what initiates the breeding season. In most temperate passerines photoperiod appears to be the proximate factor, but Farner & Lewis (1971) found that photoperiod was never the only mechanism that set the precise time of reproduction, and that in many species additional factors modified the timing. Whatever the ultimate stimulus is that influences Palila breeding, it appears proximately to be related to the timing of mamane phenophases. The major breeding effort coincided with that time of year when mamane bore pods (Fig. 2). Not only did the breeding periods seem to be adjusted to optimal resource availability, but the birds were able to make fine adjustments to yearly differences in the timing and abundance of these food supplies. In 1974, when pods appeared earlier, the breeding season was earlier than in 1975, when pods matured much later. Food supply as a determinant of breeding effort is probably common to many avian groups. Harris (1969), Lack (1954) and Perrins (1970) all argued that availability of food acted as the ultimate determinant governing initiation of the breeding season. Tordoff & Dawson (1965) have shown that food acts as the timing mechanism in the breeding cycle of the Red Crossbill *Loxia curvirostra*, which nests only when a good conifer seed crop is produced.

The length of the breeding season in comparison to the length of the nesting cycle becomes important when one considers that a nesting sequence (nest building to independence of young) takes at least 90 days. This indicates that a pair is probably able to raise only one set of young in a season. Moreover, if the season is terminated early, due perhaps to decreased food availability, the total number of young produced that year could be severely reduced.

NESTLING GROWTH AND MORTALITY

The principal cause of the protracted Palila nesting cycle is the slow growth of the young. Palila nestlings normally took 22–23 days to fledge, which is a long period for an open-nesting passerine species (Ricklefs 1968, 1969a, Skutch 1945). To compare this growth period to other altricial birds, data were analysed by methods suggested by Ricklefs (1967). This involved fitting nestling weights to a sigmoid curve and using the specific rate constant of the equation for comparisons. The growth rate (K) for Palila (0.321) was less than all passerines analysed by Ricklefs (1968), except the Formicariidae, Tyrannidae and Corvidae. It was also lower than the average (0.462) reported by Maher (1973) for seven ground-nesting passerines. A comparison of these constants shows that Palila nestlings grow more slowly than most passerines measured to date, and are therefore confined to the nest for an extended time period.

Ricklefs (1969b) proposed a model whereby natural selection would maximize the growth rates of altricial birds. He indicated that the rate of growth in body weight was not correlated with nestling mortality, but was rather a function of adult body size (of the species) and the mode of development of the young. I believe that in Hawaii long nestling periods were able to evolve because of the (former) absence of ground predators. With minimum nestling mortality from predation there would have been little directional selection against a later fledging date. This hypothesis is supported by the fact that adults exhibited a decreased feeding rate over the nestling period (Fig. 6). This type of feeding rate is unusual for passerines, but perhaps with the extended nestling period, physiological adjustments evolved in the young and food requirements were able to be spread out over a longer time period. The impact of a prolonged nestling period in the presence of introduced predators is magnified by the accumulation of pungent faecal material around the nest. Certainly predators have contributed their share to the decline of the Palila.

REPRODUCTIVE SUCCESS

While reproductive success (the number of eggs laid that fledged young) was comparable to that found in other open-nesting passerine species (Nice 1957), this can often be a misleading criterion when analysing total young produced per year by a population. Drury (1961) was one of the first to point out that total production of young per year depended upon the number of broods raised as well as clutch size.

The relative productivity of Palila was 1.8 young/pair/year. With approximately 14.8 pairs/100 ha (van Riper *et al.* 1978), total productivity was only 26.1 young/100 ha. In the same habitat, the Amakihi *Loxops virens* had a relative productivity of 203.5 young/100 ha/year (van Riper 1978). The low potential productivity of Palila was in a large part due to the already low numbers of breeding birds, coupled with a small clutch size and a long nesting cycle.

Ricklefs & Bloom (1977) examined productivity in birds and found that in a dry montane subtropical area of Ecuador (a habitat similar to Puu Laau) the most important variables of productivity were season length and clutch size. The similarity suggests that in savanna ecosystems throughout subtropical regions the two most important factors regulating productivity in small passerine birds are breeding season length and clutch size.

GENETIC FITNESS

Another problem associated with the low Palila numbers is reduced fitness. Evidence today indicates that approximately 1600 birds remain (van Riper *et al.* 1978), and the effective breeding population (McClearn & DeFries 1973: 228) is in all probability much less. When an effective breeding population is small, reduced fitness (survival value and reproductive capability of a given genotype relative to other genotypes in a population) often results (McClearn & DeFries 1973: 253). Loss of fitness in the extant population may be evidenced in the high degree of infertility. Of the 18 eggs that were incubated to term, 17% were either infertile or died as embryos. In studies of other passerines (Nice 1937: 146, Bull 1946, Mumford 1964, Seel 1968, Siegfried 1973), average infertility was 6.8% (range = 3.7–12.0).

Lack of dispersal could also be one reason for reduced fitness in Palila today, as it may have interrupted (or reduced the rapidity of) gene flow within the population. Baldwin (1953) suggested that dispersal rates were unaccountably low in Hawaiian birds, and historical data indicate that this is so. As late as 1900 two colonies existed, one on Mauna Loa, the other on Mauna Kea. The Mauna Loa population has disappeared, although what appears to be good habitat still remains in the area. Had dispersal between the two habitats been continuous, the Mauna Loa colony might have survived.

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SUMMARY

The behavioural ecology and breeding biology of the endangered Palila *Psittirostra bairdii* was studied from 1971 to 1975. The most intensive breeding occurred from June to August, and coincided with peak production of mamane *Sophora chrysophylla* seeds, the bird's major food source. The Palila was able to make adjustments in its breeding to compensate for yearly differentiation in the timing and abundance of this food supply.

Sexual chasing and courtship feeding were the most frequently encountered pre-nesting behaviours. Territory was a mate-defended area, which later in the nesting sequence was confined to the nest site. A total of 26 nests was found; most were placed on larger branches of mamane trees. Nest construction occurred primarily in the morning hours and lasted up to 20 days. Both sexes took part in nest construction, albeit the male rôle was minimal. Unless the nest was placed in the terminal fork of a tree, it usually contained a large stick base.

The modal clutch size was two; eggs were laid early in the morning and in all cases one per day. Incubation sometimes began with the first egg and lasted 15–16 days. Only the female incubated, and she covered the eggs for about 75% of the daylight hours and throughout the night. Egg hatching was asynchronous, with the first young emerging early in the morning and the second not until later that same day.

Only the female brooded, and the rate declined until day 15 when essentially it stopped. Both parents fed the young by regurgitation, and the number of feedings per hour decreased slightly over the nestling period. It is thought that insects and finely masticated plant material formed the bulk of the nestling diet until about day 5 when mamane seeds became important. Helpers were found at one nest. Young developed slowly and did not leave the nest until 21–27 days old. It is believed that these prolonged nestling periods were able to evolve because of the (former) absence of ground predators. After fledging, young remained with their parents for at least 30 days.

Productivity was regulated by small clutch size, low population numbers and by the length of an individual nesting sequence (in that a pair could potentially raise only one brood each year). The primary reason for the endangered status of this bird appears to be the effect of habitat alteration upon a specialist, coupled with the fact that the small effective breeding population and low dispersability of the species may have resulted in decreased genetic fitness.

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