

# BREEDING BIOLOGY AND NESTING SUCCESS OF PALILA<sup>1</sup>

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**Abstract.** We studied the breeding biology of Palila (*Loxioides bailleui*) at 85 nests from 20 April to 14 September 1988. Eggs were laid over a 139-day period and incubation averaged 16.6 days. The female incubated 85.2% of daylight hours and males fed incubating females. Modal clutch size was 2 ( $\bar{x} = 2.0$ ) and an average of 1.4 nestlings fledged per successful nest. Nestlings were in the nest an average of 25.3 days. Both females and males fed nestlings with the rate of feeding decreasing as the nestlings grew older.

Palila nesting success was 25%, reduced primarily by hatching failure and depredation of nestlings. Hatching failure, due to inviable eggs or desertion, occurred in 41% of nests with eggs (55% of nest mortality). Egg depredation was rare (5% of nest mortality). Inbreeding and low food availability are postulated as the major causes for poor hatching success. Twenty-one percent of nests with nestlings were depredated (35% of nest mortality). Brood reduction was observed in 47% of nests with two nestlings. Nest success decreased significantly late in the breeding season, from 46.4% to 12.8%. During this same period, the abundance of mamane (*Sophora chrysophylla*) pods, the Palila's primary food, also decreased significantly. Stepwise discriminant analysis correctly classified the fate of 79% of nests using egg-laying date, nest-tree area, and distance between the nest tree and adjacent trees as variables.

**Key words:** Palila; *Loxioides bailleui*; Hawaii; endangered species; nesting success; hatching success; brood reduction.

## INTRODUCTION

The Palila (*Loxioides bailleui*) is an endangered finch-billed Hawaiian honeycreeper (Fringillidae, subfamily Drepanidinae) with a range limited to the subalpine woodland of Mauna Kea on the island of Hawaii. The highest densities of Palila have been found near Puu Laau between 2,100 m and 2,500 m elevation (Scott et al. 1984, 1986). The Palila occupies the mamane (*Sophora chrysophylla*) ecosystem and uses the mamane tree for food, nesting, and shelter. They feed primarily on immature seeds in green mamane pods but also eat mamane flowers, insects, and naio (*Myoporum sandwicense*) berries (van Riper 1980a).

Habitat destruction by feral ungulates beginning in the early 1800s is believed to have been a major factor in the decline of Palila (Berger et al. 1977, Scott et al. 1984). Elimination of most of the feral goats and sheep from the Mauna Kea

Forest Reserve in 1980 and Mouflon sheep in 1988 is allowing regeneration of the mamane forest. Van Riper (1978, 1980a) reported on many aspects of Palila breeding biology, but because his sample size was small ( $n = 20$  nests), little is known about nesting success or causes of nest failure. Further research on Palila breeding biology is necessary to identify factors limiting Palila population growth. The objectives of our research were to: (1) obtain additional information on the breeding biology of the Palila; (2) determine nesting success; (3) evaluate factors that limit nesting success; and (4) make recommendations for further research.

## STUDY AREA AND METHODS

Field research for this study was conducted in the Mauna Kea Forest Reserve east of Puu Laau on the western slope of Mauna Kea, Hawaii (Fig. 1). The study site extended from 2,300 m to 2,800 m elevation and covered approximately 410 ha. The habitat is dry subalpine woodland dominated throughout by mamane. Naio is sparsely scattered in the lower elevations. Trees are short (3–10 m) with an open canopy. The understory is also relatively open, dominated by both native and introduced grasses.

Twenty-two transects, 900 m to 1,300 m in length and 100 m to 500 m apart, were estab-

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lished systematically throughout the study area. Transects were carefully searched for nests on four occasions between late March and mid-September 1988. Nests were located by examining each tree within 30 m of a transect, yielding a total of 153 ha searched per sample period. Nest contents were viewed with a mirror, 10 cm in diameter, attached to the end of a 4-m telescoping pole. To minimize nest disturbance, the observer left the nest area immediately after nest contents were determined. Nest contents and the parents' behavior were monitored every second or third day. Placing a mirror above a nest with nestlings older than 17 days can cause the nestlings to prematurely leave the nest. Therefore, nestlings older than 17 days were monitored from a distance by watching for activity with binoculars or spotting scope. To determine nest fate and fledging date, nests were watched every day after nestlings were 20 days old.

Most nests were found after the onset of incubation, therefore nesting success was estimated using the Mayfield method (1961, 1975). Standard errors and tests of differences in nesting success were calculated according to Bart and Robson (1982). The computer program "Contrast" (Hines and Sauer, unpubl.) was used to compute the tests of differences between groups. The possibility that visiting a Palila nest increased the risk of nest failure for a short time after a visit was investigated by estimating the daily mortality rate for several days after a visit (Bart 1977). Nests that fledged at least one young were considered successful. Depredation was assumed when eggs or young nestlings (<22 days old) disappeared from a nest. Depredated nests were carefully examined for clues of the predator responsible. A nest was considered abandoned when an adult was not seen on or near the nest and the eggs were cold or nestlings dead. Abandoned Palila eggs were collected and preserved in 10% formalin and later examined for development.

Ten Palila nests were monitored by observing them for 1 or 2 hr every second day. Except during the initial discovery, Palila on these nests were never flushed or otherwise disturbed. Nests were observed using a spotting scope located in a blind approximately 10 m from the nest. Observations were made between 07:00 and 18:00. During a nest watch, all Palila activity in and around the nest was timed and recorded. Sex was determined by plumage differences on the head

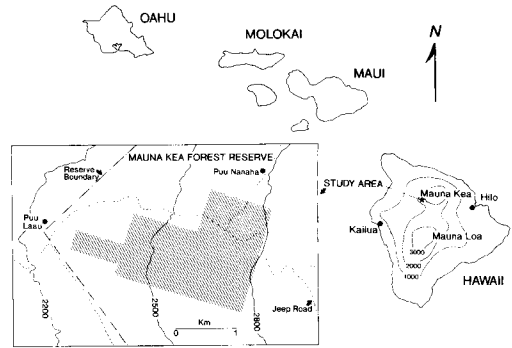


FIGURE 1. Location of study site (shaded area) on the western slope of Mauna Kea.

with males having more extensive and brighter yellow than females.

During nest searches, frequency of mamane pods on terminal branchlets was estimated for four randomly selected trees (>3 m tall) along transects at 150-m intervals. In addition, frequency of pods was estimated for each nest tree and four surrounding trees (nest-area trees). For each mamane tree, frequency of immature, but fully expanded pods, was estimated to the nearest 5% and very little was recorded as less than 5%.

Nest-site characteristics were measured after the completion of nesting. An index of crown area was calculated from the product of widest nest-tree diameter and diameter perpendicular to widest (nest-tree area). Nest location in the canopy was the distance from nest center to ground, to end of vegetation above nest (canopy top), to center of vegetation surrounding nest (center of canopy), and to nearest canopy edge. Percent foliage cover around the nest was used as an index of nest concealment. Cover (to the nearest 5%) 0.5 m above, below, and in each of the four cardinal directions (0, 90, 180, and 270°) was estimated by viewing the nest at eye level from a distance of 1 m in each of the six directions. An average of the six cover estimates was used for analysis.

Other habitat measurements were taken along lines starting at the nest center and extending in four cardinal directions. These included the linear distance of foliage cover from the nest to a break in cover of at least 1 m (end of foliage cover), and the lowest foliage in the outer part of the canopy (canopy bottom). Each of these was averaged for analysis. The distance from the nest tree to the nearest tree (>3 m tall) was mea-

sured in each of four quadrats defined by the cardinal lines. The average of these four distances was used for analysis (nearest trees).

Nest placement was categorized as: (1) "terminal" when in limbs forming the most distant group of stems from the trunk and in the top 20% of the nest tree; (2) "lateral" when in end clusters of limbs in the lower 80% of the nest tree; and (3) "central" when in limbs not the most distant groups.

Two-sample comparisons were made with the Wilcoxon's rank-sum test and paired comparisons were performed with the Wilcoxon's signed-rank test. Frequencies were compared using Fisher's exact test. Stepwise discriminant analysis was used to derive classification functions from habitat variables and egg-laying date to predict nesting success. Cross validation estimated how well these functions predicted correct classification as to the fate of the nests. Except for nesting success, all statistical analyses were performed using SAS computer software (SAS Institute 1985).

## RESULTS

### GENERAL NESTING CHARACTERISTICS

From 20 April to 5 September 1988, we found 85 active Palila nests in the Puu Laau study site. Seventy-six percent (65) of these nests were located within a 110-ha area between the elevations of 2,620 m and 2,800 m. This is a much greater density of nests and higher elevation than was found by van Riper (1978). Only one nest was located below 2,410 m in the area where van Riper conducted his Palila research between 1972 and 1975. The Palila nesting period from the start of incubation to fledging lasted a mean of 42.3 days (SD = 2.2,  $n = 6$  nests) with a range of 40 to 46 days. This is considerably longer than most passerines that nest in an open cup (Nice 1957, Harrison 1978).

Palila nested in woodland habitat composed almost entirely of mamane trees and all 85 nests were built in mamane trees. Mean nest height was 3.9 m (SD = 1.1, range = 0.25–8.5 m) and mean tree height was 5.0 m (SD = 1.1, range = 1.5–10.0 m). These were much lower than the mean nest (5.2 m) and nest tree (6.9 m) heights found by van Riper (1980a). There was a significant positive correlation between nest height and tree height (Spearman's rank,  $r_s = 0.82$ ,  $P < 0.001$ ). The majority of nests were placed in forks

of two or more branches. Nest placement was predominantly in terminal forks (67%), with 22% built in the center and 11% in lateral forks.

### INCUBATION PERIOD

The earliest date of egg laying was calculated to be 7 April and the latest 24 August with the peak of egg laying in mid-June (Fig. 2). Incubation averaged 16.6 days (SD = 0.49, range = 16–17 days,  $n = 6$  nests) (day 0 was the day on which the clutch was completed). Among 52 nests, clutch size ranged from one to four eggs and the mean clutch size was 2.0 eggs (SD = 0.35). Two-egg clutches were the mode, making up 87% of the total. Only three nests had more than two eggs (one with four eggs and two with three eggs). Four nests had one egg, but these were late in season and failed to hatch. Of the 27 nests with eggs that hatched, 25 were two-egg clutches and the remaining two were three-egg clutches.

Ten Palila nests were observed during incubation for a total of 72 hr (49 watch periods). All incubation was done by the female. The mean amount of time spent incubating per hour was 51.1 min (SD = 3.19, range = 44.1–54.5 min,  $n = 10$  nests) or 85.2% of daylight hours. Incubation recesses averaged 4.8 min (SD = 1.6, range = 2.6–7.5 min,  $n = 10$  nests), which suggests that incubating females did not travel far to feed. Males were observed feeding females in the nest area, and probably were important in allowing the female to remain on the nest.

The eggs failed to hatch in two of the 10 nests under observation. One was abandoned 9 days after discovery and the other after 19 days; however, we do not know when the eggs were laid in either nest. The behaviors of these Palila were not noticeably different than other incubating Palila and the amount of time each nest was incubated was near the mean: 50.5 (SD = 8.9,  $n = 8$  hr) and 54.5 (SD = 5.5 and  $n = 8$  hr) min per hour. The eggs from these nests did not have detectable embryos and probably were either infertile or died after a few days of incubation.

Near two other nests, juvenile Palila begged regularly from the incubating female. This suggests that these nests were second broods. The eggs in one nest were laid on about 7 July and the other near 1 August. The juveniles continually flushed the females off their nests, resulting in lower than average incubation times: 47.7 (SD = 4.1,  $n = 11$  hr) and 44.1 (SD = 12.3,  $n = 4$  hr) min per hour. The eggs in both of these nests

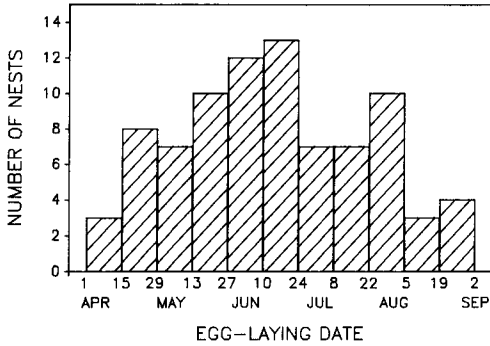


FIGURE 2. Timing of Palila egg laying during 1988.

hatched; however, the nestlings in the first nest were depredated on day 3, whereas two young fledged from the other nest.

NESTLING PERIOD

The earliest date of fledging was 19 May and the latest 14 September. Nestlings spent an average of 25.3 days (SD = 1.7, range = 23–29 days, *n* = 19 nests) in the nest (with hatching day equal to day 0). The nestling period for nests fledging two young averaged slightly longer ( $\bar{x}$  = 25.8 days, SD = 1.4, *n* = 6 nests) than for nests fledging only one young ( $\bar{x}$  = 24.7, SD = 1.2, *n* = 10 nests) (*P* = 0.1). For nests with eggs that hatched, a mean of 1.8 nestlings hatched per nest (SD = 0.43, *n* = 22 nests). We never observed more than two nestlings in a nest. An average of 1.4 Palila (*n* = 26 nests) fledged per successful nest, with 17 nests fledging one young and nine fledging two.

Eight Palila nests were observed during the nestling stage for a total of 124 hr (88 watch periods). Virtually all brooding was done by the female. A male was observed brooding on two occasions at the same nest and each bout lasted less than 10 min. Daytime brooding decreased steadily as nestlings grew (Fig. 3). Young nestlings (0–12 days old) were brooded a mean of 38.5 min per hour (SD = 5.8, *n* = 8 nests). Mean brooding time for old nestlings (>12 days old) was 14.8 min per hour (SD = 5.8, *n* = 7 nests) which was significantly less than for young nestlings (*P* < 0.01, *n* = 7 nests). The mean length of a brooding session was similar for young and old nestlings; however, recesses were much longer for old nestlings (Table 1).

Although both males and females participated

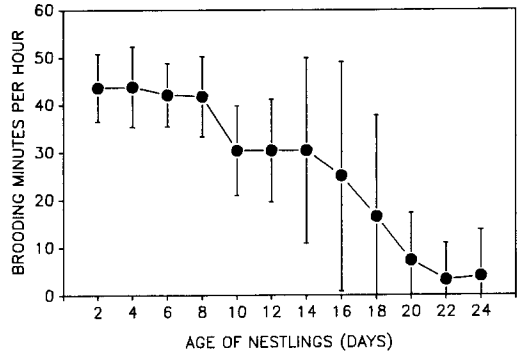


FIGURE 3. The relationship of mean ( $\pm$  SD) brooding time per daylight hour and age of nestling for eight Palila nests.

in feeding nestlings, females were responsible for 63% of feedings (*n* = 224). Nestlings were fed by regurgitation. The amount and type of food that nestlings were fed was not measured and often it was not possible to determine how many nestlings were fed. The majority of regurgitate appeared to be green mamane pods, but insects and mamane flowers were also observed. Adults fed young nestlings (0–12 days old) a mean of 2.6 times per hour (SD = 0.73, *n* = 8 nests). Feeding rate decreased significantly for old nestlings (>12 days old) to a mean of 1.6 per hour (SD = 0.64, *n* = 7, *P* < 0.02; Fig. 4). Whereas the mean number of nestlings per nest decreased from 1.7 (SD = 0.30, *n* = 8 nests) for young nestlings to 1.3 (SD = 0.24, *n* = 7 nests) for old nestlings, the number of feeding visits per nestling per hour for young nestlings ( $\bar{x}$  = 1.9, SD = 0.73, *n* = 8 nests) was significantly greater than for older nestlings ( $\bar{x}$  = 1.4, SD = 0.52, *n* = 7 nests) (*P* < 0.05). This indicates that the decreased number

TABLE 1. Mean length of incubation, brooding, and recesses at Palila nests. Young nestlings were 0–12 days old and old nestlings were 13 days and older. An asterisk indicates a significant difference from the previous stage.

|                | No. nests | Incubation or brooding session (min) |     | Recess (min) |     |
|----------------|-----------|--------------------------------------|-----|--------------|-----|
|                |           | $\bar{x}$                            | SD  | $\bar{x}$    | SD  |
| Incubation     | 10        | 21.2                                 | 9.0 | 4.8          | 1.6 |
| Young nestling | 8         | 10.6*                                | 2.7 | 6.5*         | 2.7 |
| Old nestling   | 7         | 14.1                                 | 9.0 | 16.6*        | 3.5 |

\* *P* < 0.05, Wilcoxon's signed-rank test.

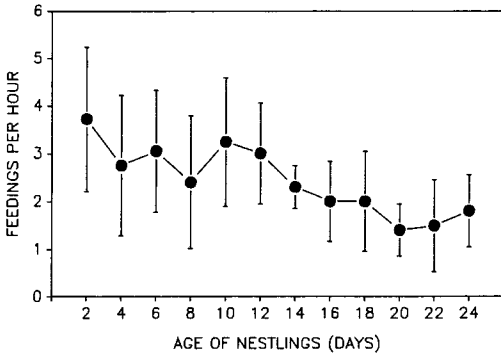


FIGURE 4. The relationship of mean ( $\pm$  SD) number of feedings per hour and age of nestling for eight Palila nests.

of nestlings in older nests was not the sole reason for the decreased feeding rate. Van Riper (1980a) also found that the number of feedings decreased slightly over the nestling period.

NESTING SUCCESS

Overall Palila nesting success using the Mayfield method (1961, 1975) was estimated to be 25% ( $n = 81$  nests). This is half the rate of nesting success (50% of 12 nests) found by van Riper (1978). During incubation, nesting success was 38% and during the nestling stage it was 67% (Table 2). Daily survival rate during incubation was significantly less than during the nestling stage ( $P < 0.001$ ). Hatching failure occurred in 41% of 54 nests monitored during incubation and was

TABLE 3. Reasons for nesting failure as a percentage of Palila nests in the incubation and nestling stages. Incubation began in early nests before 15 June and after 14 June for late nests.

|       | Incubation stage |                    |             | Nestling stage |             |             |
|-------|------------------|--------------------|-------------|----------------|-------------|-------------|
|       | No. nests        | Hatching failure % | Predation % | No. nests      | Desertion % | Predation % |
| Early | 24               | 16.6               | 8.3         | 35             | 0           | 14.3        |
| Late  | 30               | 60.0               | 0           | 22             | 18.2        | 31.8        |
| Total | 54               | 40.7               | 3.7         | 57             | 7.0         | 21.1        |

the primary cause of nest mortality (Table 3). Van Riper also found that nest failure was largely due to hatching failure (43% of 14 nests).

Of 100 eggs laid, 47 hatched, four were depredated, and 49 failed to hatch because of desertion or inviability. For the 26 nests with eggs that hatched, partial hatching was found in 23% (six nests) and the hatching rate was 88.7% ( $n = 53$  eggs). In all cases, the unhatched egg remained in the nest with the nestling for several days. Two of these eggs were examined and neither had embryo development.

We examined 35 unhatched eggs from 19 nests abandoned after discovery. The eggs in 10 nests had no embryo development (14 eggs), three nests had both developed (four eggs) and undeveloped eggs (five eggs), and six nests had developed embryos (12 eggs). All but two of these nests were found after incubation had begun, thus we were uncertain how long most nests were incubated.

TABLE 2. Palila nesting success for incubation ( $n = 54$  nests) and nestling ( $n = 57$  nests) periods between April–September 1988 calculated using the Mayfield method. Incubation began in early nests before 15 June and after 14 June for late nests. Low elevation nests were below 2,650 m and high elevation nests above 2,650 m.

|                   | No. successful/<br>unsuccessful | Successful nests % | Daily survival (SE) | Success rate % | $P^*$ |
|-------------------|---------------------------------|--------------------|---------------------|----------------|-------|
| <b>Incubation</b> |                                 |                    |                     |                |       |
| Early             | 18/6                            | 75                 | 0.966 (0.0137)      | 56.4           | 0.07  |
| Late              | 12/18                           | 40                 | 0.926 (0.0170)      | 27.9           |       |
| Low               | 16/9                            | 64                 | 0.963 (0.0122)      | 53.8           | 0.05  |
| High              | 14/15                           | 48                 | 0.915 (0.0211)      | 22.8           |       |
| All               | 30/24                           | 56                 | 0.943 (0.0114)      | 37.8           |       |
| <b>Nestling</b>   |                                 |                    |                     |                |       |
| Early             | 27/5                            | 84                 | 0.992 (0.0037)      | 81.0           | 0.03  |
| Late              | 10/11                           | 48                 | 0.971 (0.0090)      | 47.6           |       |
| Low               | 20/8                            | 71                 | 0.986 (0.0061)      | 69.3           | 0.70  |
| High              | 17/8                            | 68                 | 0.983 (0.0054)      | 64.1           |       |
| All               | 37/16                           | 70                 | 0.984 (0.0040)      | 66.8           |       |

\* Bart and Robson (1982).

Nonetheless, at least seven nests (12 eggs) with eggs that had no embryo development were incubated for three or more days. If these eggs were fertile, some embryonic development should have occurred.

Hatching failure due to infertility or embryo death (unhatchability) was  $\geq 18\%$  of all eggs. Unhatchability was determined by the percentage of eggs incubated to term and not hatched, and eggs incubated for  $\geq 3$  days that had no embryo development. This is a minimum percentage because there were undoubtedly inviable eggs among the remaining 35 unhatched eggs.

In addition, the eggs from seven nests abandoned before discovery were examined. The eggs from four nests had no embryo development and three had development. Abandoned eggs with embryo development were equally common in nests found before and after our discovery (Fisher's exact test,  $P = 0.66$ ), which suggests that monitoring tests did not cause a significant amount of egg abandonment.

Depredation of eggs was rare (Table 3). When the two active nests were depredated, one of two eggs was depredated and the nest was immediately abandoned. The daily mortality rate of eggs due to hatching failure was 0.052, whereas daily mortality due to depredation was only 0.005. Unhatched eggs provided further evidence of the low rate of egg depredation. The eggs in 30 abandoned nests (10 abandoned prior to our discovery) were monitored for 397 nest exposure days and in only one nest were the eggs depredated. The daily mortality rate of these abandoned nests was only 0.0025.

Nest mortality during the nestling stage was primarily due to depredation of nestlings, whereas abandonment was uncommon (Table 3). Nestling remains, scats, and other signs indicated that both feral house cats (*Felis catus*) and black rats (*Rattus rattus*) depredated Palila nestlings. In many cases the species of predator could not be determined, thus the relative influence of each species is unknown. All four cases of nestling abandonment occurred after 15 July and may have been related to the decrease in mamane pod frequency (see below).

Of 39 eggs that hatched young, 20 fledged for a fledging rate of 51% ( $n = 21$  nests). This is much lower than the fledging rate (80% of eight nests) found by van Riper; however, he trapped mammals extensively during his Palila research which probably reduced predation on nestlings.

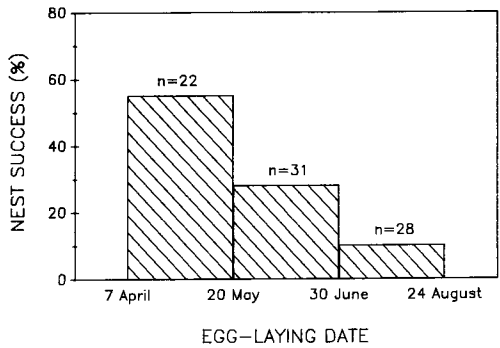


FIGURE 5. Palila nesting success during 1988 calculated using the Mayfield method.

Brood reduction was found in 47% of the successful nests that hatched two eggs ( $n = 17$  nests). All eight instances of brood reduction occurred when the nestlings were in their second week. The causes of death were not determined. A dead nestling was never observed in a nest with a living nestling. Apparently nestlings were removed soon after their death.

Low Palila nesting success was due largely to nest failures late in the breeding season. Nesting success of clutches completed before 15 June was 45.7%, with 71% of 38 nests fledging young, but after 14 June nesting success decreased significantly to 13.3%, with 26% of 39 nests fledging young (Table 2). Nesting success became progressively worse through the breeding season (Fig. 5). Hatching failure, due to desertion or inviability, increased significantly late in the breeding season (Fisher's exact test,  $P < 0.001$ ; Table 3). Predation also increased, but not significantly (Fisher's exact test,  $P = 0.11$ ) and abandonment of nestlings only occurred in late nests.

A high daily mortality rate (DMR) the day after we visited a nest followed by a lower DMR would indicate that the visit decreased nest survival. The DMR for the day after a visit was 0.0625 ( $n = 32$  nests) and the average DMR for 2 to 7 days after a visit was 0.0545 ( $n = 49$  nests;  $P = 0.87$ ). Thus nest survival was not affected by our inspections and monitoring nests did not decrease nest survival.

#### SUCCESSFUL VS. UNSUCCESSFUL NESTS

Nest-site characteristics of successful nests were significantly different than failed nests for four of 12 variables (Table 4). Nest height tended to be greater in successful nests, but the difference

TABLE 4. Average nest-site characteristics for successful vs. unsuccessful Palila nests.

| Variable                   | Successful ( <i>n</i> = 37) |      | Unsuccessful ( <i>n</i> = 40) |      | Z*       |
|----------------------------|-----------------------------|------|-------------------------------|------|----------|
|                            | $\bar{x}$                   | SD   | $\bar{x}$                     | SD   |          |
| Elevation (m)              | 2,645                       | 383  | 2,664                         | 323  | ns       |
| Egg-laying date            | 29 May                      | 27   | 30 June                       | 35   | -3.98*** |
| Percent cover              | 44.8                        | 15.3 | 46.8                          | 13.5 | ns       |
| Nest-tree:                 |                             |      |                               |      |          |
| Height (m)                 | 5.2                         | 1.26 | 4.6                           | 0.9  | 2.16*    |
| Area (m <sup>2</sup> )     | 68.0                        | 46.3 | 41.6                          | 35.0 | 3.01**   |
| Canopy bottom (m)          | 1.1                         | 0.4  | 1.2                           | 0.4  | ns       |
| Distance from nest to (m): |                             |      |                               |      |          |
| Ground                     | 4.1                         | 1.2  | 3.6                           | 1.1  | ns       |
| Canopy top                 | 0.74                        | 0.44 | 0.86                          | 0.71 | ns       |
| Nearest canopy edge        | 0.94                        | 0.89 | 0.80                          | 0.63 | ns       |
| Canopy center              | 2.1                         | 1.5  | 2.8                           | 2.4  | ns       |
| Nearest trees              | 7.0                         | 7.6  | 3.3                           | 4.2  | 2.89**   |
| End of foliage cover       | 4.6                         | 1.5  | 4.5                           | 1.5  | ns       |

\* Wilcoxon's rank sum, significant at \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ , unless not significant (ns).

was not significant ( $P < 0.1$ ). Using stepwise discriminant analysis three variables were found to distinguish between successful and unsuccessful nests (Table 5). Egg-laying date was the most important variable in discriminating between the two groups, with successful nests initiated earlier in the season. The second most important variable was average distance between nest tree and nearest trees, with a greater distance between trees for successful nests. The third discriminant was nest-tree area, which was greater for successful nests. The number of correctly classified cases, 79% overall, indicates that the discriminant function performs well when trying to predict the fate of a nest based on these three variables.

#### MAMANE POD FREQUENCY

After 30 June, mean frequency of mamane pods on randomly selected and nest-area trees decreased significantly, but increased slightly on Palila nest trees (Table 6). Late in the season, mamane pod frequency on nest trees was significantly greater than random trees ( $P < 0.05$ ).

Mamane pod frequency on nest-area trees was significantly greater than on random trees for both early ( $P < 0.01$ ) and late ( $P < 0.001$ ) time periods.

#### DISCUSSION

Hatching failure, due to inviability or desertion, was the primary cause of nest failure. Depredation was primarily responsible for nest losses during the nestling stage. Nesting success decreased as the breeding season progressed, largely due to a nearly fourfold increase in hatching failure. Abandonment of nestlings also increased late in the season. Overall, our results indicate that four factors limited Palila nesting success: inviable eggs, food limitations, depredation, and habitat quality. Other factors that may have been important, but we did not study, include the number of broods raised per year, age and experience of breeding birds, relatedness of breeding pairs, and availability of food resources other than mamane pods.

For most bird species, hatching failure due to

TABLE 5. Stepwise discriminant analysis of successful vs. unsuccessful Palila nests.

| Variable                  | Wilk's lambda | P      | Discriminant coefficients |              |
|---------------------------|---------------|--------|---------------------------|--------------|
|                           |               |        | Successful                | Unsuccessful |
| Egg-laying date           | 0.797         | 0.0001 | 10.76                     | 10.80        |
| Distance to nearest trees | 0.705         | 0.0001 | -3.09                     | -3.20        |
| Nest-tree area            | 0.644         | 0.0001 | -1.00                     | -1.02        |
| Constant                  |               |        | -55,779                   | -56,178      |
| Correctly classified      |               |        | 75.7%                     | 81.6%        |

TABLE 6. Mean percent cover by mamane pods for early (before 1 July) vs. late (after 30 June) trees. Wilcoxon's rank sum was used for all comparisons except early random vs. late random trees, where Wilcoxon's signed rank was used for the means of 15 areas.

|              | Random |           |        | Nest area |           |       | Nest tree |           |      |
|--------------|--------|-----------|--------|-----------|-----------|-------|-----------|-----------|------|
|              | n      | $\bar{x}$ | SD     | n         | $\bar{x}$ | SD    | n         | $\bar{x}$ | SD   |
| Early        | 612    | 16.4      | 20.7** | 32        | 19.6      | 17.0* | 34        | 11.0      | 13.5 |
| Late         | 1,229  | 8.7       | 13.7   | 37        | 12.4      | 14.0  | 37        | 15.1      | 19.0 |
| Successful   |        |           |        | 33        | 16.9      | 17.2  | 34        | 11.5      | 14.6 |
| Unsuccessful |        |           |        | 36        | 14.7      | 14.5  | 37        | 14.6      | 18.4 |

\*\*  $P < 0.001$ , \*  $P < 0.05$ .

infertility and embryo death is infrequent. Koenig (1982) analyzed 155 nesting studies and found that a mean of 9.4% of eggs were unhatchable, and open nesters and granivores had even lower hatching failure (9.0% and 7.4%, respectively). However, the syntopic Common Amakihi (*Hemignathus virens*), also a Hawaiian honeycreeper, was found to have a hatching failure rate of 11.3% (van Riper 1987). Nonetheless, the high incidence of unhatchability ( $\geq 18\%$ ) we observed in the Palila was above normal. Van Riper (1980a) also found a high frequency of unhatchable eggs in the Palila (17% of 18 eggs).

Low population size in the Palila may have led to inbreeding resulting in reduced fertility and high incidence of lethal recessives exposed during embryo development. Evidence that inbreeding reduces both fertility and embryo survival exists for domestic fowl (Shoffner 1948) and the Japanese Quail (*Coturnix japonica*, Sittmann et al. 1966). In a wild population of Great Tits (*Parus major*) hatching failure was found to increase with degree of inbreeding (van Noordwijk and Scharloo 1981). However, the degree of inbreeding in Palila and the genetic fitness of the population are unknown.

Decreased hatching success late in the breeding season indicates that a seasonal factor may have been influential. We found that mamane pod abundance decreased as the breeding season progressed, suggesting that late nesters may have been more stressed for food. Eggs laid by poorly nourished birds may have lower hatchability (Scott 1973, Martin 1987). Eggs formed at the time of poor food availability had reduced hatching success in the House Martin (*Delichon urbica*, Bryant 1975), European Swift (*Apus apus*, O'Connor 1979), and Pied Flycatcher (*Ficedula hypoleuca*, Järvinen and Väisänen 1984). In addition, birds faced with diminished food resources may have to leave their eggs more often

to forage, thus exposing their eggs to variable temperatures which could lead to reduced hatching (Romanoff 1972, Martin 1987). Alternatively, a severe food shortage might cause Palila to abandon viable eggs.

The high incidence of unhatched eggs late in the breeding season may have been partially due to younger Palila breeding later than older birds. Young and inexperienced Palila may lay eggs with lower hatchability as was found in the European Blackbird (*Turdus merula*, Snow 1958), American Goldfinch (*Carduelis tristis*, Middleton 1979), and California Gull (*Larus californicus*, Pugsek and Diem 1983). Young birds of many species breed later and are less successful than older birds (Ralph and Pearson 1971, De Steven 1978, Reese and Kadlec 1985). Young Palila may have nested late in the season and had a tendency to abandon eggs due to inexperience.

Many of the late nests may have been second broods which tend to be less successful than first broods (Perrins 1970). Hatchability decreased in second and/or late nests in Eastern Bluebirds (*Sialia sialis*; Norris 1958, White and Woolfenden 1973). Our observations of juvenile Palila begging from females at two nests indicated that Palila will attempt a second brood even if their first was successful. Van Riper (1980a) believed that Palila were able to raise only one brood in a season. Young Palila stay with their parents for at least 30 days after fledging (van Riper 1980a), and second nests may be initiated while adults are still feeding the first brood. Juvenile Palila may regularly flush adults off their nests, causing exposure of eggs and difficulties in feeding nestlings. Clearly, feeding young from a previous brood while incubating eggs or feeding nestlings would be difficult, especially if food was scarce. Nonetheless, one of two pairs that laid second clutches fledged two young.



Palila nesting success early in the season was similar to that of many open-nesting passerine species (Nice 1957). If the majority of the experienced breeding population nested early in the season and late nests were primarily second clutches and first attempts of young birds, then reproductive success was within the normal range.

Predation is commonly cited as the major factor limiting nesting success in arboreal open-cup nesting birds (Nice 1957, Ricklefs 1973, Wilcove 1985, Martin and Roper 1988). The absence of mammalian predators during Palila evolution suggests that Palila may be particularly vulnerable to predation by introduced feral cats and rats. The large accumulation of pungent feces around Palila nests during the nestling phase (van Riper 1980a, pers. observ.) may increase the vulnerability of nests to depredation during the nestling stage. The degree of depredation on adults is unknown. The high incidence of egg abandonment could, in part, be due to predation of parents. The accessible placement of Palila nests make adults sitting on nests easy prey for cats and rats. Van Riper (1980a) observed a feral cat prey upon a brooding Palila without harming the nestlings. During 1988, feral cats were common, and rats were present in at least the lower portion of the study area (pers. observ.; U.S. Fish and Wildlife Service, unpubl. data).

Our analyses show that nests in widely spaced large trees were more successful than nests in smaller, closely spaced trees. That many unsuccessful nests were located in small, closely spaced trees indicates that some extrinsic factor, such as predation, may render large, widely spaced trees better nesting habitat. The advantage of widely spaced trees may relate to a behavioral characteristic, to the presence of fewer predators, or to some other environmental factor, such as food or temperature. Large trees provide more potential nest sites that may be higher off the ground than smaller trees and may provide greater protection from ground predators, as is typical of other areas (Martin 1988). In addition, large trees can produce more mamane pods and thus provide more food.

Three of our findings indicate that food resources may limit Palila productivity: brood reduction, variability of fledging age (23 to 29 days), and greater fledging age in nests with two nestlings. Brood reduction is commonly associated with unpredictable and limited food availability (Ricklefs 1965; Howe 1978; O'Connor 1978,

1979; Bechard 1983). In the Mauna Kea Forest, mamane flowering and pod production vary considerably between years and between sites (van Riper 1980b). When local food supply is favorable, nestlings probably develop more rapidly and fledge earlier than when food is scarce (Skagen 1988), which could account for the variability of Palila fledging age.

In conclusion, hatching failure and depredation limited Palila nesting success. Inbreeding is postulated as a cause for hatching failure, but because hatching success decreased late in the season, inadequate food supply is also suspected. Depredation by feral house cats and black rats was documented. Clearly, more research is needed to determine the importance of these factors. A long-term study of the reproductive success of known individuals along with measurement of nest habitat and food availability and quality is necessary. In addition, research is needed to determine the influence of mamane pod, insect, and other food availability on Palila nest success. To determine Palila productivity, data should be collected on survivorship, the number of broods raised per year, and the age, timing, and success of first breeding. Information on the amount of inbreeding and degree of genetic variability would help determine the genetic fitness of the Palila.

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