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Technical Reports 42 & 43
Breeding Ecology of Palila
and
'Amakihi Parasites

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42. A BREEDING ECOLOGY OF THE ENDANGERED PALILA (PSITTIROSTRA BAILLEUI) ON MAUNA KEA, HAWAI'I

43. A SURVEY SHOWING THE EFFECT OF ENVIRONMENT AND BEHAVIOR UPON PARASITE LEVELS IN THE HAWAI'I 'AMAKIHI (LOXOPS VIRENS) (AVES: DREPANIDIDAE)

September 1981

UNIVERSITY OF HAWAII AT MANOA

NATIONAL PARK SERVICE Contract No. CX 8000 7 0009

Contribution Number CPSU/UH 022/~~11~~ Final
022/12

A BREEDING ECOLOGY OF THE ENDANGERED PALILA (PSITTIROSTRA BAILLEUI) ON MAUNA KEA, HAWAI'I

ABSTRACT

The behavioral ecology and breeding biology of the endangered Palila (*Psittirostra bailleui*) was studied from 1971 to 1975. The most intensive breeding occurred from June to August, and coincided with peak production of māmane (*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 behaviors. 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 māmane 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 role 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 to 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 māmane seeds became important. Helpers were found at one nest. Young developed slowly and did not leave the nest until 21 to 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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INTRODUCTION

A plethora of plants and animals have been introduced by man into the Hawaiian Islands, and some of these have had a profound influence upon native organisms. Today, approximately 40% of the endemic Hawaiian bird species are thought to be extinct, and many of the survivors cling to a tenuous existence. There still remain, however, a few endemic strongholds, one being the ecosystem on the upper slopes of Mauna Kea, which provides habitat for an endangered Hawaiian honeycreeper, the Palila (Psittirostra bailleui).

Presently this ecosystem on Mauna Kea is, like so many other native Hawaiian forests, threatened. Habitat degradation has been extensive, primarily because of overbrowsing by introduced feral sheep, and little work has been carried out concerning the effects of habitat alteration on endemic organisms. Here was an opportunity to provide some of the needed answers concerning the relationships of the Palila with its environment. With this in mind a study of its breeding ecology with the following objectives as guidelines was undertaken:

1. To define parameters of the environment (climate, forest composition, phenology, and productivity of major tree species) and understand how they relate to the biology of the birds in terms of time of breeding season and population regulation;

2. To define the breeding biology of the Palila;

3. To determine general patterns of population regulation.

MATERIALS AND METHODS

From late 1970 through 1975 I spent 757 days on Mauna Kea, with approximately 6100 observational hours; during the last three years observations were made in every month. Study sites were established at 1980, 2130, and 2290 m in the Ka'ohe and Mauna Kea Game Management Areas at Pu'u Lā'au (Fig. 1). Adult birds were captured in mist nets and marked with U. S. Fish and Wildlife Service metal and colored plastic bands. Nestlings were weighed daily; feather tracts and physical development were described from photographs. Observations made in the field (especially at nests) included data on incubation rhythm, brooding rates, feeding of young, fledging of young, nest sanitation, courtship behavior and displays, and vocalizations.

Nest measurements included nest height (distance from ground to nest base), nest-tree height and species, circumference at breast height (CBH) of nest tree (1.4 m from ground), distance of nest from axis of trunk to end of branch, nest placement within the tree (terminal fork--limbs that formed the most distant group of stems from the trunk in the topmost 20% of canopy; lateral fork--end clusters of limbs in remaining canopy; branch--any horizontal or vertical limb within the canopy cover), nest dimensions (nest height and width, bowl depth and diameter, rim thickness), and nest weight. The long and short axis of each egg was measured, and egg shape index was calculated on the basis of the following:

$$\text{Egg Shape Index} = \frac{\text{lesser egg diameter}}{\text{greater egg diameter}} \times 100.$$

Annual productivity was calculated indirectly from clutch size, breeding success, length of nest cycle, and length of breeding season by the equation:

$$\text{Productivity} = \frac{C \cdot B \cdot S}{N}$$

where C = clutch size, B = length of breeding season in days, S = breeding success (proportion of eggs laid that fledge young), and N = length of nest cycle in days. Length of the breeding season was considered the average number of days per year when active nests were found (160 days). Length of the nest cycle was:

$$N = b + l + y + n + f$$

where b = nest building interval (18 days), l = number of days for egg laying (2 days), y = incubation period (16 days), n = nestling period (24.8 days), and f = fledgling period (30+ days). It took about 91 days for the Palila to complete one successful nest cycle. To determine the number of young produced per unit area of forest, the following formula was used:

$$T = P \,.\, D$$

where P = relative productivity and D = density of breeding birds. This was then divided in half to account for pairs and modified according to the approximate percentages of floaters in the population with the following:

$$D = \frac{d \cdot z}{2}$$

where d = observed population density and z = percentage of population not floating, which in the Palila is approximately 0.8.

Weather data were collected at the 2290 m study site. Temperature was recorded with two maximum-minimum thermometers, one under the tree canopy and one in the open. Data obtained from the National Weather Service were used for monthly rainfall analysis. Wind direction and percent cloud cover were noted daily in field records. Phenological parameters of the flora are reported elsewhere (van Riper 1980), as are results of predation (van Riper 1978).

RESULTS

I. Historical Overview

The Palila was first collected in the Kona District of Hawai'i by Bailleu in 1876, and was described scientifically by Oustalet (1877), who named the species Loxioides bailleui. Amadon (1950) revised the classification of the Hawaiian honeycreepers and placed the bird in the subfamily Psittirostrinae as one of the six species of the finch-billed genus Psittirostra.

Historically the range of the Palila included only the māmane (Sophora chrysophylla (Salisb.) Seem.) and māmane-naio (Myoporum sandwicense Gray) ecosystems of Mauna Kea, Hualālai, and the southwestern slope of Mauna Loa. It has never been reported from the forest on the eastern slope of Mauna Loa. The bird was apparently limited to the upper forest regions as Perkins (1903) found it only from 1220 m to 1830 m on Hualālai. Wilson and Evans (1890-1899) likewise reported it as being confined to upland districts of Hualālai and Mauna Kea. This range has been greatly reduced since the turn of the century, and all available information today indicates that the Palila is found only in the māmane-naio ecosystem on parts of Mauna Kea. A recent census estimated the present population to be from 1500 to 1700 individuals (van Riper et al. 1978). The Palila is limited to only 10% (5560 ha) of its former range at densities of approximately 37 birds per 100 ha.

II. Population Parameters

Population Structure.--Palila were studied mainly at 2290 m, that area with the highest density of birds (van Riper et al. 1978). This population consisted of adults and juveniles moving in small flocks during the nonbreeding season (October to April), and breeding pairs around māmane pod concentrations from May to September. Fifteen adults and 10 nestlings were color banded (Table 1).

Adult Palila could be sexed by plumage dimorphism, but it was often difficult to differentiate between immature and female birds except by the presence or absence of a brood patch. There were more males than females in the population. At one nest in 1974, four unmated males were present and singing on the periphery of the territory throughout the entire nest-building period. One of the males was banded, and also remained unmated the following season. A surplus of nonbreeding birds is also suggested by the presence of helpers at one nest. Amadon (1950), in his sex-ratio analysis of museum specimens, likewise found a disparity of male to female birds.

<u>Length of the Breeding Season</u>.--Active Palila nests were recorded from March through September with young fledging from May to September; the most intense breeding occurred from June to August (Appendix I). Renesting was never observed but it may occur especially if the first nest is unsuccessful. A possible attempt was made by one pair, but they were not color-banded until the second nest had been started. A nesting cycle takes at least 90 days, which may limit the birds to only one successful brood each year.

<u>Patterns of Molt</u>.--Molting patterns were examined for all captured individuals and observations were made of museum specimens. Amadon (1950) noted that the molting period for the Palila and other species of <u>Psittirostra</u> was usually later than for other members of the subfamily Psittirostrinae. Molt occurred from late May until early December (Fig. 2), and, of three birds captured while nesting, two were in molt. Baldwin (1953) showed that drepanidids have longer periods of molt than North American birds. These observations substantiate and extend his limits.

<u>Weight Patterns</u>.--When male and female Palila were viewed together in the field, the latter appeared smaller, although this was not reflected in weight. Live weights were recorded for eight adult birds, giving a mean of 39.1 g for males and 40.0 g for females. The higher female weight may be due in part to one individual captured in July 1973 which weighed 45.5 g; another netted in March 1974 weighing 37.4 g; and one captured in August 1974 which weighed 37.1 g. Males weighed 43.5, 35.5, 37.5, 38.6, and 40.6 g.

<u>Feeding Habits</u>.--Munro (1944) reported that Palila fed on naio fruit when they were green and still soft. In this study they ate only ripe white fruit, that portion eaten being the soft exterior (possibly for moisture content) and the rest discarded. However, the importance of māmane in the Palila diet cannot be overemphasized. Wilson and Evans (1890-1899), Perkins (1893), Rothschild (1893-1900), Munro (1944), and Berger (1972) all reported a predilection for green seed pods of the māmane tree. Berger (1972) also reported that the Palila ate flowers and dry, brown seed pods. Palmer (in Rothschild 1893-1900: 198) saw it once eat a green 'a'aka (naio) seed, as well as various berries. In addition to seeds and flowers, the bird consumes caterpillars and other larvae (Perkins 1903: 436). The Palila diet was monitored through visual observations over a two-year period; māmane was the major food (particularly green pods and flowers) with the bird also taking naio fruits and insects (Table 2).

The technique employed in feeding on māmane pods was predictable. The bird would rip open the pod and bite the seeds out. The seeds were bitten in half and since they were not mature, it was unlikely seeds were dispersed in this manner. Māmane seed dispersal was probably accomplished by the bird carrying a pod to an adjacent area, eating part, and then dropping the rest of the seeds onto the ground, a frequently observed occurrence.

Although there were many green pods on a tree apparently not all were potential food. Because the bird is fairly large, it was unable to obtain pods that hung from smaller branches. Pearson (1971) found in Central America that the larger body size of a bird excluded several species from the denser foliage and smaller branches. It may be that tree size influenced Palila distribution as they were found in greater numbers at the 2290 m study area where māmane trees were significantly larger (van Riper 1975; van Riper et al. 1978).

Palila usually fed on insects by slowly gleaning over a tree trunk or by gnawing at a branch and working off the outer bark. On one occasion a bird tried to hawk an insect, but it missed by a considerable distance. Insect larvae may also have been obtained from infected māmane pods. Large numbers of the family Tortricidae (three species of the genus Adenonema) were observed in young seeds. In analysis of 385 pods, 7% of the seeds were infected with these larvae.

Vocalizations.--The Palila had two songs: a primary song given by the male and extended subsong given by either sex. There were a variety of calls and location notes given during foraging, courtship interactions, and distress situations. There was no flying predator call. Singing gradually decreased over the breeding cycle, and birds sang more during early morning hours and just before noon (Fig. 3). Weather had a marked influence on the frequency of vocalization. Whenever a region became blanketed in fog, calling would increase. Calling continued during light rains at a slightly higher than normal rate, but if precipitation increased further almost all calling ceased. Wind, although infrequent, seemed to cause a reduction in the amount of calling.

III. Breeding Biology

Courtship Behavior and Displays.--Pairing probably occurred prior to the breeding season. A low advertising flight, given by the male, was characterized by a slow fluttering of wings followed with a short glide. Sexual chasing was either a low rapid straight-line chase or high rapid flight. Chases occurred mainly during the early breeding season (April to May) but one such flight was observed in December. Chasing probably was important as a means of synchronizing the sexual cycle and bringing birds into breeding condition.

Palila frequently courtship fed, with the sequence initiated by either sex. This behavior usually involved vocalizations and wing quivering by the female after which the male fed her. In the nesting cycle courtship feeding was most common during incubation (Table 3). From late incubation to the end of the nesting cycle, courtship feeding became more ritualized and was often replaced by mutual billing where the birds touched bills from side to side but no food was exchanged.

Territory.--The territory of the Palila is best described as a "mate defended area" because males excluded all conspecifics from near the female especially early in the cycle. Defense included song and direct chase (rarely claw-to-claw combat), with the former more important during initial establishment and chase assuming a greater role after nest building. For example, at nest 5-73 on the third day of nest building, the male followed and chased other Palila from the vicinity while the female collected material. From 0730 to 0930 hours the female made 19 trips for nesting material and was accompanied 13 times by the male, who chased intruders on nine occasions. As the nesting cycle progressed and incubation began, defense shifted to the area around the nest. Females chased other birds much less than males, and aggression was closer to the nest site (Fig. 4). These territories, or the area bounded by the outermost points of aggression with neighboring Palila, included 3900 m^2 and 600 m^2 at nest 5-73 and 1-73, respectively. Only three cases of interspecific aggression were observed, all at one nest on the day of hatching; species chased were the Japanese White-eye (*Zosterops japonicus*), 'Amakihi (*Loxops virens*), and 'Elepaio (*Chasiempis sandwichensis*).

When young fledged, the territory was abandoned and birds joined small feeding flocks which centered activity around a feeding area rather than a nest site. Little aggression was noted in these feeding congregations. Palila would return to the same area to nest year after year, and one banded female came back for three consecutive seasons. During the nonbreeding season birds appeared to follow shifts in māmane pod concentrations, and one bird, color-banded as an adult, was sighted 2.5 km away in a pod concentration near Pu'u O Kauha. There were insufficient color-banded birds to say if some stayed in an area throughout the year.

The Nest.--The first, and prior to this study only other active Palila nest, was found by Berger (1970). Of the 26 active nests found from 1972 through 1975, all but three were in māmane trees. Larger māmane were preferred, as the mean height of nest trees (6.9 m) and CBH (83.4 cm) were both nearing 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. 5). Nest placement was predominantly on horizontal branches (15 nests) while four nests were found in terminal and seven in lateral forks. Nests located in terminal forks were all on solid main stems where at least three branches formed a cup in which the nest was built. As a rule nests were placed in from the end of the limb. The average distance of nest placement from the trunk was 2.7 m and from the end of the branch, 105 cm.

Nest site selection was observed on one occasion only, 8 July 1973. A banded female flew into a large māmane tree with a grass stem in her beak. She moved throughout the tree, came to a large fork and proceeded to wriggle her body into a crotch for some time, trying a number of different positions. On 9 July there was no material at the site, but on the morning of 11 July a few pieces of grass were present. By that afternoon much of the nest-base had been completed.

Twenty-seven hours of observation were made on 14 days of nest building at four different sites; most construction occurred during the morning hours. Length of nest building varied considerably; nest 1-72 took over 20 days to complete whereas nest 5-73 was finished in seven days.

Apparently male and female Palila took part in construction of the nest, but both birds were never observed building or at the nest at the same time. In one instance a male was on the nest molding the cup with his body as the female approached; when she reached the nest he left immediately. The female was responsible for a major portion of nest building, as she gathered the materials and built while the male only incorporated materials into the nest. Males helped only during very early nest building, until the bowl had been completed. 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 molding and reweaving grasses into the structure.

Nests usually had a base of large dead twigs. These twigs were collected from the nest tree, broken off and piled onto a fork or branch. If the nest was situated in a terminal fork, sticks were not used for a base. The bowl was composed of interwoven grasses (sometimes sheep wool; van Riper 1977) and lined with either lichens (Usnea spp.) or fine grasses and rootlets. Palila nests were impressive structures as the width of 26 nests averaged 14.7 cm (range = 9.6 - 18.8 cm) and total height was 7.7 cm (range = 4.6 - 9.6 cm). The bowl depth (mean = 3.9 cm; range = 2.5 - 5.3 cm) and bowl width (mean = 7.4 cm; range = 5.8 - 8.9 cm) were similar throughout the population. Rim thickness was the most variable measurement as it ranged from 1.5 to 6.9 cm and was dependent upon whether a nest contained a stick base. 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 at varying intervals after the nest appeared completed. For example, nest 1-72 was finished on 20 May and the first egg was not laid until 4 June. At nests 5-73 and 1-75, 1.5 and 2.0 days respectively elapsed between the end of construction and laying of the first egg. Eggs were laid early in the morning and in all cases (n = 12) one per day. At one nest the first egg was laid before 0745 and the second before 0800 hours the following day. At nest 5-73 the female laid the first egg at 0746 hours.

Clutch size of 11 nests was two eggs; at one nest apparently only one egg was laid. Palila are determinate layers; removal of the second egg of one clutch on the morning of laying did not result in any subsequent laying.

Eggs were oval and characterized by a whitish ground color with superimposed reddish-brown markings, usually forming a dense cap around the larger end. Eight eggs were measured; average length 25.0 mm and width 16.8 mm. The egg shape index was 67.1. Four eggs were weighed with a mean of 2.8 g (range = 2.6 - 3.0 g) and two shells averaged 0.2 g.

Incubation Period.--Incubation in the Palila probably commenced with the laying of the first egg. In two nests observed on the day that the first egg was laid, birds were present at the nest approximately 50% of the time (13.4 hours of observation). In one case it was a banded female, but at nest 1-72 apparently only the unbanded male attended the nest; length of attentive periods were protracted at this nest, as he remained for 101, 73, and 55 minutes in three different sitting periods. It was possible, therefore, that some heat may have been applied to the first egg of a clutch. Incubation periods at two other nests were 16 days 6 hours and 15 days 22 hours; a third was between 15 and 16 days.

Only females incubated the eggs and covered them for an average of over 75% of the daylight hours (Fig. 6). Turning of the eggs averaged 1.6 turns per hour (Fig. 7). Eggs were incubated throughout the night as probes in the nest lining revealed constant heat in the nest.

Nestling Period.--Nestling periods of 21, 23, 24, and 27 days were recorded. The first egg started hatching either late at night or early in the morning, and the second not before the middle of that day. At nest 1-72, when the female left the nest at 0837 hours, one young had hatched and was dry, while the other was still sitting in half of its shell with the other half over its head. At nest 4-74 one young had hatched by 0930 hours and the other egg was pipped. This same pattern held at nest 7-74 (only one hatched by 0900) and at 1-75 where one of two eggs had hatched at 1110 hours.

Parental Care of the Young.--Only the female brooded and time on the nest declined steadily throughout the nestling period until day 15 when brooding essentially stopped (Fig. 8). If a heavy rain occurred during brooding, the female stayed on the nest. At night the nest was covered until at least day 18.

After hatching the female carried egg shells from the nest. In one instance she dropped the shell over the edge. At nest 1-75, where only one egg hatched the shell was soft and pliable. In this case small pieces of shell remained in the nest and eventually were worked into the bottom. It may be that the stimulus of sharp edges releases egg shell disposal, and in this case the soft shell did not elicit this response.

Nestling feeding rates, as measured by the number of trips to the nest by adults, showed that female Palila fed the young more than males (Fig. 9). The number of feedings decreased slightly over the nestling period (regression: $Y = 2.57 - 0.034 X$). On day 16 of the nestling period at nest 4-74, a feral cat ate the brooding female. The male, over the next 10 days, increased his feeding rate presumably to compensate for the absence of his mate (Fig. 9). This was the only nest where helpers were observed (Skutch 1961). At least two helpers made five trips to the nest with food from days 16 to 26. The feedings of the helpers were quite irregular, and when they occurred, often followed shortly after a feeding of the parent male.

Although young were not sacrificed for crop analysis, I was able to gather some information on the food they were fed, as the color and shape of items could be discerned through the skin of the neck. In early nest life (day 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 from a māmane tree, and after repeated regurgitation fed them to the young. I was unable to conclusively prove insects were fed during the first few days of the nestling period; however, adult Palila did take more insects during the breeding season than during the rest of the year (Table 2). This suggested insects were probably fed to the young (see also Perkins 1903). On day 2 (one case) and 3 (three cases), māmane 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, but there was also a viscous white milky substance fed to the young.

The most striking feature of a used Palila nest was an accumulation of fecal material (Fig. 10). Both parents removed fecal 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. Rate of fecal sac removal increased from 0.2 per hour at day 2 to a peak removal rate of 4.6 per hour 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. I observed a female eating a sac on day 14, but by this time the buildup on the nest rim was tremendous. By day 22 the nest, limbs of the tree, and ground below were covered with dried fecal material. The odor from this accumulation was rather pungent.

Nestling Development.--At hatching, young were completely helpless and pinkish-orange in color with small areas of black nestling down in the pterylae. Eye slits, grasping reflex, fear response, ability to stand, beak color, preening, and flapping of wings all appeared at different times and developed gradually (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. 11). Young probably fledged at weights slightly less than those of adults. Feather development was slow in the young Palila with tracts beginning to open about day 12 to 14 (Table 5).

Fledging of Young.--Before fledging, young repeatedly moved from the nest to nearby branches and returned. Apparently fledging in the Palila constitutes leaving the nest tree and not just departure from the nest. Young either fledged separately or as a group. When asynchronous fledging occurred, one parent accompanied the fledgling while the mate remained at the nest site. This was the case at nest 1-72 where the first young fledged at day 21 and the male accompanied it. Neither bird was observed in the vicinity thereafter. The female remained with the other nestling and it fledged on day 24. During this three-day period the female repeatedly coaxed the young off the nest with food items.

When Palila nestlings fledged they could fly well, and at nest 4-74 both young flew to a tree over 20 m from the nest. Young never returned to the nest once they had fledged. The first week of the fledgling period was characterized by a sedentary existence. Fledglings would remain in a single tree, sometimes for a 2-day period, and adults would forage out from that point returning to the tree only for feedings. Young, when not being fed, spent most of their time preening and sleeping; often they would bite at leaves and flowers. Feeding of fledglings was observed for three days; the rate was much the same as in the last days of the nestling period. In one case the single young was fed by a male 1.2 times per hour and in another, once in 2 hours of observation. After leaving the nest area, young remained with the parents for an extended time period, as they moved in small postbreeding flocks. Banded young were observed with their parents over 30 days after fledging, about 100 m from the nest site.

Reproductive Success.--Little can be said about adult mortality because of the small number of banded birds, but all indications are that it is low. One female banded as an adult was observed over a 2.5 year period; therefore, some birds will live to be at least 4 years of age. Of 11 mature birds banded in 1972-1973, all but three were relocated at least one year later, yielding an absolute maximum turnover rate of 27% in the banded population.

From 1972 through 1975, reproductive success (number of eggs laid that fledged young) was 52.2% (Table 6). 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 either due to embryonic death or infertility (17% of all eggs not deserted), desertion, unexplained nestling death, weather, or poor nest construction. Predation was observed at only one nest, but was probably a greater factor at Pu'u Lā'au than these data indicate. Because the 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 nests observed.

DISCUSSION AND CONCLUSIONS

Many different mechanisms have been shown to influence population productivity, but as in many areas of ecology it is difficult to discern between cause and effect. In the Palila population at Pu'u Lā'au, length of the breeding season, clutch size, hatching sequence, nestling growth, and mortality, all gave evidence of regulating productivity. No single mechanism was alone responsible, but all acted together in an intricate system of checks and balances.

<u>Timing and Length of Major Breeding Effort</u>.--The Palila breeding season was protracted, lasting 6 to 8 months, but most birds bred within a 2 to 3 month seasonal span. The period of most intense breeding was June to August. It is still uncertain what initiates the breeding season. In most temperate passerines photoperiod appears to be the primary factor, but Farner and 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. Lewis and Orcutt (1971) listed such modifiers as social behavior, ontogenetic factors, experience, resource availability, temperature, and various geophysical and ecological factors. These modifiers appear even more important in nontemperate passerines as Skutch (1950) could find no single stimulus that explained the initiation of breeding in tropical and subtropical species.

There were a number of environmental factors at Pu'u Lā'au which might have acted as a timing mechanism for breeding season initiation. Rains after the dry summer period may have acted to initiate breeding as Keast (1959) found that certain Australian desert birds can breed at any time of the year, but do so only after rains. Greening of vegetation could also have been a stimulus as Lehrman (1964) showed that this was true for weaver finches. The effects of photoperiod (both direct and indirect) cannot be ruled out, and age and experience may contribute to the asynchrony of individual pairs (Perrins 1965, 1970). It may well be that the Palila depends both upon exogenous and endogenous timing mechanisms to set an appropriate time for reproduction.

Each of the above hypotheses needs to be tested in controlled laboratory situations. But whatever the immediate stimulus that influences the initiation of breeding, ultimately it appears to be the timing of māmane phenophases. The major breeding effort was spaced into that time of year when māmane bore pods (Fig. 12). Not only did the breeding periods seem adjusted to optimal resource availability, but the birds appeared able to make fine adjustments to yearly differentiation 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 came much later. Lack (1954), Harris (1969), and Perrins (1970) all argued that availability of food acted as the ultimate determinant governing initiation of the breeding season. Tordoff and Dawson (1965) have shown that food acts as the proximal timing mechanism in the breeding cycle of the Red Crossbill (Loxia curvirostra) as these birds nested only when a good seed crop was produced by conifers.

Small concentrations of nesting pairs are separatd by long distances in which no birds were nesting. Because of relatively low Palila numbers, it may be that the social group is the exteroceptive factor important in the timing and integration of reproduction. Most work in this area has been done with seabirds (Darling 1938; Coulson & White 1960; Schreiber & Ashmole 1970), but recently it has been shown important in other avian groups as well (Brockway 1964; Hall 1970; Lewis & Orcutt 1971).

Mechanisms that terminate breeding are poorly understood. The selective factors that have been effective in shaping the termination in Hawai'i are, no doubt, less intense than the postnuptial demands of temperate species that must undergo energetically demanding autumnal migration. Payne (1972) pointed out that periodic molt of birds usually occurs at the end of the breeding season after reproductive activities have been completed. In the Palila there was a large period of breeding-molt overlap (Fig. 12). Greater than 25% of skins and birds examined were in molt during the breeding season, and two of three birds captured while breeding were in molt; one female could hardly fly due to worn and molting feathers. This is unusual in passerines. In African birds Payne (1969) and Moreau (1936) reported only a 3.9 and 4.2% overlap, respectively; Foster (1975) documented a 10% breeding-molt overlap in birds from Costa Rica.

This raises the question: Why does the Palila initiate molt at the height of the breeding season? Possibly because the most abundant food supply was later in the year, molt had been pushed back as far as it was physiologically capable in the species, and eventually the factors which served to stimulate molt (possibly photoperiod) overrode the inhibiting effects of gonadal hormones. Ligon and White (1974) found this true when years of differing food supply and molt were compared in the Piñon Jay, Gymnorhinus cyanocephalus. They also inferred that gonadal activity decreased somewhat because of molt initiation, and this may at times cut short the Palila breeding season. It cannot be ignored, however, that breeding may be timed in such a manner that the most abundant food supply is made available at that time of year when both Palila adults and juveniles are present.

The length of the breeding season as a factor in population productivity becomes important when one considers that a Palila 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. Furthermore, if the season is terminated early due to lack of food or for some other reason, the number of young produced could be severely affected.

Nestling Growth and Mortality.--The rate at which birds grow is an important ecological parameter of productivity regulation, because it determines the nestling period and hence the time young are exposed to possible predation and adverse climatic conditions (Maher 1973). Ricklefs (1969a) proposed a model whereby natural selection would maximize growth rates of altricial birds. He indicated that 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.

Palila nestlings normally took 22 to 23 days to fledge. These are fairly long periods for open-nesting passerine species (Skutch 1945; Ricklefs 1968, 1969b). To compare these growth periods to those of other altricial birds, data were analyzed 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 comparison. The growth rate (K) for Palila (0.321) was less than all Passeriformes analyzed by Ricklefs (1968), except the Formicariidae, Tyrannidae, and Corvidae; furthermore, it was also lower than the average of 0.535 for 21 fringillids, and the average (0.462) reported by Maher (1973) for seven groundnesting passerines. This shows that the Palila grows more slowly than most passerines measured to date, and are therefore relegated to the nest for an extended time period.

In Hawai'i prolonged nestling periods probably evolved in the former absence of ground predators. With minimum nestling mortality from predation, there would have been little directional selection against a later fledging date. Also adult Palila exhibited a decreased feeding rate over the nestling period (Fig. 9). This is unusual for passerines, but perhaps with the extended nestling period, physiological adjustments were made in the young, and food requirements were spread out over a longer time period.

Reproductive Success.--Reproductive success, the number of eggs laid that fledged young, for Palila (52.2%) was comparable to that found in other open-nesting passerine species (Nice 1957). However, reproductive success can be a misleading criterion when analyzing 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 number of broods raised as well as clutch size. Recently, population biologists have treated this aspect of avian demography in great detail (Cody 1971; Ricklefs 1973; Ricklefs & Bloom 1977).

The productivity per unit area for the Palila was determined as shown below:

Relative Productivity	Breeding Pairs/100 ha (Density)	Total Productivity/100 ha
1.8	14.8	26.1

Total production was quite low and was, of course, due in a large part to the already low numbers of breeding birds. However, another factor that cannot be ignored was the length of the breeding season in comparison to the length of a nesting cycle: Palila can raise only one set of young in a season.

Ricklefs and Bloom (1977) examined productivity in birds from diverse habitats, and found that in a dry montane subtropical area of Ecuador (a habitat similar to Pu'u Lā'au) the most important variables of productivity were season length and clutch size. The similarity of the Palila data with Ricklef and Bloom's might indicate that in savanna ecosystems throughout subtropical regions, the two most important factors regulating productivity in small passerine birds are season length and clutch size.

Conclusions on Abundance.--In studying the Palila one must eventually confront the question of why it is rare and today maintains such a precarious existence. The reasons are: first, and probably most important, the ecological role of the species (a specialist) and the effects habitat alteration and reduction have on population numbers; and secondly, the small effective breeding population and low dispersibility of the bird may have resulted in genetic problems.

The Palila has evolved into a rather specialized niche, becoming almost totally reliant upon the māmane-naio ecosystem. Pianka (1974: 188) argued that highly specialized organisms usually had narrow tolerance limits along one or more of their niche dimensions. Often these specialists had very specific habitat requirements and, as a result, were not very abundant. In contrast, organisms with broad tolerances were typically more generalized, had more flexible habitat requirements, and were usually much more common. 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 its ecological niche in a way predetermined low Palila abundance.

This immediately raises the question: Why did the Palila become specialized when it involved becoming less abundant? An insight to this dilemma was provided by Hutchinson (1957) when he defined the "fundamental niche" and elegantly showed that specialized individuals were more efficient on their own ground. Problems, therefore, probably did not begin for the Palila until man and feral mammals had significantly altered their habitat. Since that time (ca. 1850) there has been a steady decline in māmane forests on Hawai'i (Warner 1960). With the reduction of this habitat has come a parallel reduction of the Palila. The bird presently occupies only 10% of its former range (van Riper et al. 1978). Giffin (1976) showed that this area is diminishing rapidly. Furthermore, as large māmane trees are preferred by the Palila for nesting and feeding, what appears at first glance to be acceptable habitat might in all reality not be so to the birds (see discussion by Whitmore 1977). Thus the already small realized niche of the Palila has become even more restricted.

Fisher's (1958) model of adaptation and deterioration of the environment showed that a random change of a given magnitude was more likely to improve the level of adaptation of the generalist than the specialist. Therefore the highly specialized Palila, with its narrow tolerance limits, would suffer greater losses in fitness due to a unit of environmental destruction.

Evidence today indicates approximately 1600 birds remain (van Riper et al. 1978), and the effective breeding population (McClearn & DeFries 1973: 228) is in all probability much less. Support comes from sightings of bachelor flocks throughout the breeding season, and this overabundance of males may in fact be an inhibiting factor to successful reproduction. For example, at nest 5-73 the continual intrusion of unmated male X-R may have contributed to nest desertion.

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). This may have happened to the extant Palila population as there is a high degree of infertility. Of the 18 eggs that were incubated to term, 17% were either infertile or died as an embryo. In studies of other passerines (Nice 1937; 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 the Palila today, as it may have interrupted (or reduced the rapidity of) gene diffusion throughout the population. Baldwin (1953) suggested that dispersal rates were unaccountably low in Hawaiian birds, and historical data of the Palila 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 that area. Had dispersal between the two habitats been continuous, the Mauna Loa colony might not have disappeared.

SUMMARY

The behavioral ecology and breeding biology of the endangered Palila (Psittirostra bailleui), a member of the endemic Hawaiian honeycreepers (Drepanididae), was studied from 1971 to 1975. Birds were color-banded and aspects of the environment monitored. The Palila population on Mauna Kea consisted of resident adults that each year returned to the same areas to breed. There was an excess of unmated males. Most intense breeding occurred from June to August, and coincided with peak production of māmane seeds, the birds' major food source. The Palila was able to make adjustments in its breeding to compensate for yearly differentiation in the timing and abundance of these food supplies.

Sexual chasing and courtship feeding were the most frequently encountered prenesting behaviors. Singing was also important and vocalizations are described. Territory was a mate defended area which later in the nesting sequence shifted to the nest site. A total of 26 nests was found and most were placed on larger branches of the māmane tree. Nest construction occurred primarily in the morning hours, and in one case lasted 20 days. Both sexes took part in nest construction, albeit the male role 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, and eggs were laid early in the morning and in all cases one per day. Incubation sometimes began with the first egg and lasted between 15 and 16 days. Only the female incubated, and she covered the eggs for about 75% of the daylight hours and throughout the night. Turning of the eggs averaged 1.6 turns per hour. 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. However, 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 larger māmane seeds became important. Helpers were found at one nest; this is the first recorded instance in the Drepanididae. Fecal material accumulated on the nest rim of all Palila nests. Young developed slowly and did not leave the nest until 21 to 27 days of age. It is believed that these prolonged nestling periods evolved because of the former absence of ground predators. After fledging young remained with their parents for at least 30 days.

Adult mortality was quite low. Reproductive success was 52%; however, infertility of eggs incubated to term (17%) was quite high. Palila 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, and that the small effective breeding population and low dispersibility of the species may have caused genetic problems.

ACKNOWLEDGMENTS

This project began while I was a teacher at The Hawaii Preparatory Academy, and for the use of their facilities and accommodating my sometime erratic hours, I am grateful. To my former students at this school, in particular R. L. Warner, I am grateful for many hours of help during the summers of 1971 and 1972.

While in the field, members of the Hawaii Division of Fish and Game were at various times of assistance: to J. Giffin for his help on the mountain, E. Kosaka for his hospitality at Pōhakuloa, and C. Branco and H. Fergerstrom for help moving camp, I am indebted. Many of the permits needed for this study could not have been obtained without the guidance and support of the U. S. Fish and Wildlife Service and Hawaii Division of Fish and Game. For places of solace while off the mountain I will always be grateful to R. and S. Johnston, S. Landsberg, and J. Spencer. To members of the International Biological Program team at Hawaii Volcanoes National Park, J. Jacobi, T. Parman, R. Warshauer, and especially the late H. E. Smith, I am indebted for assistance. In addition, my warmest appreciation to I. and J. Q. Casey for their continued support and gracious hospitality during my stays in Honolulu.

For access to unpublished information I thank P. H. Baldwin, A. J. Berger, T. L. C. Casey, J. Sincock, and J. M. Scott. J. Beardsley kindly identified insects, T. Nakata assisted with some of the illustrations, J. Q. Casey helped gather field data, and D. Weiner gave clerical assistance. My wife, Sandra, has been invaluable in many ways, particularly in reading and typing the numerous drafts of this manuscript and making many suggestions, most of which I accepted.

This work has been supported by a number of organizations, to which I express my sincere thanks: The Frank M. Chapman Memorial Fund of the American Museum of Natural History; The Hawaii Audubon Society; The Hawaii Volcanoes National Park (Contract No. CX 8300 5 0035); The International Council for Bird Preservation; The McInerny Foundation; a National Science Foundation grant to A. J. Berger and D. Mueller-Dombois; and The World Wildlife Fund of Morges, Switzerland, with a grant extension (US-35) from the U. S. Section. During the final stages of preparation I was supported by Contract No. CX 8000 7 0009 from the U. S. Department of the Interior National Park Service to the Cooperative National Park Resources Studies Unit at the University of Hawaii at Manoa. The following people were indispensible in procurement of these fundings: W. King; U. Kojima; W. and M. Mull; D. Reeser; C. W. Smith; and to each many thanks.

This work was done as partial fulfillment for the degree of Doctor of Philosophy from the University of Hawaii. I am pleased to thank the members of my doctoral committee, Professors A. J. Berger, R. Kinzie III, C. Lamoureux, A. Miyahara, and A. Popper, for their critical reading of my work and their help in many other ways. H. G. Baker, T. L. C. Casey, A. Kamil, R. Raikow, C. J. and C. P. Ralph, R. Scowcroft, and J. Sincock made useful comments on some sections. Finally, I thank A. J. Berger, J. Emlen, and J. M. Scott for reading the entire manuscript and for offering valuable suggestions for its improvement.

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TABLE 1. Capture and subsequent sightings of marked Palila on Mauna Kea, Hawai'i.

Date Captured	Sex	Subsequent Sightings Within the 2290 m Study
22 Dec 1972	Male	July 1973
4 Jan 1973	Unknown	---
5 Jan 1973	Male	June 1974
7 Jan 1973	Male	June, July 1974; April, June, July 1975
4 June 1973	Male	August 1974
4 June 1973	Female	March 1974
20 June 1973	Immature	July 1973
12 July 1973	Male	---
13 July 1973	Female	February, July 1974; June 1975
13 July 1973	Male	---
14 July 1973	Immature	July 1973; March, April, October 1974
26 March 1974	Female	May 1974
16 July 1974	Immature	July 1975
25 July 1974	Male	August 1974
19 Aug 1974	Female	---

TABLE 2. Types of food Palila were observed eating during 152 days of observation on Mauna Kea, Hawai'i.

Observation Period	Number of Days Observed	Times* Recorded Feeding	Percent of Food type Taken per Month					
			Māmane			Naio		
			Rods	Flower	Leaves	Fruit	Insects	Other
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

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

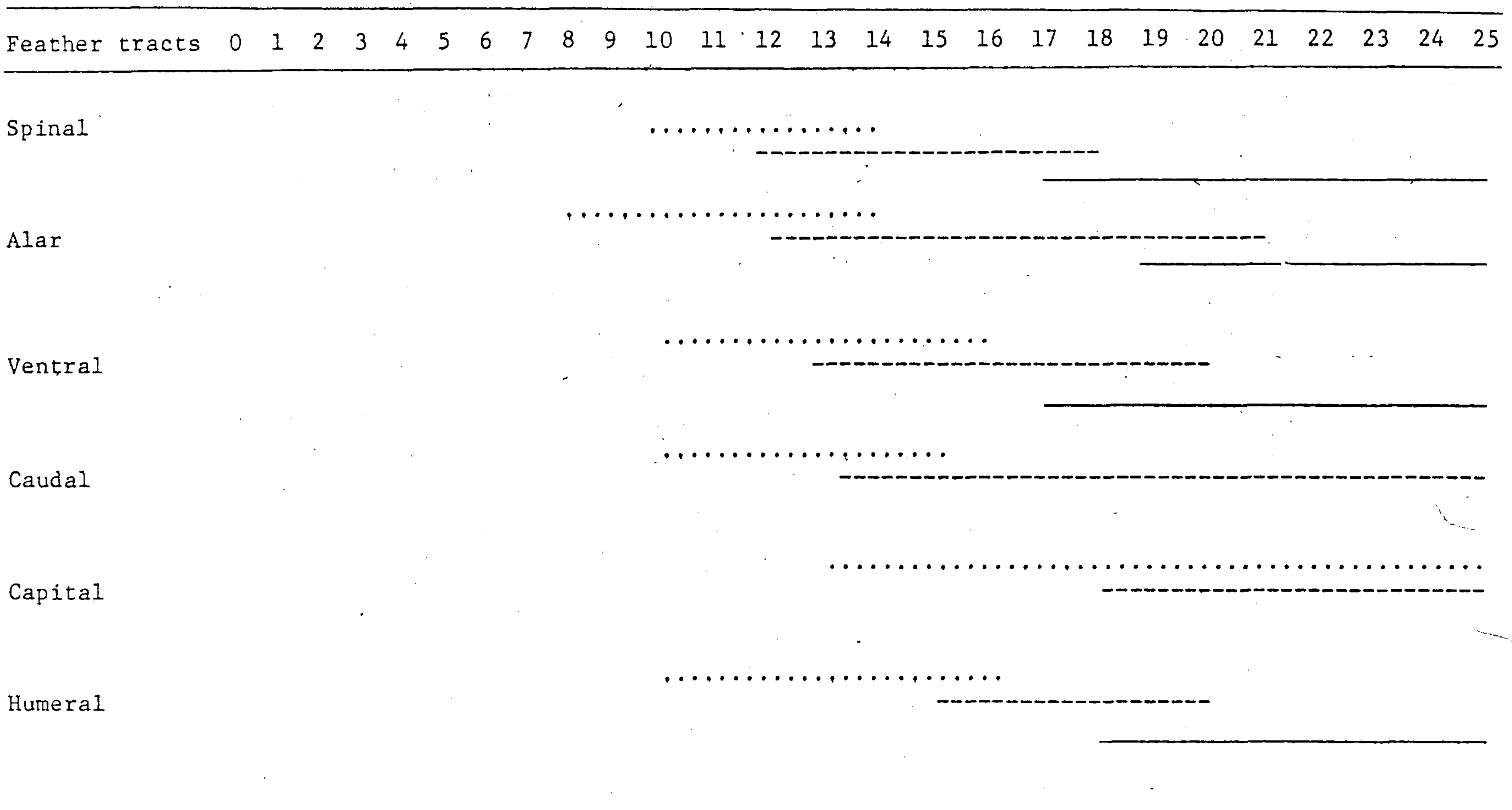
TABLE 3. Palila courtship feeding rates throughout the nesting cycle.

Days of Cycle		Total Hours Observed	Total No. of Courtship Feedings	No. of Courtship Feedings/hr
(Clutch Completed)				
0 - 3	Incubation Period	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
(Hatching)				
16 - 19	Nestling Period	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)				

TABLE 4. 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	cowering in nest	
Ability to stand	unable to stand	standing well	
Color of beak	yellow	orange	black
Preening	none	some	vigorous
Flapping of wings	no flapping of wings	flapping	

TABLE 5. Development of feather tracts in Palila nestlings*.



* .... = pin feathers; --- = unsheathing of feathers; —— = feathers completely unsheathed.

TABLE 6. Summary of Palila nest histories from 1971 to 1975 on Mauna Kea, Hawai'i.*

Total Number of Nests	26
Nests with Complete Records	16
Total Number of Complete Clutches	12
Total Eggs Laid	23
Total Eggs Hatched	15
Total Young Fledged	12
Hatching Success	65.2%
Nestling Success	80.0%
Reproductive Success	52.2%

* See Appendix I for complete nest histories.

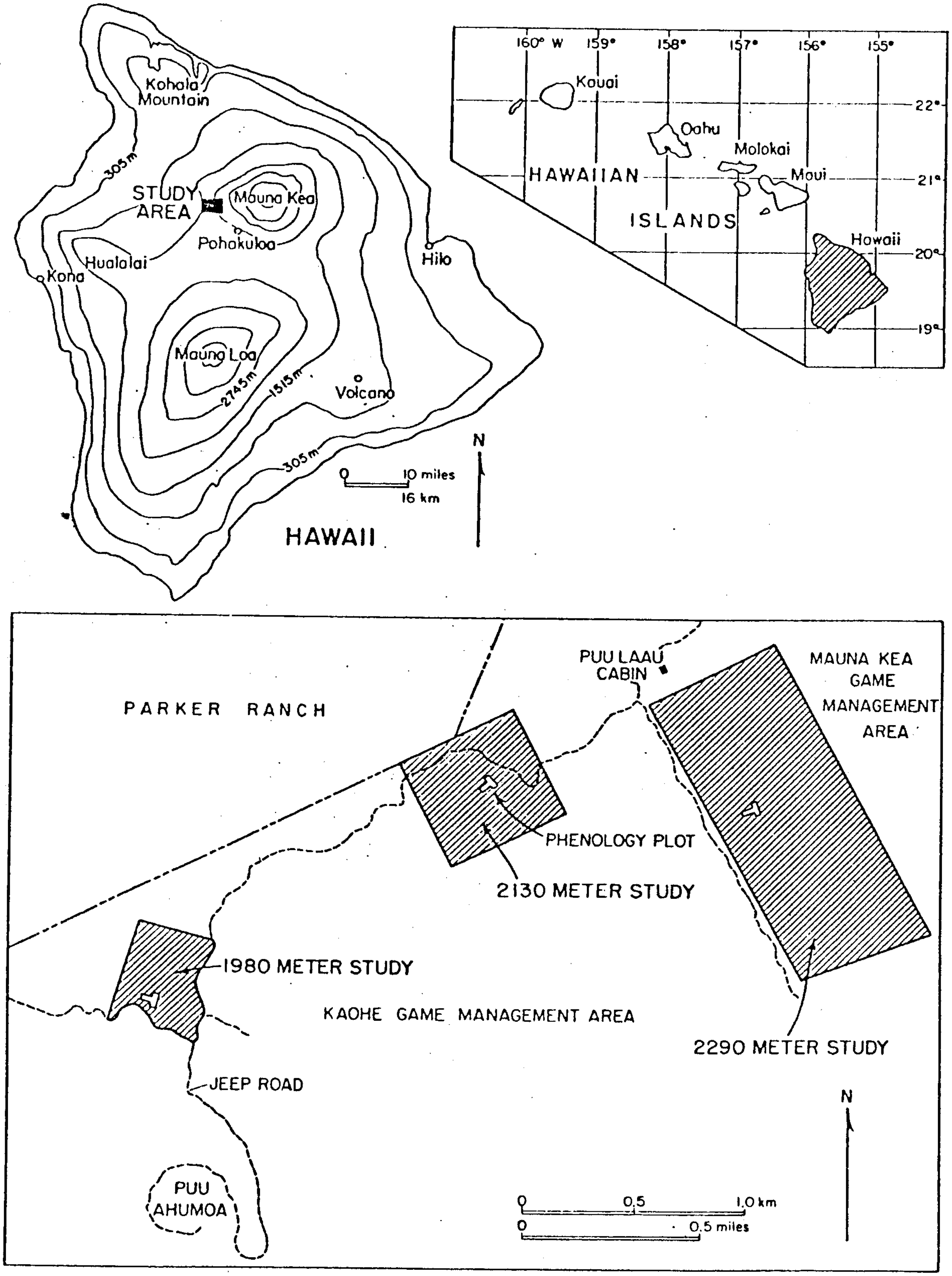


FIGURE 1. The island of Hawai'i showing study sites on Mauna Kea.

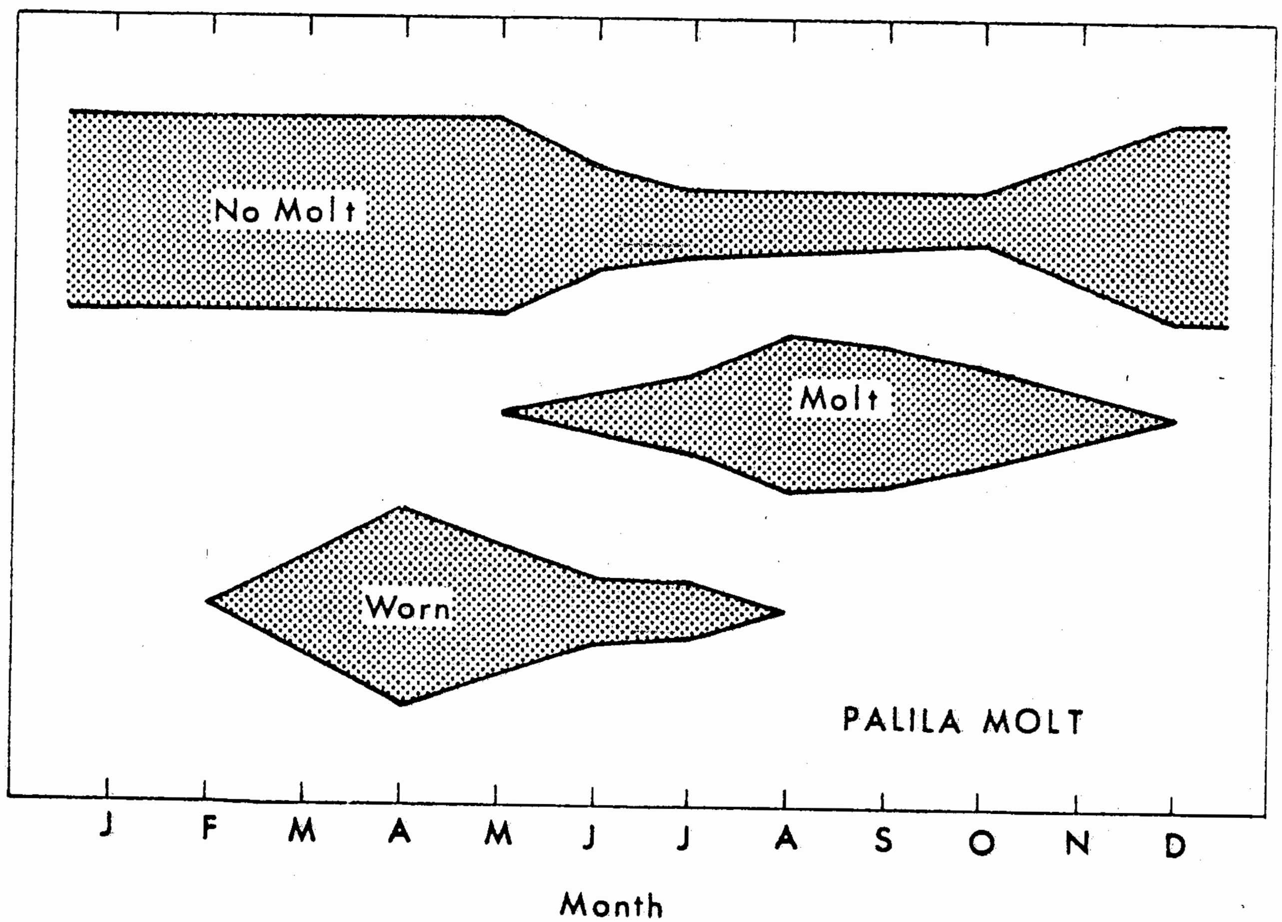


FIGURE 2. The yearly molt pattern in the Palila as recorded from six banded birds, 36 museum skins, and field observations.

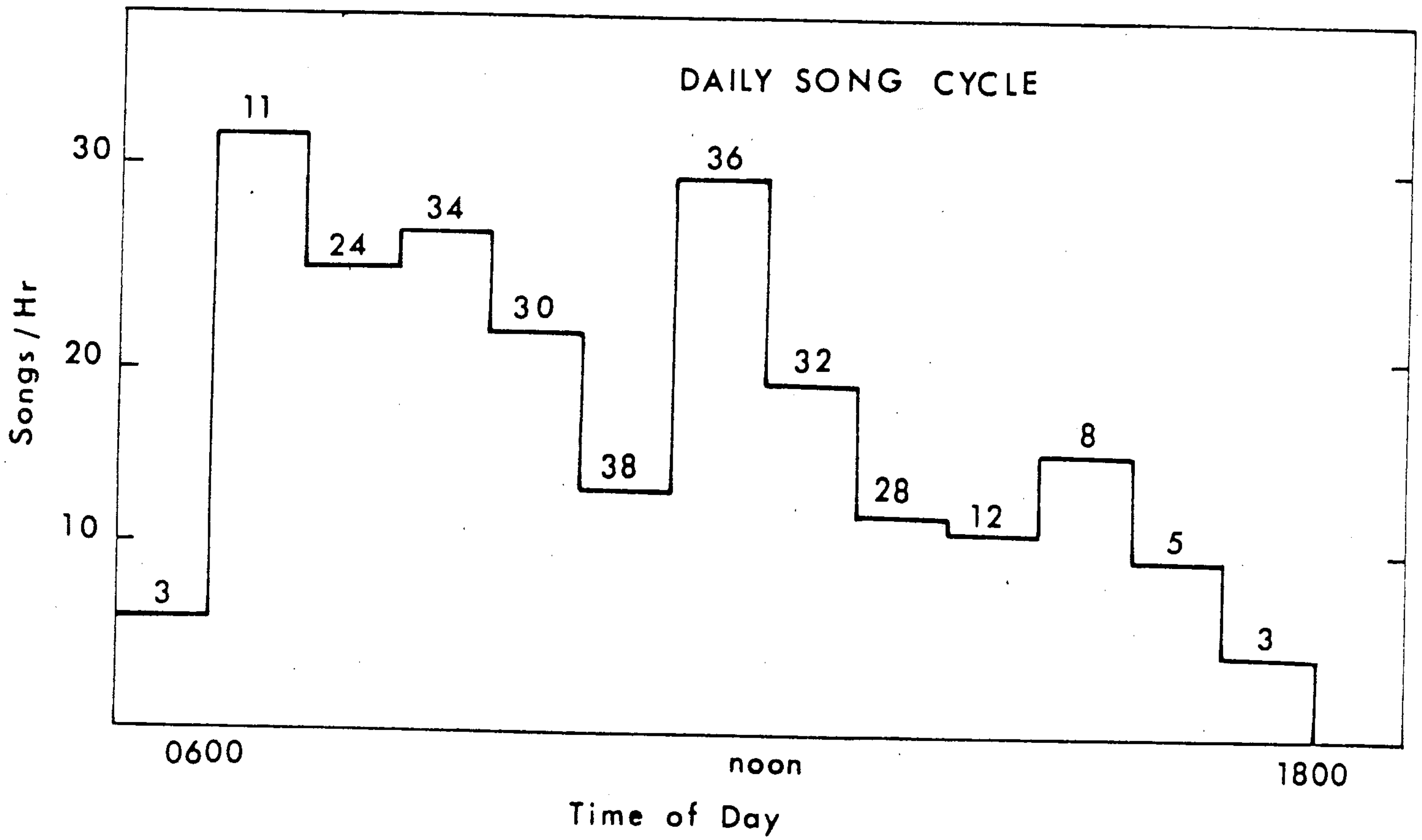


FIGURE 3. The daily song cycle of the Palila on Mauna Kea, Hawai'i. Numbers denote hours of observations.

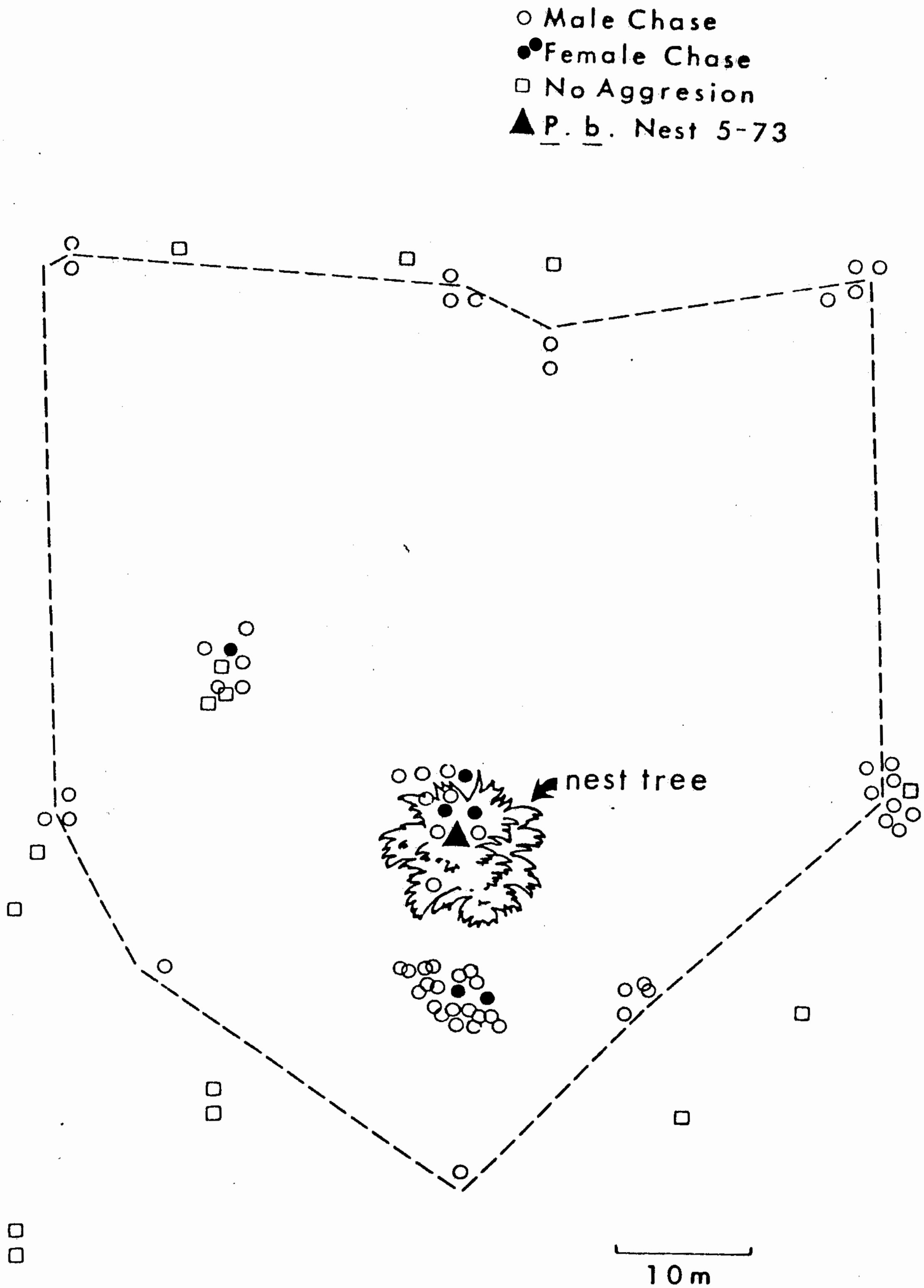


FIGURE 4. Territorial encounters and proposed boundary during nest building and early incubation at Palila nest 5-73.

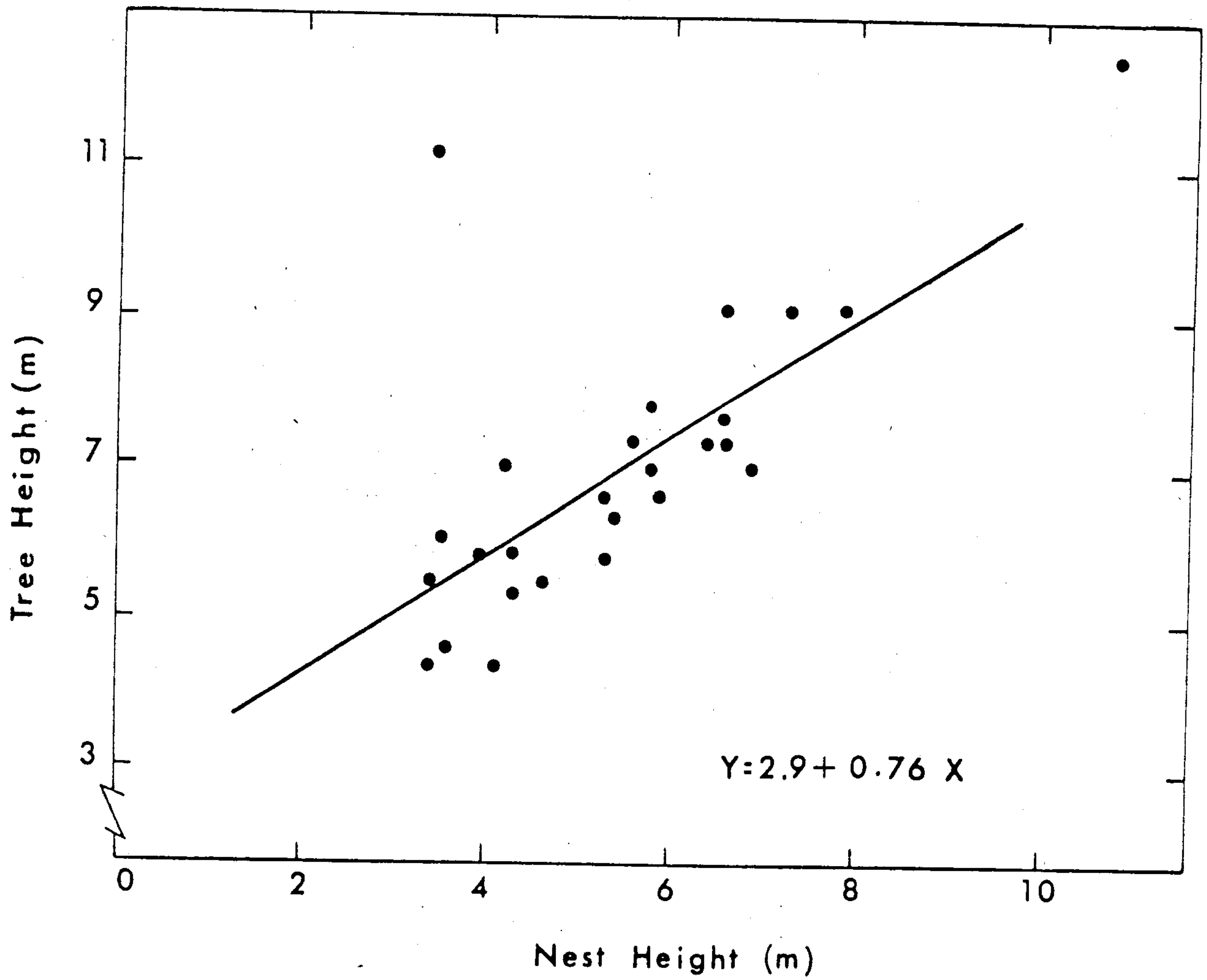


FIGURE 5. The relationship between 26 Palila nest heights and nest-tree heights in māmane and naio trees on Mauna Kea, Hawai'i.

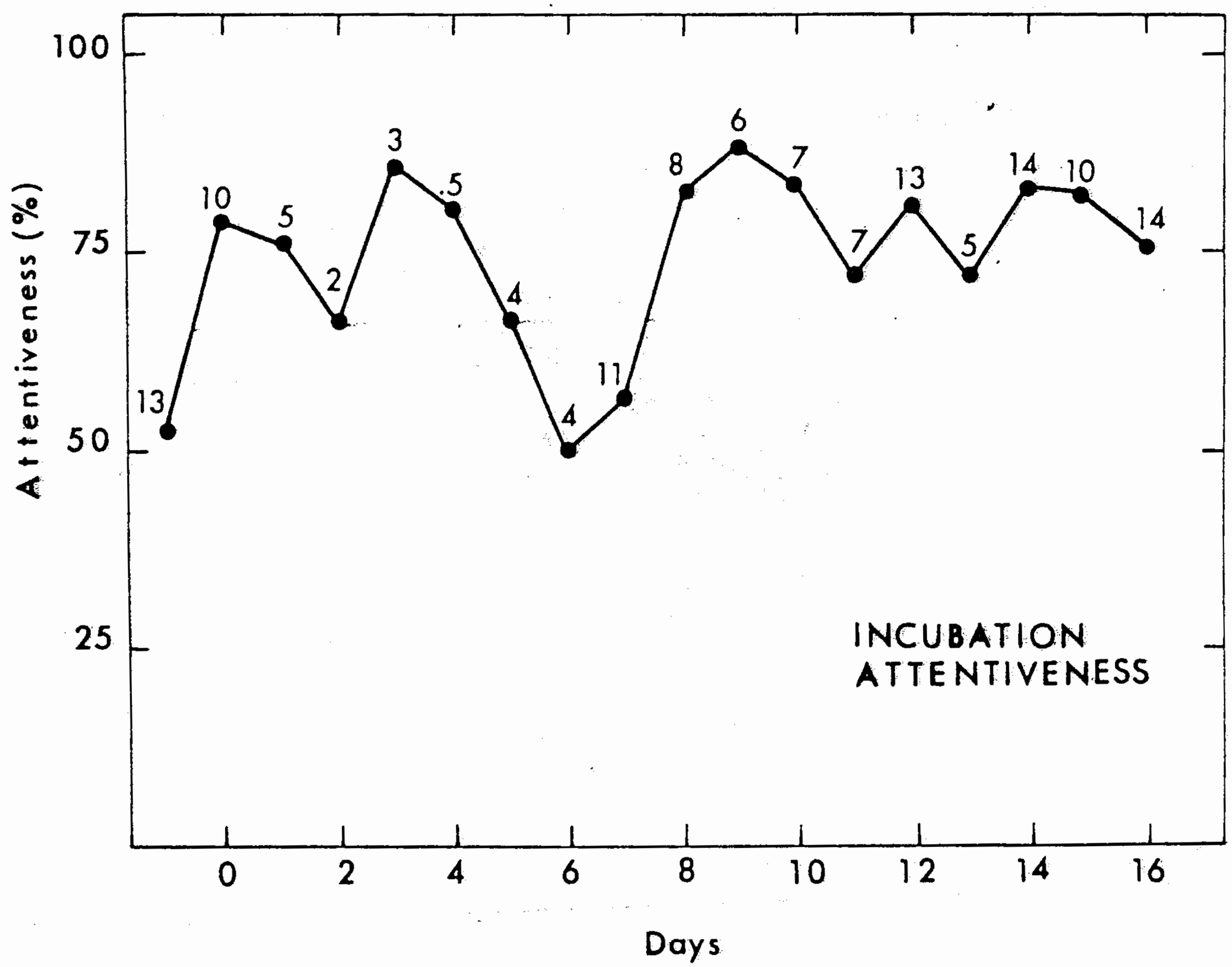


FIGURE 6. Palila attentiveness during incubation as measured at six nests during 141 hours of observation. Numbers denote hours of observation.

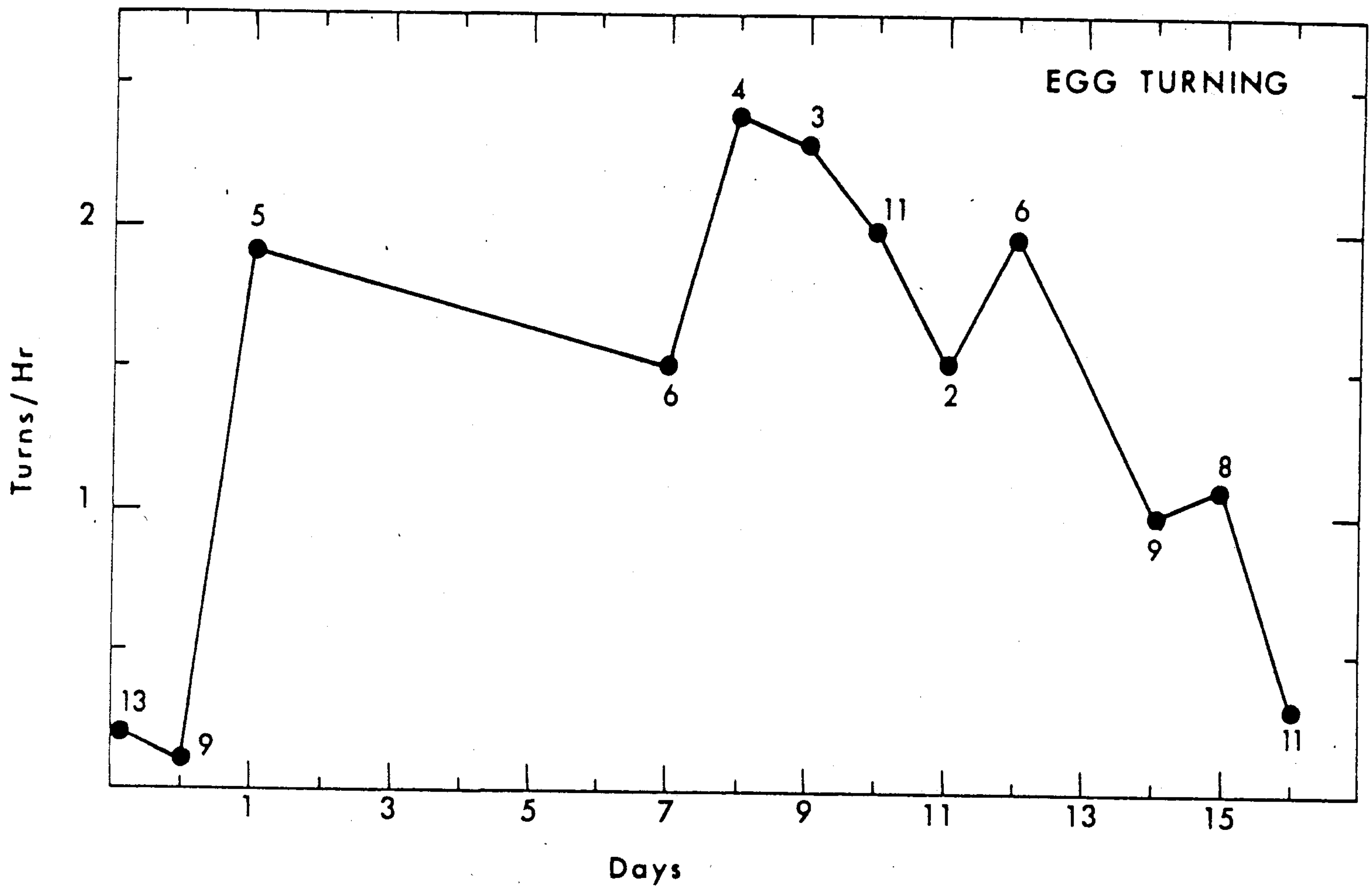
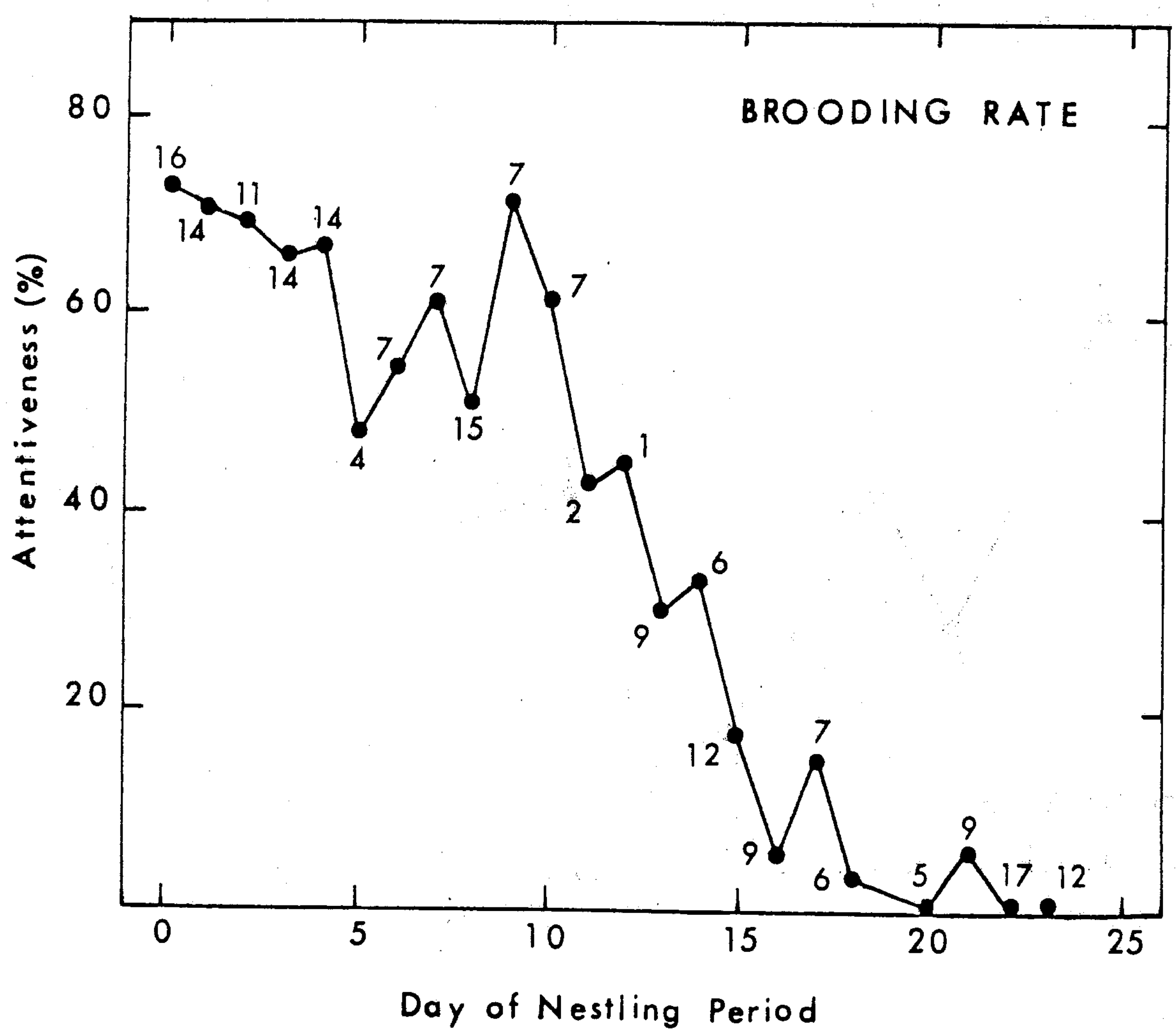


FIGURE 7. Frequency of egg turning by female Palila as measured at six nests during 87 hours of observation. Numbers denote hours of observation.

FIGURE 8. Palila brooding rate as measured at four nests during 211 hours of observation. Numbers denote hours of observation.



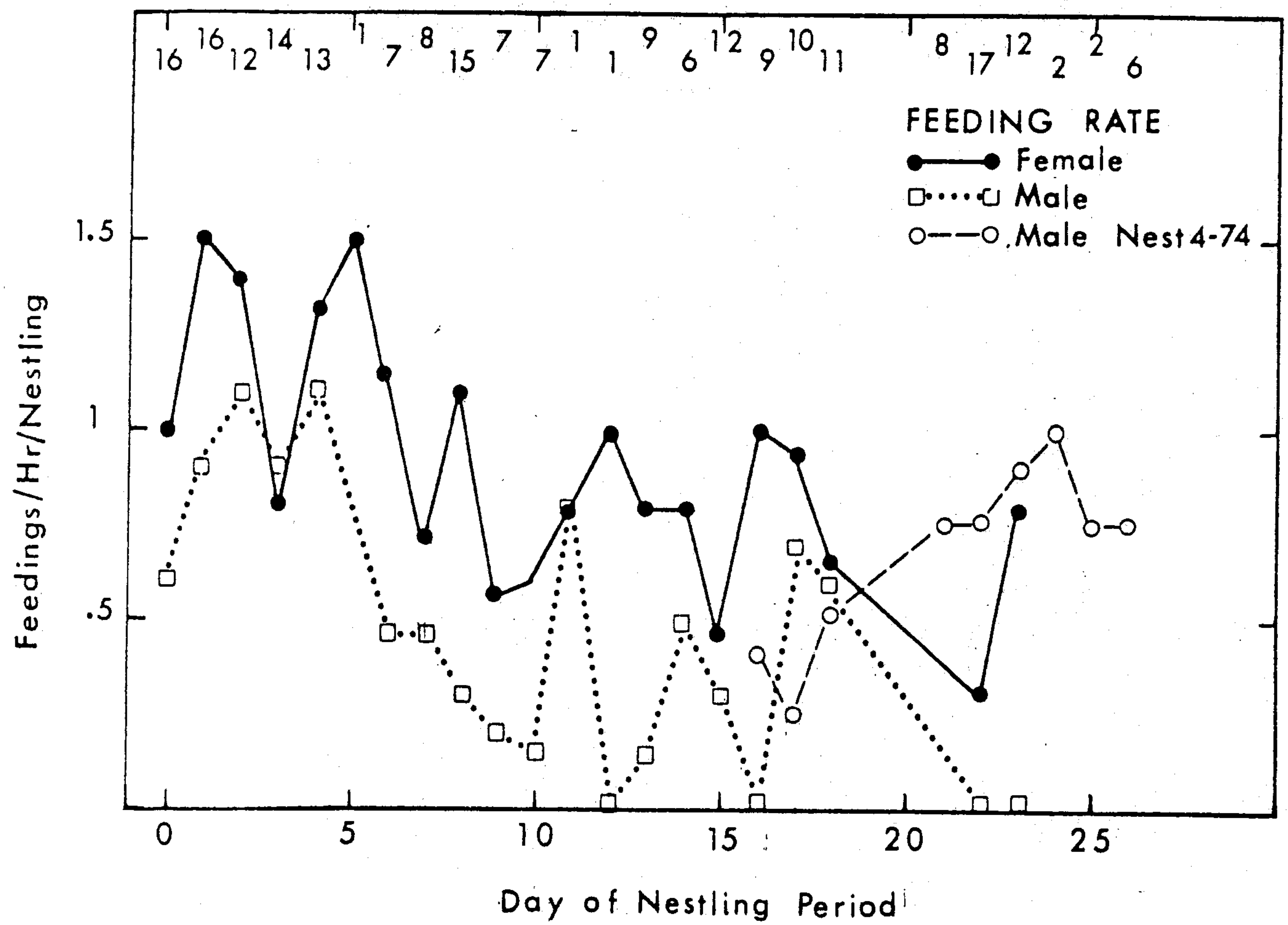


FIGURE 9. The number of hourly feeding sessions at a nest for each nestling by male and female Palila as measured at four nests during 222 hours of observation. Numbers denote hours of observation.

FIGURE 10. Palila nest and young with fecal accumulation evident on the nest rim.

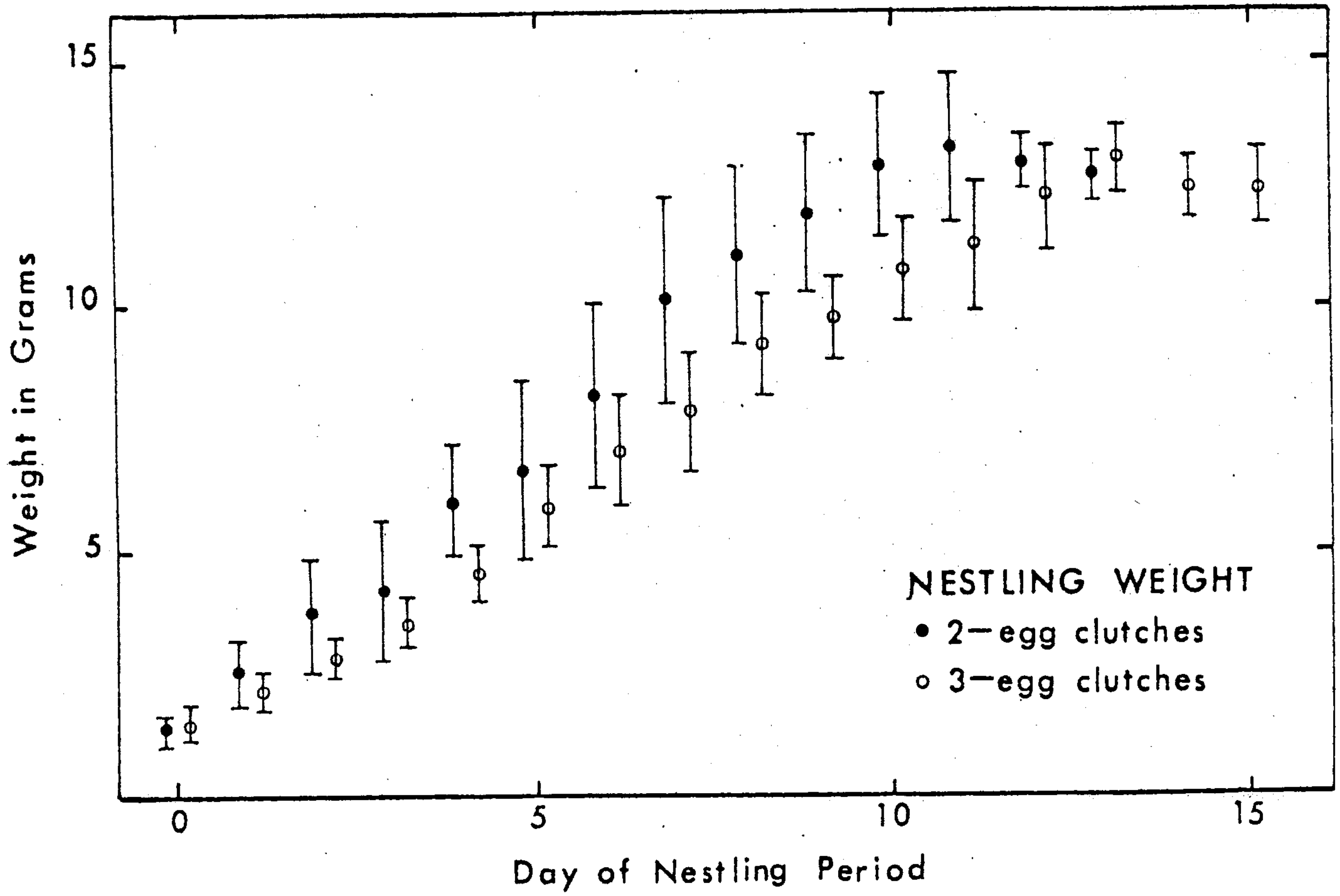


FIGURE 11. Daily nestling weights of Palila young from seven nestlings at four nests. Circles are means and vertical lines ±95% C.I.

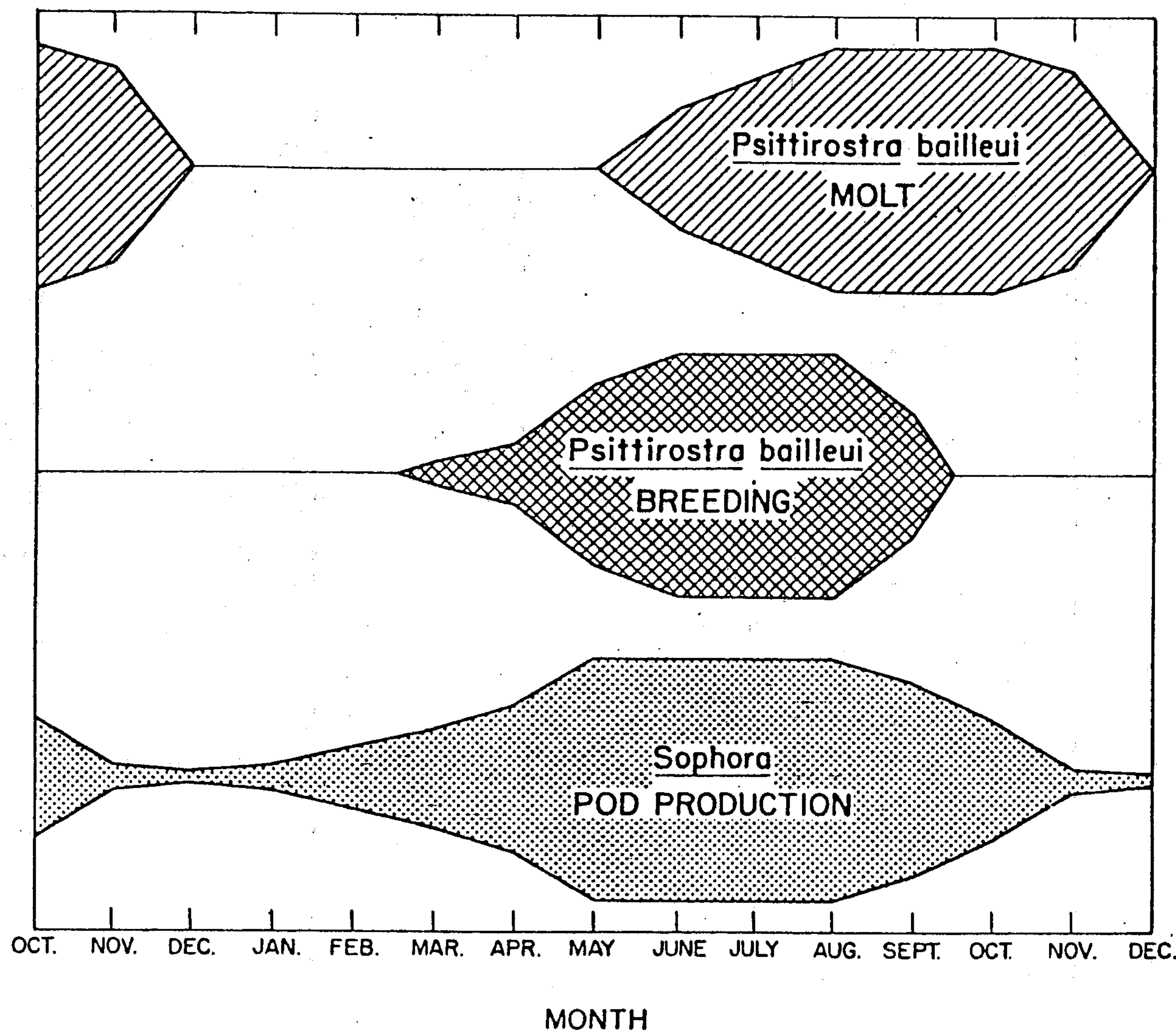


FIGURE 12. Comparison of the Palila breeding season with molt and māmane pod production.

APPENDIX I

Palila nest histories from Mauna Kea, Hawai'i

Nest Number	Date Started	Eggs Laid	Eggs Hatched	Young Fledged	Reasons for Failure
1-72	29 May	2	2	2	
1-73	29 May	2	1	0	Failure to hatch; Young died in nest
2-73	10 June	0	0	0	Deserted
4-73	28 Mar	+	2+	2	
5-73	8 July	2	0	0	Deserted
6-73	1 May	+	1+	1	
3-74	29 April	+	2+	2	
4-74	8 June	2	2	2	
6-74	30 June	2+	0	0	Poor nest construction
7-74	1 June	2	2	0	Weather
8-74	28 April	+	2+	1+	
9-74	20 July	1	0	0	Deserted
10-74	17 June	2+	0	0	
11-74	1 June	+	1+	0	Died in nest
12-74	1 July	+	1+	1	
15-74	3 Sept	0	0	0	Deserted
1-75	24 June	2	2	2	
2-75	15 July	2	0	0	Failure to hatch
3-75	1 July	0	0	0	Deserted
4-75	16 July	2	2	2	
6-75	20 July	2	2	2	
7-75	15 Aug	2	0	0	Deserted
9-75	6 Aug	2	2	2	
11-75	15 Aug	+	2	1+	
13-75	29 Aug	0	0	0	Deserted
15-75	25 July	+	1+	1	

+ = incomplete nest history; not used in determination of success.