

BREEDING ECOLOGY OF THE HAWAII COMMON AMAKIHI¹

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Abstract. The ecology and breeding biology of the Common Amakihi (*Hemignathus virens*) was studied on Mauna Kea, Hawaii, from 1970 through 1981. Common Amakihi retained mates for more than one season and returned each year to the same area to breed. There was an excess of unmated males in the population. First-year birds were rarely successful in their initial breeding attempt. The species had a protracted breeding season, with nests found in every month of the year except August through October. However, the most intensive breeding occurred from March to May, that period of greatest mamane (*Sophora chrysophylla*) flowering.

Ritualized courtship in the Common Amakihi included high altitude and low altitude chases. Territories encompassed the nest site and all food resources, and was a fixed location that often had the same boundaries in succeeding years. The size and location of territories were related to available food resources. Nests were statant, open cupped, with mamane trees the preferred nesting substrate. Clutch size averaged 2.5 eggs and varied between years such that, in a year of low food availability, birds with smaller clutch sizes fledged more young than did those with larger clutches. Incubation period was 14 days and clutches hatched asynchronously. Difference in nestling sizes resulted in brood reduction through elimination of the smallest individual in years of decreased food supply. The nestling period averaged 17 days and young usually fledged synchronously. Both parents fed the young but only the female incubated and brooded. Based on 150 nests with complete records, hatching success was 53.5%, fledging success was 64.9%, and overall reproductive success was 34.7%. The major mortality factor during the breeding cycle was nest desertion by the adults.

There were six major factors which influenced productivity on Mauna Kea. The two most important were length of the breeding season and clutch size. Other factors were territoriality, hatching sequence, nestling growth rates, and nestling mortality.

Key words: Hawaii; Common Amakihi; breeding biology; productivity; effective territory; clutch size; reproductive success.

INTRODUCTION

The endemic land birds of the Hawaiian archipelago provide one of the most striking examples of insular adaptative radiation and convergent evolution. Despite this fact, very little intensive behavioral field work has been done on this group of birds. In an effort to provide much needed base-line information on the breeding ecology of this unique group, I conducted a 10-year study of the Hawaii Common Amakihi (*Hemignathus virens*).

The Hawaii Common Amakihi, described as the Olive-green Creeper by Latham in 1782 (Wilson and Evans 1890-1899), has been placed in several genera (*Himatione*, *Chlorodrepanis*, *Loxops*), with the most recent being *Hemignathus* (Pratt 1979). Four subspecies are recognized from the islands of Hawaii, Kauai, Oahu, and the Maui complex. It is the second most abundant native

forest bird in Hawaii (Scott et al. 1986). Baldwin (1953) analyzed food habits and monitored population movements at Hawaii Volcanoes National Park; Eddinger (1970) studied the breeding biology of the Kauai subspecies (*H. v. stejnegeri*); Berger (1969) worked on the breeding season of the Hawaii race on Mauna Kea; MacMillen (1974) measured bioenergetics of both Kauai and Hawaii forms; Richards and Bock (1973) analyzed Common Amakihi feeding adaptations; Kamil (1978) and Kamil and van Riper (1982) studied systematic patterns of foraging for nectar; Kern and van Riper (1984) looked at the insulative quality of their nests along an altitudinal gradient.

The purpose of this study was to examine what regulatory mechanisms were operative in the Common Amakihi population on Mauna Kea, Hawaii. Specific objectives were to: (1) determine the timing and length of the breeding season and what factors most greatly influenced them; (2) describe the breeding biology, includ-

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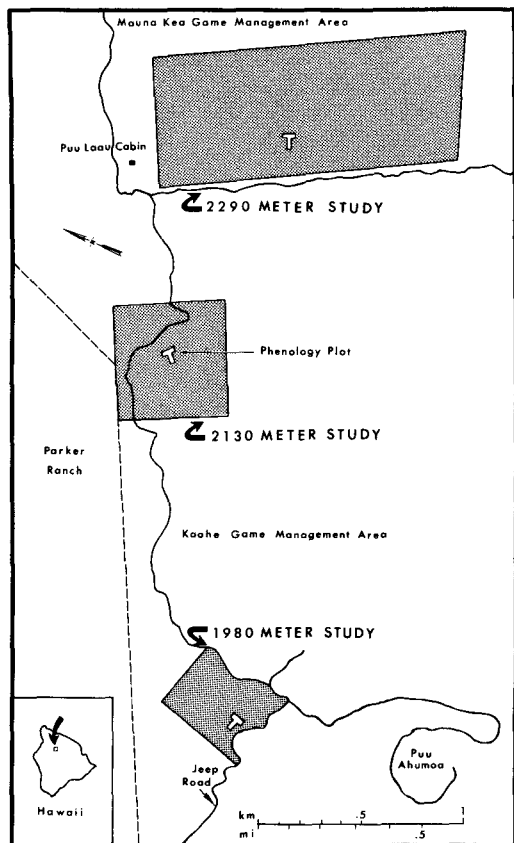


FIGURE 1. Study areas on the southwestern slope of Mauna Kea, Hawaii. Stippled areas are study sites and white "T" inside each are vegetation phenology plots.

ing courtship, territory, nesting, and reproductive success; (3) determine the type of territoriality and how it influenced productivity; and (4) relate the breeding ecology to population productivity.

MATERIAL AND METHODS

From late 1970 through 1981, I studied the ecology and behavior of the Common Amakihi. During 1970 to 1975, I concentrated on the breeding biology, while from 1976 to 1981, I monitored this color-banded population to determine the species' feeding ecology and longevity. Study sites were in the Kaohe and Mauna Kea Game Management Areas at Puu Laau, on Mauna Kea, Hawaii (Fig. 1). I captured adults by mist-net and marked each with U.S. Fish and Wildlife Service metal band, and unique combinations of col-

ored plastic bands. Nestlings were banded between 8 and 10 days of age.

Adult Common Amakihi 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. I took the following measurements: beak length (measured with a flexible celluloid rule, see Amadon 1950:178), tarsus length, weight (using a Pesola scale), and rectal temperature (with a size 402 rectal probe from YSI model 43 Single Channel Tele-thermometer). Molting patterns were examined for all captured individuals and observations were made of museum specimens. I also weighed nestlings daily, and described feather tract and physical development from photographs.

Territory size was determined by plotting known boundaries from color-band sightings, then using an overlay with a known density of dots. Nest measurements included nest height (distance from ground to nest base), nest-tree height and species, circumference at breast height 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 the 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 color patterns were recorded for each clutch. Egg shape index was calculated on the basis of the following:

$$\text{Egg Shape Index} = \frac{\text{short egg axis}}{\text{long egg axis}} \times 100$$

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

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

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 sea-

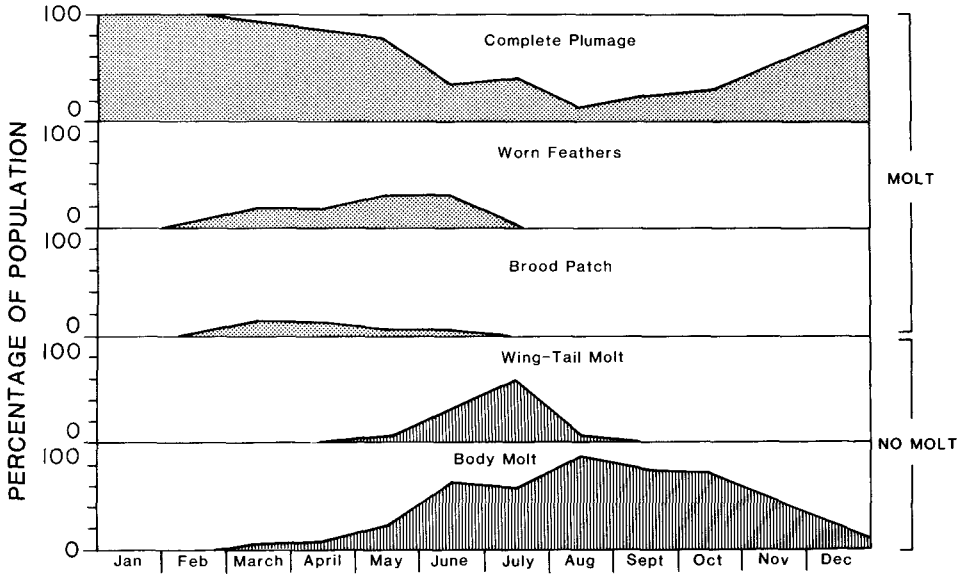


FIGURE 2. Yearly molt pattern in the Common Amakihi as recorded from 579 birds captured on Mauna Kea, Hawaii.

son was considered the average number of days per year when active nests were found. Length of the nest cycle was:

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

where *b* = nest building interval, *d* = number of days for egg laying, *y* = incubation period, *n* = nestling period, and *f* = fledgling period, or when young are still dependent upon the adults. In order to determine the number of young produced per unit area of habitat, 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:

$$D = \frac{(d)(z)}{2}$$

where *d* = observed population density and *z* = percentage of population not floating. The *z* value was calculated from a comparison of mist-net capture data of breeding and nonbreeding birds, and is expressed as a seasonal value.

Data obtained from the National Weather Service Puu Laau station were used for monthly

rainfall analysis, while I recorded daily wind direction and percent cloud cover in the field. Temperature and humidity were recorded with a hydrothermograph placed under a tree canopy.

RESULTS

SEX RATIOS, WEIGHT AND MOLT PATTERNS

I captured and banded over 1,000 Common Amakihi during this study. A total of 579 breeding adults was captured between 1970 and 1975. By 1974, 78% of the resident breeding birds were

TABLE 1. Common Amakihi measurements.

Measurement	Number measured	Range	\bar{x}	SE
Beak Length (mm)				
Male	77	12.0-16.0	14.4	0.1
Female	48	11.0-15.5	13.1	0.1
Immature†	148	10.5-16.0	13.2	0.1
Tarsus length (mm)				
Male	19	21.0-24.0	22.8	0.2
Female	9	21.0-23.0	22.1	0.2
Immature	48	19.0-24.0	21.9	0.1
Weight (g)				
Male	144	11.0-15.6	14.0	0.1
Female	88	10.5-16.2	13.4	0.1
Immature	172	9.8-14.9	13.0	0.1

† Birds in subadult plumage.

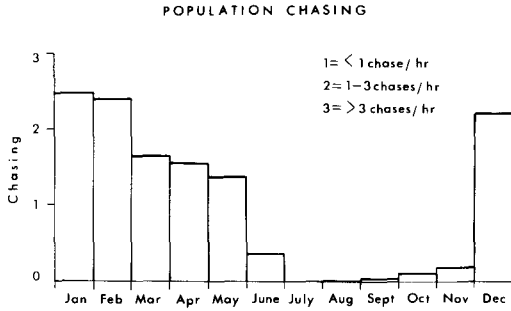


FIGURE 3. Numerical index of intraspecific Common Amakihi chases by month, as recorded during 98 hr of observation during 28 days in 1974 and 1975 ($n = 107$ chases).

color-banded and by 1975, 84% were marked. Of all recaptures, 56.8% were within one month after initial capture. More males than females were captured ($\chi^2_c = 20.0$; $P \leq 0.001$). Amadon (1950), in his sex-ratio analysis of museum specimens, also found a disparity of male to female birds in many of the Drepanidinae.

Weights of male, female, and immature Common Amakihi were significantly different (one-way analysis of variance; $P \leq 0.001$). The average male was 4.3% heavier than the female and 7.5% greater than immature birds (Table 1). Greatest weight variance occurred in the female. From the beginning of the breeding season, males lost weight over the next five months, so that the average weight in June (13.5 g) was significantly less than the mean February weight (14.3 g). Females, on the other hand, gained approximately 0.8 g from February to May.

Molting birds can be found in every month except January (Fig. 2). Male Common Amakihi do not develop their adult body plumage (bright yellow) until after their first breeding season, that is, after their first postnuptial or second prebasic molt at an age of 15 to 17 months.

COURTSHIP BEHAVIOR, VOCALIZATIONS, AND DISPLAYS

Common Amakihi retained one mate for a number of years ($n = 42$). However, courtship behavior between unmated birds was observed each year, especially during the protracted initiation of the breeding season from December to February. Courtship chasing was common and of two types: (1) in high courtship chase, males pursued females slowly in a gentle rising arc up to 30 m altitude, with a slight fluttering at the apex;

TABLE 2. Common Amakihi courtship feeding rates.

Day of cycle	Hr observed	Total feedings	\bar{x} number of feedings/hr
0-3	7.0	6	$\bar{x} = 0.86$ SE = 0.28
4-6	7.0	7	$\bar{x} = 1.00$ SE = 0.22
7-9	8.5	8	$\bar{x} = 0.88$ SE = 0.23
10-12	16.5	13	$\bar{x} = 0.75$ SE = 0.17
13-15 (Hatching)	25.3	11	$\bar{x} = 0.44$ SE = 0.12
16-18	21.5	11	$\bar{x} = 0.52$ SE = 0.11
19-22	28.0	11	$\bar{x} = 0.39$ SE = 0.09
22-24	23.5	3	$\bar{x} = 0.13$ SE = 0.07
25-27	15.5	5	$\bar{x} = 0.33$ SE = 0.16
28-30	12.0	2	$\bar{x} = 0.17$ SE = 0.11
31 (Fledging)	7.0	0	0

and (2) in low courtship chase, males rapidly pursued females, usually in a straight line and at lower altitudes. Both types of displays were often interrupted by conspecifics. Chasing in the population increased during the early breeding season, peaking from December through February (Fig. 3). The daily chase pattern revealed greatest chasing at 09:00 and 15:00. In the Common Amakihi these chases may serve as an adaptive mechanism of ensuring synchronization of the sexual cycle between members of a pair, and possibly stimulating other members of the population as well.

I consistently observed two types of advertising displays. High advertising flight involved males making four or five concentric circles over an area, hovering, then returning to a perch. Low advertising flight, characterized by slow fluttering wing beats followed with a glide, was usually given in a gentle arc over an established territory, either in silence or accompanied by primary song.

A flitting display, observed principally during pair formation of unmated individuals, took two forms depending upon the female's reaction (Fig. 4). In the case of a "stationary nonresponsive female," the male either: (A) flew directly at the perched female, veering off at the last moment; (B) hopped around her; or, as was most usual (C)

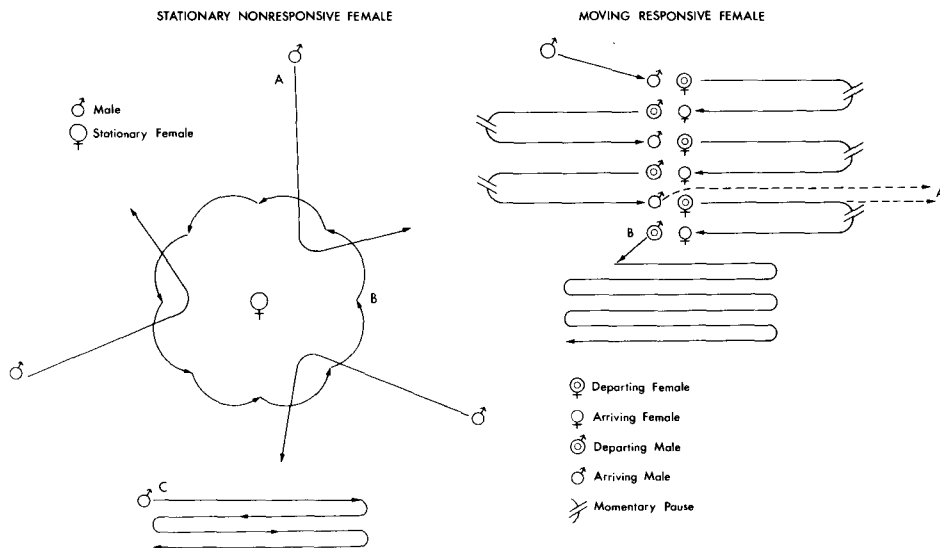


FIGURE 4. Pair formation flitting display of the Common Amakihi. Each behavioral sequence involves only one male and one female. The “Stationary Nonresponsive Female” sequence occurred between a mated female and an intruding male. The “Moving Responsive Female” sequence occurred between unmated birds.

flew rapidly back and forth below her. The display was given in silence or accompanied by subsong, and the female typically changed direction to face the male. On several occasions males gave low advertising flight after this flitting display. In the case of a “moving responsive female,” she would fly to the edge of the tree, pause, then quickly return to the original perch. It looked as if the birds were knocking each other off the limb, but no actual contact was made. The usual sequence was about six turns, but sometimes lasted longer. The display was terminated by either: (A) the female flying away, with the male in immediate chase; or (B) the male flying rapidly back and forth below the female, followed by a courtship chase.

Courtship feeding, often initiated by female wing quivering, was common during the nesting cycle, particularly during the incubation period (Table 2). This behavior not only helped to maintain the Common Amakihi pair bond, but also supplied food to the female, a function emphasized by Royama (1966). Males fed females an average of 7.1 (SE = 0.82) times during a single feeding bout ($n = 59$ feeding bouts).

The Common Amakihi utilized two songs, a primary song given by the male and extended subsong given by either sex. The birds also gave a variety of calls and location notes during foraging, courtship interactions, and distress situ-

ations. This species did not use a flying predator call.

Common Amakihi singing, measured by monitoring all songs heard in study areas throughout 194 days of the annual breeding cycle, showed increases in late October and again in late February (Fig. 5). During the breeding season, Common Amakihi song peaked during nest building and incubation, then gradually decreased over the remainder of the breeding cycle. The frequency of daily song steadily increased during the morning hours, diminished during the afternoon, then peaked just before dusk (Table 3). Evening song was measured on four nights, two during early and two during late breeding. In March, a large number of songs were recorded from 17:30 to 18:00 ($\bar{x} = 17.1$ songs/5 min; SE = 4.9), followed by a sudden drop, presumably as birds prepared to roost for the night. Just before sunset there was another outburst of primary song usually lasting 15 to 20 min. In May, when territorial song was rarely heard, there was still an increase of song just prior to sunset (van Riper 1978).

I observed copulation on 22 different occasions, and no consistent pre or postcopulatory display was used. The usual sequence began when the female lowered her body, wing quivered, and gave a soft call. The male then mounted, usually from the side. I observed copulation from three

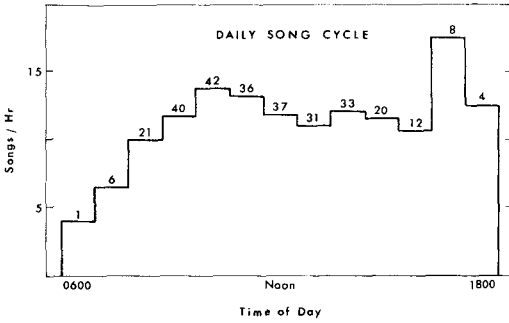


FIGURE 5. Mean number of daily songs/hr recorded during each month of the year in the Common Amakihi population at Puu Laau, Hawaii. Numbers denote hr of observation during that month ($n = 194$).

weeks before, and through nest building. Reverse copulation occurred only in the very early breeding period.

TERRITORY

For approximately one month prior to the breeding season, each pair occupied a loosely held, often overlapping area that would be classed as a home range rather than territory (Fig. 6). The 31 home ranges that I measured in January 1975 averaged 0.45 ha (SE = 4.1), and were significantly larger (t -test = 2.97; $df = 67$; $P \leq 0.005$) than were 38 territories which averaged 0.33 ha (SE = 1.7) during late April. As the breeding season progressed, boundaries became more clearly defined (see March of 1975, Fig. 6), and once established, territories were mutually exclusive. There were, however, still uncertain and disputed boundaries throughout the breeding season. Territorial defense was primarily the male's role and was done by song, chasing, and/or perch displacement. Minor alterations in territory boundaries occurred throughout a breeding season, but original territories were not significantly reduced in size (Table 4). A territory was held by the same pair for more than one season ($n = 33$), and one male banded in 1971 held the same territory until 1980. If either the male or female died, the survivor retained the territory and attracted a new mate.

Common Amakihi territories ranged in size from 610 m² to 7890 m². In an attempt to explain this size variation, I selected six territories in 1974 and delineated with a tape measure all substrate that was not covered by tree canopy (Fig. 7). In all six, the remaining area (effective territory size) was similar (range = 1,000 to 1,400

TABLE 3. Daily song cycle of the Common Amakihi during 1974 at 2,130 m elevation on Mauna Kea, Hawaii. Sample sizes are the number of 30-min observational periods made during that hour of the day ($n = 291$).

Hour of day	Sample size	Mean number of primary songs/hr	SE
06:00-07:00	1	4.00	—
07:00-08:00	8	4.75	2.23
08:00-09:00	25	8.56	2.36
09:00-10:00	43	11.37	1.73
10:00-11:00	44	13.14	3.46
11:00-12:00	38	13.24	3.73
12:00-13:00	39	11.28	3.24
13:00-14:00	35	12.03	2.82
14:00-15:00	35	13.66	3.35
15:00-16:00	22	10.50	2.72
16:00-17:00	14	8.43	3.34
17:00-18:00	9	16.00	4.23
18:00-19:00	4	12.26	6.14

m²). This implied that differences observed in territory size were influenced by the amount of tree cover. Moreover, nests were placed closer to each other in predominantly mamane habitat than they were in naio habitat ($t = -4.2$; $df = 20$; $P \leq 0.001$). However, there was no significant difference in distances between nests in predominantly mamane habitat ($t = 1.1$; $df = 21$; $P = 0.27$). This suggests that tree-species composition in an area was also an important selection factor in territory size.

Although Common Amakihi are intraspecifically territorial, they exhibited little interspecific aggression. Many bird species were tolerated within the territory, sometimes as close as 1 m from the nest. Palila (*Loxioides bailleui*), Elepaio (*Chasiempis sandwichensis*), Red-billed Leiothrix (*Leiothrix lutea*), House Finch (*Carpodacus mexicanus*), Melodious Laughing-thrush (*Garrulax canorus*), Eurasian Skylark (*Alauda arvensis*), and numerous game birds all nested regularly within Common Amakihi territories.

THE NEST

I obtained nest histories on 174 nests from Mauna Kea. All nests were statant and cup-shaped, averaging 6.9 cm in height by 9.4 cm in width (Table 5). At Puu Laau, mamane was the preferred nesting tree (88% of all nests). Within the study areas, 352 naio and 265 mamane trees were classed according to mean height and then compared to heights of 174 trees that contained nests (Fig. 8). In general, nest trees were somewhat

TABLE 4. Seasonal changes in select Common Amakihi territory sizes (in m²) during 1975 at the 2,130-m study area, Puu Lauu, Hawaii.

Territory number	Early February	Early March	Early April
65-75	2,450	2,910	2,300
32-75	3,450	3,220	2,300
21-75	1,610	3,840	3,300
18-75	610	540	690
70-75	3,990	4,060	4,220
23-75	3,760	5,680	3,990
53-75	2,530	—*	2,530
16-75	840	2,680	2,450
169-75	3,300	3,990	3,450
180-75	1,380	—	—
29-75	1,610	1,690	1,840
37-75	3,220	2,070	3,140
35-75	1,610	1,840	4,220
49-75	2,680	—	2,680
42-75	2,380	2,990	4,300
40-75	7,890	—	3,450
28-75	2,530	2,150	2,450
55-75	1,530	3,070	3,450
43-75	2,380	1,760	1,760

* Missing numbers (—) are where territory boundaries were not clearly ascertained.

taller than would be expected if birds selected trees solely on the basis of their availability ($\chi^2 = 28.19$; $P \leq 0.01$). As larger trees have more foliage, they have more potential nest sites and this may in part explain the increased number of nests in the larger trees. Furthermore, nest height in both mamane and naio was influenced by tree height in that as tree height increased, so did nest height.

More than 78% of 386 Common Amakihi nests that I found in mamane were either in terminal or lateral forks; however, in 126 naio nest placements, only 45 were in lateral and 32 in terminal forks. Both male and female took part in nest-site selection. Usually the female moved from branch to branch with a large blade of grass in her bill, continually testing sites by pushing the grass into forks and onto branches, while the male followed closely behind.

Nest building lasted from 8 to 17 days for the first nest ($\bar{x} = 10.6$ days; $n = 20$); however, most construction was usually completed by day 7 (Table 6). Renesting attempts were completed in less time and ranged from four to eight days ($\bar{x} = 5.7$ days; $n = 9$). I observed only the female building; on one occasion a male carried material, but it was not incorporated into the nest. Construction of the nest lining took one to three

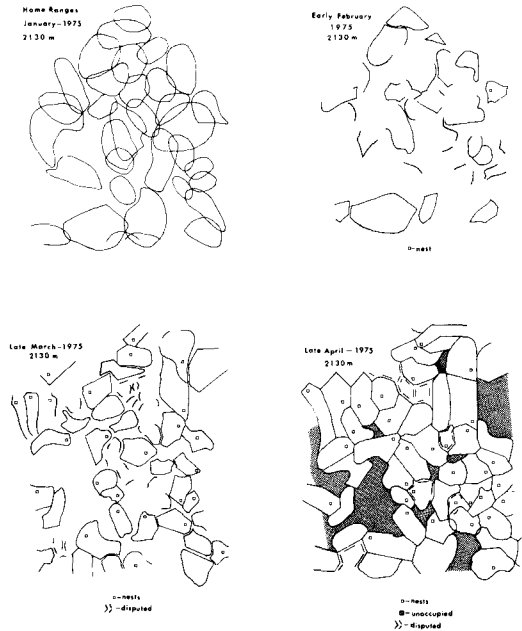


FIGURE 6. Sequential development of Common Amakihi territories during the 1975 breeding season at 2,130 m elevation on Mauna Kea, Hawaii. "January" shows overlapping home ranges; "Early February" shows formation of partial territory boundaries, but the majority of birds were still in a home range situation; "Late March" shows that early breeders have established complete territory boundaries and begun to nest, whereas new breeders are still defining their boundaries; "Late April" is the peak of the breeding season and most territory boundaries are well defined. In this last period of the breeding sequence, birds that still have disputed boundaries were invariably unsuccessful breeders. Moreover, grey stippled areas are, apparently, not suitable breeding habitat (see van Riper 1984).

days. The daily nest construction cycle showed most building in the morning, slowing somewhat during the middle of the day (12:00 to 14:00), and then a slight upsurge of activity. Rarely did birds build in the late afternoon. From day eight to egg laying, little time was spent at the nest site.

Techniques of building involved first laying large pieces of grass into the nest site, until a circular structure resembling a doughnut was formed. Material was woven into the structure and bulky material was continually added to the bowl until the body of the nest had been completed (usually before day 5). During the last two days of bowl construction, the female often sat in the nest and molded the rim with her body, at times picking out strands of grass and reweav-

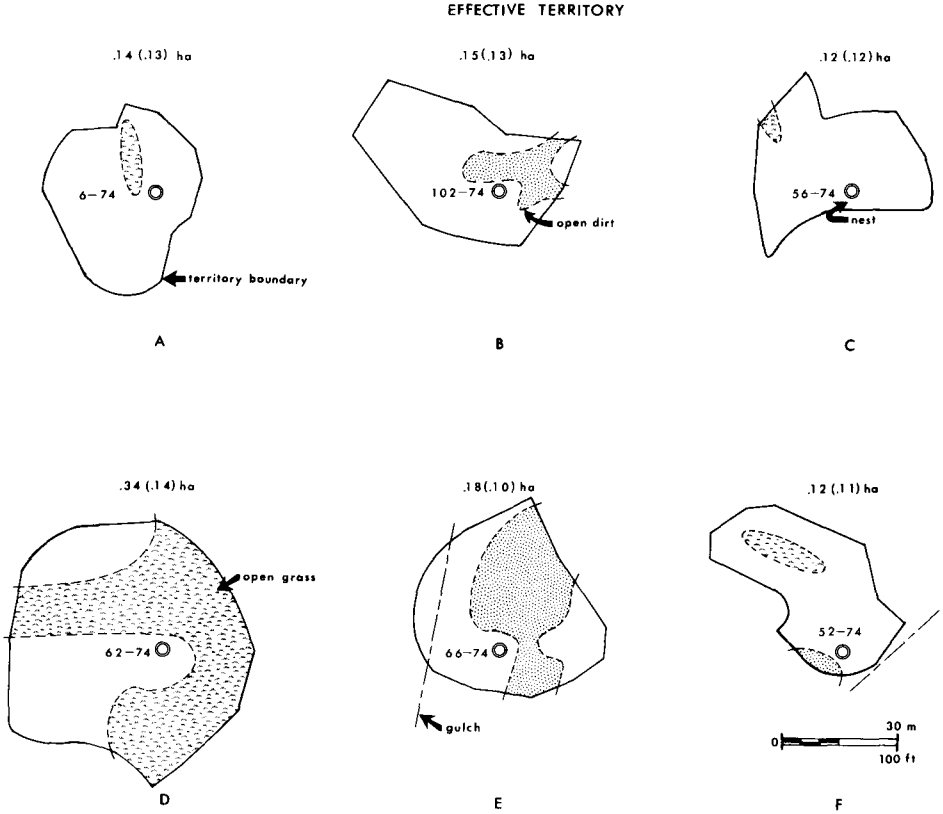


FIGURE 7. Size and shape of six randomly selected Common Amakihi territories in relation to habitat types within each territory. Circles denote location of nests within the territory, and numbers adjacent to the circles are nest numbers. The nonstippled portions of each territory is that area covered by tree canopy. Numbers above each territory are the original size (ha), while the numbers in parenthesis are the sizes of the territory after those portions without tree cover were removed.

ing them back into the sides. The principal material used in construction of the nest were coarse grasses and sometimes sheep wool (van Riper 1977); materials used in the lining were lichens, rootlets, pig hair, and fine grasses (Kern and van

Riper 1984). When lichen (especially *Usnea* sp.) was used, the female body packed rather than wove the nest lining. Most nest constituents were gathered on the ground within the territory. Ed-dinger (1970) reported frequent stealing of nest

TABLE 5. Dimensions and mass of Common Amakihi nests collected from Puu Laau, Hawaii.

Nest feature	Number measured	Mean (SE)	Range
Nest height	115	6.9 cm (0.15)	3.0-11.9 cm
Minimum nest width	74	9.0 cm (0.16)	5.6-11.9 cm
Maximum nest width	86	10.9 cm (0.20)	6.1-17.3 cm
Bowl width	152	5.2 cm (0.08)	3.0-9.6 cm
Bowl depth	83	3.5 cm (0.08)	1.3-6.4 cm
Minimum rim thickness	71	1.5 cm (0.07)	0.5-3.8 cm
Maximum rim thickness	84	3.0 cm (0.11)	0.5-5.6 cm
Nest lining weight	21	5.4 g (0.53)	2.0-11.6 g
Nest weight	18	18.8 g (1.26)	13.6-33.5 g

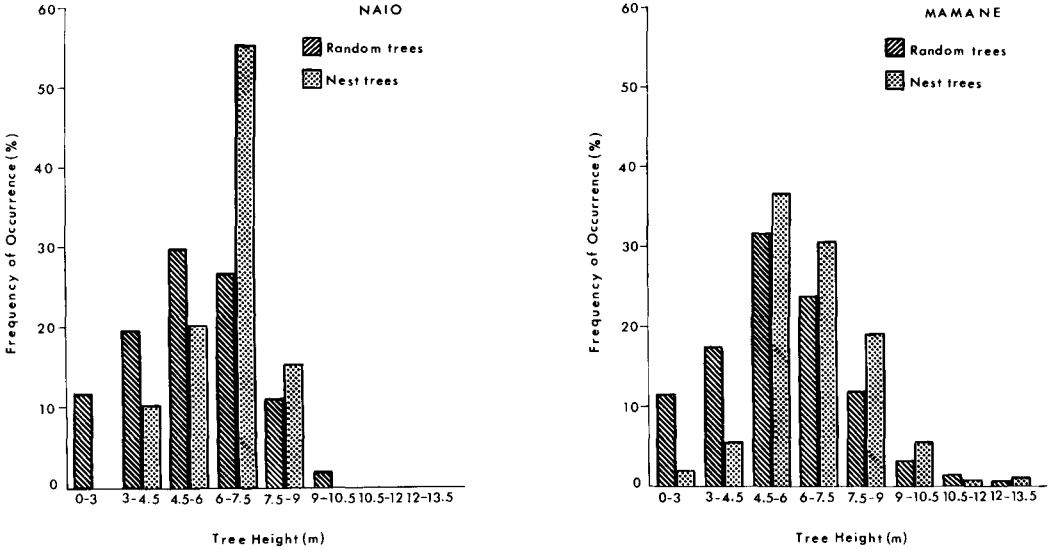


FIGURE 8. Heights of 173 Common Amakihi nest trees in relation to heights of a random sample of 265 mamane and 352 naio trees at Puu Laau, Hawaii.

materials in the Kauai Common Amakihi, whereas I observed only one case of this on Mauna Kea.

Mean distance between first and second nests was 21.1 m ($n = 59$; $SE = 2.3$), with the re-nesting attempt usually towards the opposite side of the territory. Second nesting after desertion was more rapid than when successful fledging occurred. If the first nest was deserted, re-nesting occurred in 6.2 days (range = 1 to 9 days; $n = 13$), while if the nest was successful in fledging young, re-nesting did not occur until an average of 22.2 days after fledging (range = 7 to 35 days; $n = 9$). There was a difference in the second nesting effort between 1974 and 1975. With approximately the same number of birds breeding each year, 35 re-nestings were recorded in 1974 whereas only 10 were noted the following year.

TABLE 6. Common Amakihi nest construction.

Day of building	Hr observed	Average time spent building (min/hr)
1	1.0	8.5
2	9.6	21.6
3	17.3	45.6
4	13.9	26.7
5	15.0	34.5
6	9.3	35.4
7	2.0	29.7
8	1.5	8.0

EGGS AND CLUTCH SIZE

The average clutch size in 185 nests (1971 to 1975) was 2.50 eggs ($SE = 0.04$). Most clutches contained two or three eggs; I found only two 1-egg and two 4-egg clutches. Size of the second clutch did not differ significantly from the first. Clutch data were analyzed for a 5-year period and differed between years (one-way analysis of variance; $F = 4.6$; $P \leq 0.01$). A S-N-K multiple range test showed that the greatest difference in clutch size was between 1971 + 1975 and 1974 (Table 7).

Average weight of 21 eggs was 1.6 g ($SE = 0.05$), while shell weight of 27 blown eggs averaged 0.11 g ($SE = 0.01$). Common Amakihi egg color was whitish with light and dark purple markings interspersed by brownish splotches,

TABLE 7. Common Amakihi clutch sizes in different years at Puu Laau, Hawaii.

Year	Number of clutches†	Range of clutch size	Mean clutch size	(SE)
1971	28	2-3	2.32	(0.08)
1972	35	2-3	2.51	(0.08)
1973	9	2-3	2.44	(0.17)
1974	72	1-4	2.68	(0.07)
1975	41	2-3	2.29	(0.07)
Total	185	1-4	2.50	(0.04)

† First and second clutches were pooled because there was no significant difference between them.

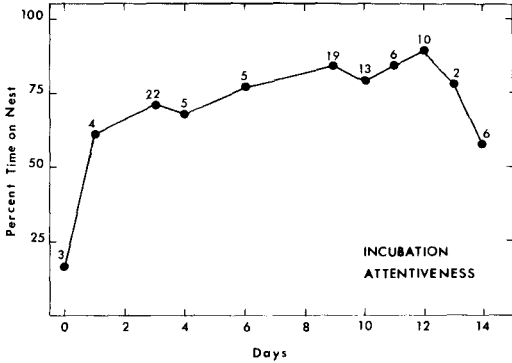


FIGURE 9. Attentiveness during incubation as measured at 12 Common Amakihi nests. Numbers denote hr of observation ($n = 95$).

usually concentrated in a cap or ring at the large end (van Riper 1978). Total amount of pigment covering the surface of an egg was variable, and Berger (1981) also noted differences in marking among Hawaii Common Amakihi egg patterns. Egg shape (after Preston 1953) was oval. Mean length of 90 eggs was 19.0 mm (SD = ± 1.1 ; range = 15.8 to 21.7 mm) and width was 13.9 mm (SD = ± 0.05 ; range = 12.6 to 15.0 mm). Mean egg shape index was $68.1 \pm 0.3\%$.

INCUBATION PERIOD

Mean duration of incubation in 22 nests was 14.1 days (range = 12 to 16 days). The modal incubation period was 14 days at 6 nests. Only the female incubated and only she developed a brood patch. Nest attentiveness throughout the incubation period showed low attendance during day 0, then a rapid rise so that on days 1 through 12 the female was on the nest most of the day (Fig. 9). Females sat the entire night throughout the incubation period. If the clutch did not hatch, incubation was extended, and in one instance lasted 30 days before abandonment.

NESTLING PERIOD

Hawaii Common Amakihi nestling periods varied from 15 to 21 days ($\bar{x} = 16.8$ days). There was a significant difference in the nestling period between 1974 ($\bar{x} = 16.4$ days; 12 nests) and 1975 ($\bar{x} = 17.3$ days; 18 nests: t -test; $P \leq 0.05$).

PARENTAL CARE OF THE YOUNG

Only the female brooded young. A decline in attentiveness started at day 3; by day 8, less than 20% of the daylight hours were spent brooding

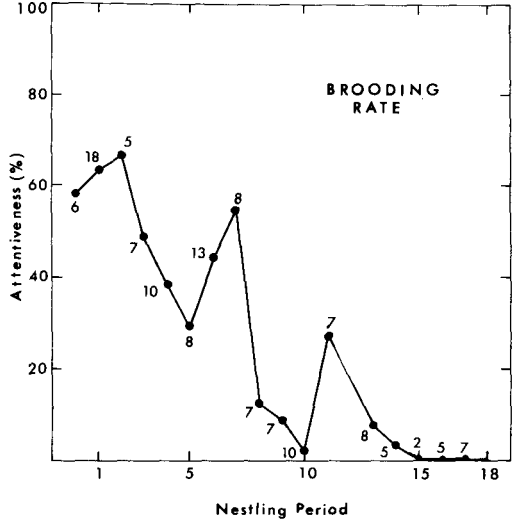


FIGURE 10. Common Amakihi brooding rates as measured at 11 nests. Numbers denote hr of observation ($n = 133$).

(Fig. 10). During rain showers, brooding rates increased slightly; however, females sometimes left the nest while it was still raining. Most Common Amakihi nests were placed well under the canopy, but in nests that did receive direct sunlight, sun-shading by the female did occur.

In most cases hatching was staggered over a 10-hr period. As a result, size of young within a clutch differed throughout the nestling period. After hatching, egg shells were removed from the nest by the female. In some instances they were carried away, but most of the time shell fragments were simply dropped over the nest rim; average distance of shell pieces from nine nests was 1.9 m. Eggs that did not hatch remained in the nest.

Both male and female fed the young. The female fed more frequently, but her feedings/nestling/hr decreased significantly ($t = 3.15$; $P \leq 0.01$) during the nestling period whereas male feedings did not increase significantly ($t = 1.20$; $P = 0.25$; Fig. 11). However, the male courtship-fed the female during this time, and she would in turn feed the young; therefore, he was contributing more food than it would appear if only feeding rates at the nest were recorded. The total number of feedings/hr for each nestling by parents was constant throughout the nestling period, in that $r = -0.35$ and did not differ significantly from zero ($t = 1.50$; $P = 0.15$). The number of times

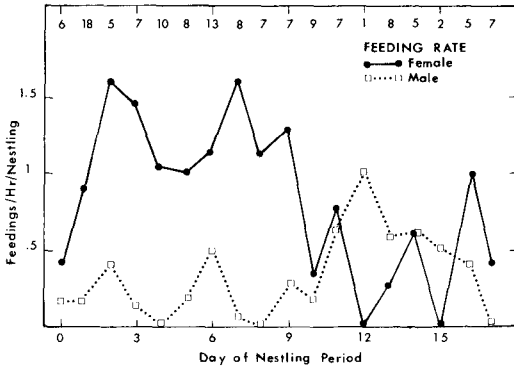


FIGURE 11. Number of feedings by male and female Common Amakihi/nestling/hr as measured at four nests. Numbers denote hr of observation ($n = 133$).

a nestling was fed during a feeding trip to the nest, however, significantly increased over the nestling cycle ($t = 2.52$; $P \leq 0.05$).

One complication in Common Amakihi nestling food analysis is the difficulty of measuring nectar (Baldwin 1953). It appeared that during the first week of nest life, insects formed a large part of the diet, after which young were fed other types of food (e.g., nectar by regurgitation). As I weighed young, they would often defecate when being held. Early in the nestling period fecal sacs were dark with many insect parts, but later (usually after day 5) they were filled with a yellow-colored fluid ($n = 115$), suggesting that more nectar was being fed at that time.

Both parents regularly removed fecal sacs from the nest. The sacs were rarely dropped because the adults either ate them, or, later in the nestling period, would flay them against a branch and eat only the covering. During the first two days of the nestling period, sacs were removed at a rate of 0.4/hr; from day three to five, disposal averaged 0.9/hr, and from day 6 until 10, the rate rose to 1.4/hr/nest. After this time, young could stand and defecate over the nest rim, and removal rate decreased to almost nothing for the remainder of the nestling period. Common Amakihi nests remained clean throughout the nestling cycle, with generally the only trace of fecal material being the last defecation of the young as they fledged.

NESTLING DEVELOPMENT

Young at hatching were flesh-pink colored with grey down in the pterygia; eyes were closed and

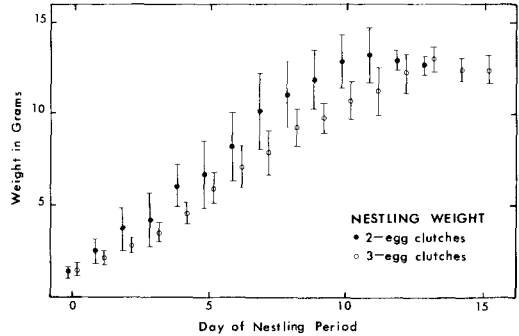


FIGURE 12. Daily weights of 23 Common Amakihi nestlings from 2- and 3-egg clutches at nine nests. Circles are means and line \pm 95% C.I.

did not open until day 5 to 7. The bill was yellowish and the gape pattern revealed a single rose-red target area. All the pterygia were dark except for the ventral, which ranged from whitish to a deep yellow. Feather tracts darkened slightly on the second or third day, and became steadily darker until the quills emerged. The tracts developed and opened at different rates (Table 8). Weight increased from hatching until day 11 (4 nests with 2 young) or day 13 (5 nests with 3 young), when it leveled off (Fig. 12). Young from clutches of three consistently weighed less than did birds from clutches of two. Nestling Common Amakihi were apparently able to regulate their internal temperature after day 8 (Table 9). The fear response followed opening of the eyes, but cowering developed gradually; young gaped readily when I tapped lightly in the nest rim usually until day 8.

FLEDGING OF YOUNG

All the young from a given nest would usually fledge on the same day ($n = 31$). In four nests, I found that the heaviest bird fledged a day prior to the others, and by the next day was dead on the ground. In most instances, young climbed onto a branch and remained there for at least one day. In three cases, I observed young fly from the nest, and after a series of rapid wing beats plummet to earth. Parents then coaxed the young into a tree; the young ascended by both flapping and climbing.

The first week out of the nest was primarily spent preening, resting, and begging for food. Both adults fed the young, but the load shifted to the male if the female readied herself for the next nesting effort. At two nests, I observed parents

TABLE 8. Development of feather tracts in Common Amakihi nestlings.*

Feather tracts	Day of nestling period																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Spinal																	
Alar								-----									
Ventral								-----									
Caudal																	
Femoral								-----									
Crural																	
Capital																	
Humeral																	

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

still feeding young from their first nest while in the process of feeding the newly hatched chicks of the second, but this was not usual.

If the first nesting was late in the season, or if two broods were successfully raised, the birds

TABLE 9. Cloacal temperatures of Common Amakihi young over the nestling period.

Day of nestling period	Number of birds measured	Average cloacal temperature °C	Cloacal temperature range °C
0	2	20.8	19.4-22.2
1	6	21.3	24.4-31.1
2	3	27.3	24.7-30.3
3	5	29.6	27.5-32.8
4	3	31.0	27.2-35.6
5	3	33.0	32.2-34.2
6	3	35.7	34.4-36.4
7	3	34.6	32.2-36.1
8	6	37.2	36.4-38.3
9	6	36.0	34.4-38.3
10	7	36.2	33.9-38.6
11	6	35.7	33.6-38.6
12	4	37.2	35.6-38.9
13	4	36.2	34.4-38.3
14	4	36.2	33.9-38.9
15	4	36.1	34.4-38.9
16	2	38.4	38.0-38.9

would leave their territories and form loose post-breeding flocks, which usually consisted of one or more small family groups. In June 1974, I found one bird that had been color banded as a nestling over 9 km from its natal area. A few adults remained within several hundred meters of their nesting site throughout the year, but their young presumably dispersed (or at least were never observed). In one case, young remained with the parents throughout the nonbreeding season; this was on a home range where a naio tree was heavily fluxing sap (van Riper 1984). During 1975, three birds banded as nestlings in 1974 tried to nest near the area where they had been raised; all were unsuccessful.

REPRODUCTIVE SUCCESS

My analysis of Common Amakihi reproductive success was based on 150 nests with complete records; 282 eggs laid, 151 eggs hatched, and 98 young fledged. Common Amakihi hatching success was 53.5%, fledging success 64.9%, and overall reproductive success 34.7%.

Reasons for Common Amakihi nest failures were compared in terms of the fate of eggs and young (Table 10). Most mortality was due to nest

TABLE 10. Summary of Common Amakihi nest histories from 1971 to 1975.

	Year					Total
	1971	1972	1973	1974	1975	
Eggs laid	10	12	10	169	81	282
Young fledged	3	5	0	63	27	98
% eggs and young lost each year due to:						
Poor nest construction	0	0	0	3.5	4.9	3.5
Failure to hatch	10	0	30	13.6	6.2	11.3
Desertion	40	0	70	26.0	29.6	28.0
Unexplained nestling death	0	8.3	0	6.5	13.6	8.2
Weather	0	41.6	0	5.3	3.7	6.0
Predation	20	8.3	0	7.7	8.6	8.2

desertion immediately following egg laying, usually early or late in the breeding season. Failure of eggs to hatch accounted for 11.3% of the eggs laid. Of eggs in 3-egg clutches, 13.7% did not hatch whereas only 3.8% of the eggs in 2-egg clutches failed. This difference might be due to freezing temperatures during the nights at Puu Laau (Kern and van Riper 1984). In the Common Amakihi there was a tendency to cover the eggs on the night the penultimate egg was laid; therefore, eggs were not subjected to lowered temperatures in 2-egg clutches while in 3-egg clutches the first egg was left unprotected for one night. Poor hatching might also have been influenced by brood patch size (its ability to cover three eggs) but one would expect all eggs to have an equal probability of being excluded. Predation and unexplained nestling death each contributed 8.2% to the mortality; weather and poor nest construction were the least important mortality factors.

Relative productivity per unit area for the Common Amakihi was 2.5, and, with approximately 81 breeding pairs/100 ha (van Riper et al. 1978), total productivity/100 ha was approximately 203 young. Although there was no significant difference in Common Amakihi nesting success between the years, 1.8 times as many young were produced in 1974 as 1975 (26 vs. 49) with the same approximate number of birds nesting. The reason for this difference was because the renesting effort was much reduced in 1975, with only 10 attempts, while in 1974 the birds made 35 attempts.

BREEDING SEASON AND POPULATION STRUCTURE

Common Amakihi are apparently long lived. One male, banded in June 1972 as an adult (at least

one year old), was observed until August 1980. Of 14 birds banded as adults in the 2,130-m study area during 1973, 10 were alive two years later; of 56 banded birds breeding during 1974, 48 were alive one year later. This indicates high survival rates and low turnover in adult Common Amakihi at Puu Laau, as compared to similar sized passerine birds in continental situations.

I found active Common Amakihi nests at Puu Laau during every month of the year except August, September and October. However, the peak of breeding activity occurred from March through May, with 89% of the 150 nests for which I had complete information being active during this time period. Most young fledged during April and May. For example, 18 of 30 nests in the 2,130-m study area fledged during this period in 1974, and in 1975 all ($n = 15$) nests that fledged were in April and early May.

The initiation of the breeding season was variable and coincided with major mamane flowering periods. For example, mamane flowering at 2,130 m elevation peaked during November in 1974, but did not peak until January in 1975 (van Riper 1980). The first Common Amakihi nest that I found in 1974 was in early December whereas in 1975 it was almost one month later. The majority of breeding terminated in June, with very few ($n = 4$) nests active into July.

DISCUSSION AND CONCLUSIONS

Many different mechanisms have been shown to influence productivity, but, as in many areas of ecology, it is difficult to differentiate cause and effect. In the Common Amakihi population at Puu Laau, length of the breeding season, territoriality, clutch size, hatching sequence, nestling growth, and nestling mortality all gave evidence

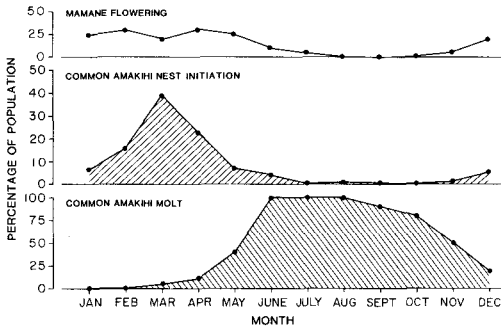


FIGURE 13. Common Amakihi breeding season, molt period, and mamane flowering pattern over the annual cycle on Mauna Kea, Hawaii.

of regulating productivity. No single mechanism was alone responsible, but all acted together in an intricate system of checks and balances.

TIMING AND LENGTH OF MAJOR BREEDING EFFORT

It is uncertain what initiates the Common Amakihi breeding season, but, for most temperate passerines, photoperiod appears to be the primary factor. In Hawaii both Berger (1969) and I have found that in some years Common Amakihi start breeding when day length is still decreasing. Farner and Lewis (1971) found that photoperiod was never the only mechanism that set the precise time of reproduction, but 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 non-temperate passerines as Skutch (1950) could find no single stimulus that explained the initiation of breeding in tropical and subtropical species.

A number of environmental factors at Puu Laau might have acted as a timing mechanism for breeding season initiation. But, whatever the immediate stimulus that influences the initiation of breeding, the major Common Amakihi breeding effort coincided with that time of year when mamane bore maximum amounts of flowers (Fig. 13). Not only did the breeding period seem adjusted to optimal resource availability, but the birds appeared able to make fine adjustments to yearly differentiation in the timing and abundance of this food supply (van Riper 1984). It may well be, however, that the Common Amakihi depends both upon exogenous and endog-

enous timing mechanisms to set an appropriate time for reproduction.

Mechanisms that terminate breeding are poorly understood. The selective factors that have been effective in shaping the termination in Hawaii are, no doubt, less intense than the post-nuptial demands of temperate species that must undergo energetically demanding autumnal migration. This may be one of the reasons that allows the large breeding-molt overlap in the Common Amakihi (Fig. 13). Baldwin (1953) found that the start of Common Amakihi gonadal regression was in May, and no doubt decreasing hormonal levels play an important role in terminating breeding after this time. Near the end of each breeding season I recorded a number of newly constructed nests that were abandoned (van Riper 1976). These may well have been deserted because of low reproductive drive, which is common late in the breeding season (Nickell 1951).

Timing of postbreeding dispersal for most Common Amakihi pairs corresponded to that time when mamane flowering terminated in their territory. When birds remained after breeding, they expanded their territories into a much larger home range (see van Riper 1984). Nice (1937: 63) reported a similar situation in Song Sparrows (*Melospiza melodia*) which wintered on their breeding grounds. These territories increased six-fold over the original breeding size.

The length of the breeding season as a factor in population regulation becomes important when one considers that a nesting sequence (nest building to independence of young) takes 66 days in the Common Amakihi. This may explain why the Common Amakihi is able to raise two sets of young in one season. However, if the breeding season is terminated early, the number of young produced could be severely affected. This did happen in 1975 when the re-nesting effort was much reduced.

TERRITORIALITY

Common Amakihi defended a classical "Type A territory" (Nice 1941). No previous worker has shown that mutually exclusive territories exist in any member of the Drepanidinae. Eddinger (1970) found that in Kauai Common Amakihi territories consisted of a small circle around the nest, usually extending to a radius of 5.5 m. Although he did not deal with color banded individuals, he felt that territory size was dependent

upon the number of available singing perches nearby. Baldwin (1953) worked with banded Common Amakihi on Mauna Loa, Hawaii, and reported that territories were established by the males, but loosely held and often shifted within limits. He also showed that territories could be compressed.

The type of territory in which feeding, mating, and rearing of young are all carried out together (Type A) poses the most difficult problem for any theory of territoriality (Brown 1964). Data from Common Amakihi breeding at Puu Laau suggests that territoriality resulted from food partitioning of the environment (van Riper 1984). The nectar-producing flowers of mamane are easily defendable in terms of their physical characteristics and provide a site-specific resource that is constantly renewed. Because territory spaced the Common Amakihi, it reduced potential usage of specific flowers, and thus increased the food available to the defending pair in terms of both the amount of nectar and its predictability (see Kamil 1978, Kamil and van Riper 1982).

Common Amakihi territorial systems seem to change with contrasting patterns of available resources. In rain forests (Kauai; Eddinger 1970) Common Amakihi had small exclusive territories around the nest site, in edge habitats (Mauna Loa; Baldwin 1953) territory was weakly held, and in dry savanna areas (Puu Laau) territories were mutually exclusive. Common Amakihi in pure mamane habitat (2,290 m) at Puu Laau had significantly smaller territories than did birds at 2,130 m where there was considerable naio. Furthermore, the similarity of effective territory sizes at 2,130 m elevation suggests that the spatial distribution of available resources greatly influences territory size in the Common Amakihi. It is, therefore, possible that in richer habitat (e.g., rain forest) nests could become close enough so that only the immediate area around the nest site would be defended. These data appear to be consistent with the general thought that temporal and spatial patterns of food availability are important factors regulating territoriality and, therefore, ultimately population levels.

CLUTCH SIZE

In the Common Amakihi it appears that clutch size can be proximately modified by prevailing environmental conditions. During 1974 in the 2,130-m study area, the relative productivity in-

TABLE 11. Comparison of clutch size and reproductive success in the Common Amakihi during 1974 and 1975 on Mauna Kea, Hawaii.

	2-egg clutches			3-egg clutches		
	No. clutches	Reproductive success	No. young fledged	No. clutches	Reproductive success	No. young fledged
1974	14	39.3%	11	34	36.3%	37
1975	22	40.9%	18	9	29.6%	8

dex of mamane flowering was 153.9 (see van Riper 1980), and Common Amakihi clutch size averaged 2.7 eggs for that year. In 1975, mamane productivity dropped to 72.9 and clutch size took a corresponding dip to 2.3 eggs per clutch. If Lack (1954) is correct in this theory, then optimal clutch size in the Common Amakihi would be the ratio of resource productivity (index of mamane bloom and insect abundance) to the mean expenditure of energy by adults to collect food for each young. Therefore, as the resources of a region increase, the energy required to harvest a given quantity would be reduced and optimal clutch would increase. The data on mamane productivity (van Riper 1980) and annual clutch size differences support this idea. Perrins (1965) documented this in a population of Great Tits (*Parus major*), which varied their average clutch size from 8 to 12 over a 17-year period, apparently in response to the density of caterpillars, their primary food source.

Berger (1981) worked in the Puu Laau region of Mauna Kea and collected information on nests of the Common Amakihi between 1966 and 1970; he found a mean clutch size of 2.8 eggs. Eddinger (1970) reported clutch sizes for 20 Common Amakihi nests from Kauai and found a mean clutch size of 3.2 eggs. Both of these differ significantly from my data (one-way analysis of variance; $P \leq 0.001$) and may indicate that more food was available (barring genetic differences in the Kauai population) at different years on Mauna Kea and in rain forest habitat on Kauai.

Variation in clutch size is only important if it is adaptive and has survival value to the species. The most meaningful measure of an adaptive value is its success in contributing the greatest total number of progeny to the next generation. Common Amakihi reproductive success in the 2,130-m study area as related to clutch size for the years 1974 (year of high mamane productivity) and 1975 (year of low mamane productivity) revealed a higher reproductive success in a year

of abundant food supplies (Table 11). It is apparent that Common Amakihi were producing an optimal clutch size for years with differing resource productivity, and the observed differences in clutch size were probably an adaptive modification to the environmental conditions at that time.

HATCHING SEQUENCE

Cody (1971) suggested that asynchronous hatching evolved as a mechanism of brood reduction and productivity control, whereby the largest young survived in poor years but all did so in years of abundant food. This was true even though for some cases he reported age spread in the young was often just less than a day. Ricklefs (1968) indicated that this mechanism was particularly beneficial to species with long incubation and nestling periods where food supply between hatching and fledging could not be predicted at the time eggs were laid. Selective starvation of nestlings appears to be of varying importance in different species, but has been cited as a significant cause of death in some birds (Nice 1937, Ricklefs 1965, Young 1963).

Common Amakihi clutches hatched asynchronously. The first egg would usually hatch during the night, the others early to late the following morning. Because of these age differences, even though often less than a day, young were of notably different sizes within a nest. Lack (1954) and Ricklefs (1965) both found that differences of weight between siblings were often the result of competition for food which parents delivered. It is difficult to say exactly how important asynchronous hatching is in the Common Amakihi, but in 15 of the 17 nests that lost members, it was the smallest member of the clutch that died.

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 that young are exposed to possible predation and adverse climatic conditions (Maher 1973). Ricklefs (1969b) proposed a model whereby natural selection would maximize growth rates of altricial birds. He indicated that rate of growth and body weight were not correlated with nestling mortality, but were rather a function of adult body size (of the species) and the mode of development of the young.

The average Common Amakihi nestling period was 17 days, which is long for an open-nesting passerine species (Ricklefs 1968, 1969a, Skutch 1945). To compare Common Amakihi growth rates 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 comparisons. Except for the Formicariidae, Tyrannidae, and Corvidae, the growth rate (K) for the Common Amakihi (0.368) was less than all passerines analyzed by Ricklefs (1968). It was also lower than the average of 0.535 for the 21 fringillids given by Ricklefs, and the average of 0.462 reported by Maher (1973) for seven ground-nesting passerines. This shows that Common Amakihi grow more slowly than most passerines measured to date and are, therefore, relegated to the nest for an extended time period.

I propose that in Hawaii prolonged nestling periods were able to evolve because of the former absence of ground predators. With minimum nestling mortality from predation, there would have been little directional selection against a later fledging date. This is further supported by the fact that Common Amakihi exhibit a decreased feeding rate over the nestling period. This is unusual for passerines, but perhaps with the extended nestling period, physiological adjustments have been made in the young so that food requirements are able to be spread over a longer time period.

In the absence of heavy predation and adverse environmental conditions at Puu Laau, food availability now appears to act as a controlling factor of nestling mortality and thus ultimately as a population regulation mechanism in the Common Amakihi. In the year food resources were highest (1974), Common Amakihi nestling mortality was 6.6%. During 1975, when food supplies were considerably decreased, nestling mortality rose to 11.3%. In 104 eggs from 2-egg clutches, a 2.9% rate of nestling death was recorded, while an 11.9% rate was found in 168 eggs from 3-egg clutches. Furthermore, young from 2-egg clutches weighed more than did young from 3-egg clutches, possibly reflecting the ability of parents to feed them.

REPRODUCTIVE SUCCESS

Reproductive success, i.e., the number of eggs laid that fledged young, for the Common Ama-

kahi (34.7%) 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/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 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 Puu Laau) the most important variables of productivity were season length and clutch size. Both of these factors became obvious in this study when the productivity rates for the Common Amakihi population were compared between 1974 and 1975. Clutch sizes were significantly different between 1974 and 1975, and breeding season lengths differed because of decreased reneating in 1975. The similarity of my data with Ricklefs and Bloom's suggest that in savanna ecosystems throughout subtropical regions, the two most important factors regulating productivity in small passerine birds are breeding season length and clutch size.

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