

TIMING OF BREEDING AND MOLTING IN SIX SPECIES OF HAWAIIAN HONEYCREEPERS¹

C. JOHN RALPH

U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Dr., Arcata, CA 95521

STEVEN G. FANCY

National Biological Survey, Hawaii Field Station,
P.O. Box 44, Hawaii National Park, HI 96718

Abstract. The timing of breeding and molting was studied in six species of Hawaiian honeycreepers with differing food habits on the Island of Hawaii. The availability of nectar was highly seasonal, whereas insect abundance was relatively constant throughout the year. All six species of honeycreeper had extended breeding and molting periods with peak breeding between April and July and peak molting in August. Breeding and molting periods for Apapane (*Himatione sanguinea*) and Iwi (*Vestiaria coccinea*), two nectarivorous species, were shorter than those for the more insectivorous Common Amakihi (*Hemignathus virens*), Hawaii Creeper (*Oreomystis mana*), Akepa (*Loxops coccineus*), and Akiapolaau (*Hemignathus munroi*). Missing or growing flight feathers and either a brood patch or enlarged cloacal protuberance occurred simultaneously in only 3.2% of 2,786 adult birds examined. Although overlap of breeding and molting was rare, some individuals may have been able to allocate energy resources to both activities because of low clutch size, extended brooding of young, and a low rate of molting.

Key words: Breeding; molt; Drepanidinae; Hawaii; *Himatione sanguinea*; *Vestiaria coccinea*; *Hemignathus virens*; *Oreomystis mana*; *Loxops coccineus*; *Hemignathus munroi*.

INTRODUCTION

Reproduction and molt are energy-demanding events in the annual cycles of birds. Seasonal patterns of food availability have exerted strong selective pressure on the evolution of annual cycles, and thus observed patterns in the timing of reproduction and molt can reveal optimal solutions to the allocation of food resources to the requirements of self-maintenance and reproduction (King 1974, Murton and Westwood 1977).

In most passerines, particularly those in temperate zones, the energy-demanding events of reproduction, molt, and migration are mutually exclusive and occur within well-defined time intervals (e.g., Farner 1964, Newton 1966, Murton and Westwood 1977). In tropical species, however, overlap of breeding and molting is more common (Payne 1969, Foster 1975). Foster (1975) listed three scenarios that might account for breeding-molt overlap in birds: (1) food resources may be extremely abundant for a short period and relatively scarce at other times, such that breeding and molt must be completed during the short period of superabundance; (2) food

resources may be relatively uniform throughout the reproductive season for a species, but particular resources for reproduction are critical for only part of the nesting cycle; and (3) a species may be able to reduce energy requirements for reproduction or molt so that both activities can occur simultaneously.

In this paper, we compare the timing of breeding and molt for six species of Hawaiian honeycreepers (Fringillidae; subfamily Drepanidinae) that specialize to varying degrees on either nectar or insects. Apapane (*Himatione sanguinea*) and Iwi (*Vestiaria coccinea*) obtain energy primarily from nectar of ohia (*Metrosideros polymorpha*) blossoms, although they also consume insects (Baldwin 1953; Berger 1981; C. J. Ralph, unpubl. data). Apapane and Iwi are strong fliers that may make long flights in search of nectar, which can be superabundant for short periods in some areas (Baldwin 1953, MacMillen and Carpenter 1980). The Common Amakihi (*Hemignathus virens*) is a generalist that feeds on nectar, fruit, and insects (Baldwin 1953, van Riper 1984, 1987). Three endangered species (USFWS 1982), the Hawaii Creeper (*Oreomystis mana*), Akepa (*Loxops coccineus*), and Akiapolaau (*Hemignathus munroi*), are primarily insectivorous and

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relatively sedentary; for these, timing of breeding and molt has not been documented (Berger 1981).

In our study area, the availability of nectar was highly seasonal, whereas availability of insects was relatively constant. Our objectives were to determine the timing of breeding and molting for the six honeycreeper species, and by comparing the timing of these events with patterns of food availability, to evaluate Foster's (1975) three scenarios for explaining overlap of breeding and molting in tropical species.

METHODS

STUDY AREAS

We recorded breeding status and molt of birds caught in mist nets (78,964 net-hours) at two sites on the Island of Hawaii between November 1976 and January 1982. The 16-ha Keauhou Ranch study area (19°30'N, 155°20'W; 1,800 m elevation) had a discontinuous canopy dominated by ohia and naio (*Myoporum sandwicense*). The site had a long history of grazing and koa (*Acacia koa*) logging, and was being grazed at the time of our study. The 16-ha Kilauea Forest study area (19°31'N, 155°19'W; 1,600-1,650 m) was a relatively pristine, closed-canopy, wet forest dominated by 20-30 m tall koa and 15-25 m tall ohia trees. We also recorded observations of unbanded birds at three additional sites on Hawaii. The 50-ha Hamakua study area at Pua Akala (19°47'N, 155°20'W; 1,700 m) was similar to the Keauhou Ranch site but had a more continuous canopy and lacked an understory because of intensive grazing by cattle. The 50-ha Kau Forest study area (19°13'N, 155°39'W, 1,750 m) had a closed canopy of ohia and a largely ungrazed understory of kolea (*Myrsine lessertiana*), olapa (*Cheirodendron trigynum*), kawau (*Ilex anomala*), and native ferns. The Mamane Forest study area (19°50'N, 155°36'W) was a 4.3-km long transect between 1,700 m and 2,800 m elevation with an open canopy, dry forest of mamane (*Sophora chrysophylla*) and naio (*Myoporum sandwichense*) and a grass understory.

DATA COLLECTION AND ANALYSIS

Each bird captured in a mist net was banded and inspected to determine its molt status and the presence or absence of a brood patch or enlarged cloacal protuberance (Pyle et al. 1987, Ralph et al. 1993). We identified juvenile birds on the

basis of plumage characteristics, skull ossification, and behavior. We recorded flight molt for birds with primary, secondary, or tail feathers that were missing or in sheath; molt of remaining feathers was designated at body molt. Juveniles were excluded from analyses of breeding and molting condition.

We quantified presence of juvenile birds and singing rates of adult birds during monthly surveys at the five study sites. At least monthly, we walked throughout each grid and recorded activities of approximately 35 individuals of each species during bouts of 5-60 sec (mean bout length = 20.0 sec). For each month, we calculated the mean number of seconds of song per minute by dividing the number of seconds of song during each bout by the length of the bout. Because rare activities such as singing are more likely to be recorded during longer bouts, we weighted each observation by the square root of the length of the bout. During each observation, we also noted the presence of any immature bird with the focal bird, or, if the focal bird was an immature, any adult bird that appeared to be associated with it.

Relative abundance of ohia flowers was determined from monthly counts at 81 stations spaced 50 m apart at the Keauhou Ranch and Kilauea Forest study areas. At each station, an observer viewed the canopy of four ohia trees > 5 m tall from a distance of 20-25 m with 8-power binoculars and counted flower clusters within the field of view. We adjusted each count to compensate for differences in field of view and pooled counts from each site. We used the logarithm of each count to calculate monthly means to lessen the effect of a few trees with large numbers of flowers.

Seasonal patterns in insect abundance at the Keauhou Ranch site were determined by sampling two substrates commonly used by foraging birds: ohia foliage and ohia terminal buds. Five times each month, we swept the foliage 50 times with a fine mesh insect beating net. The sample was placed in a plastic bag, frozen, and later inspected under a dissecting scope. Invertebrate remains were measured to the nearest millimeter and converted to biomass (Rogers et al. 1977). Each month we also collected five samples of 50 ohia terminal buds in plastic bags. Within 5 hr, each sample was placed in a Berleze funnel for 5 days, and any insects collected were measured as described above.

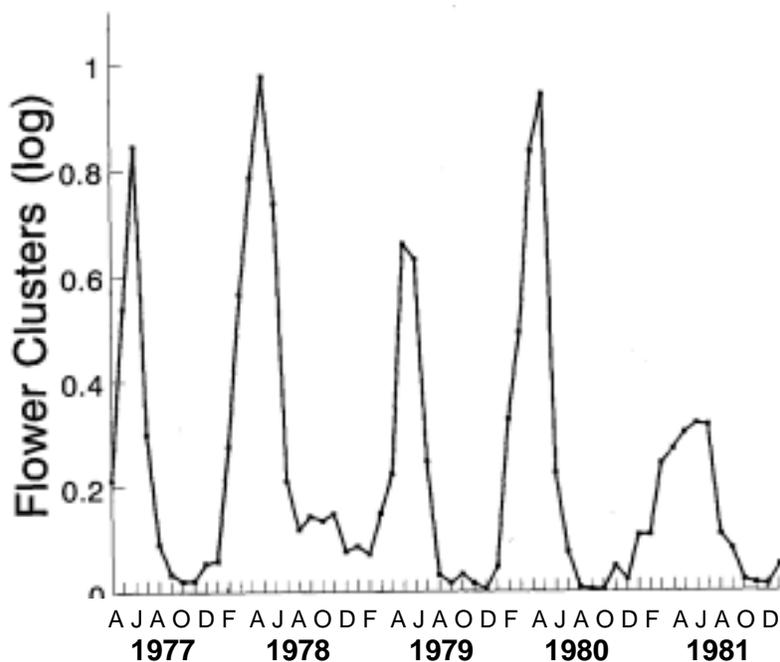


FIGURE 1. Mean monthly number of ohia flower clusters at the Keauhou Ranch and Kilauea Forest study areas on Hawaii, 1977-1981.

RESULTS

Availability of ohia blossoms was highly seasonal (Fig. 1). We recorded the highest number of flowers in May and June each year and found similar annual patterns at each study site. The proportion of ohia trees in bloom followed the same seasonal pattern as mean number of flowers. In contrast to nectar availability, we found no seasonal pattern in biomass of insects on ohia foliage or ohia terminal buds (Fig. 2).

All six species of honeycreeper had an extended breeding season with peak activity between April and July (Figs. 3-8). We recorded increased rates of singing for Apapane, Iiwi, and Common Amakihi as early as October and November, and we began capturing birds with enlarged cloacal protuberances by December and January. The occurrence of birds with cloacal protuberances peaked in April or May for all six species, although we captured Apapane, Common Amakihi, Hawaii Creeper, Akepa and Akiapolaau males in breeding condition during most months. The highest proportion of birds with brood patches occurred between May and July for each species, although many of the brood patches in

July were receding. We captured Akiapolaau with brood patches in six different months from January to October. Most birds completed breeding by July, and except for Akiapolaau, which has an unusually long period of parental care (T. Pratt, pers. comm.), we recorded the highest number of immature birds for each species during surveys in June.

Molting of flight feathers extended over a period of at least six months for all species except Hawaii Creeper, for which sample sizes were small (Figs. 3-8). We captured Akepa and Akiapolaau with flight feathers in molt as early as March and as late as November, and we recorded flight feather molt for Apapane, Iiwi, and Common Amakihi between June and November. Peak molting of flight feathers occurred in August for all species except Common Amakihi and Akiapolaau.

We captured 88 individuals (54 males, 34 females) of all six species that were molting flight feathers and had either an enlarged cloacal protuberance or brood patch. Twenty-one of the 34 females had a receding brood patch (i.e., grayish and wrinkled skin on the abdomen), but we captured Apapane with an active brood patch and

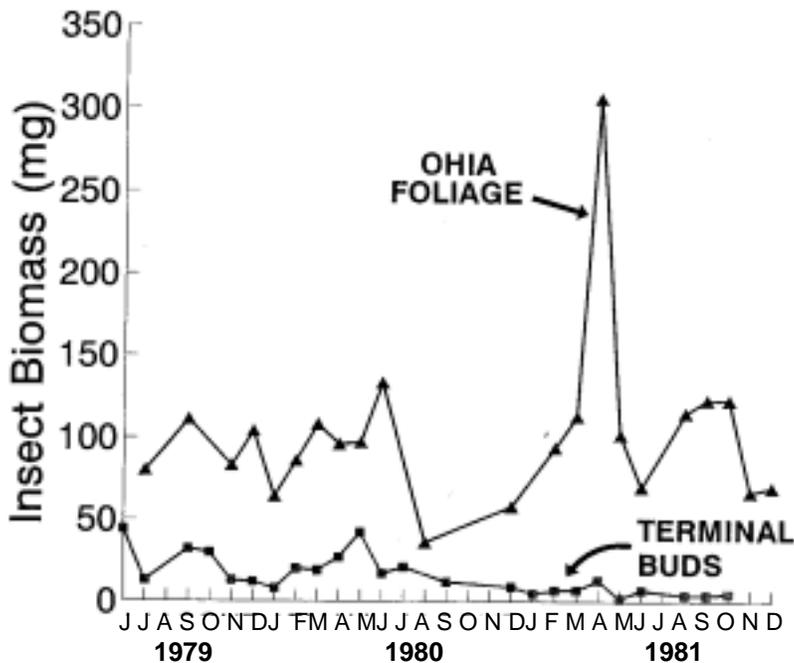


FIGURE 2. Biomass of insects on ohia foliage and ohia terminal buds at Keauhou Ranch, Hawaii, 1979-1981.

molting flight feathers in January, March, April, June and July, and three female Iiwi with an active brood patch and molting flight feathers in April, June and July. One Akiapolaau captured in May had an active brood patch and was molting its flight feathers.

Van Riper (1987) found that singing rates for Common Amakihi in the dry mamane-naio forest peaked in April and in December. We found that singing in the Common Amakihi also peaked in April and December (Fig. 5). Monthly singing rates at the Mamane Forest study area did not differ from those at the other three sites combined (paired *t*-test, $t = 0.50$, $P = 0.6253$).

DISCUSSION

We documented extended breeding and molting periods for all six species of Hawaiian honeycreeper and found that frequency distributions for birds molting flight feathers and those for birds in breeding condition overlapped by ≥ 2 months for most species. However, the occurrence of individual birds with molt-breeding overlap was rare. Only 88 of the 2,786 (3.2%) birds captured were molting flight feathers while in breeding condition, and most of the females

had receding brood patches that usually appear after the young have fledged. Overlap of breeding with molt of body feathers (excluding those with $<5\%$ of body feathers in sheath) was also rare: only 2.2% of birds were molting $\geq 5\%$ of body feathers while in breeding condition. Other studies that reported molt-breeding overlap for species in the tropics (Moreau 1936, Payne 1969, Foster 1975) recorded similar low rates of overlap (3.9%, 4.2%, and 8.1%) for individual birds. In Venezuela, none of the 869 birds ($n = 49$ species) captured by Poulin et al. (1992) that were undergoing primary molt were simultaneously in breeding condition.

Although molting of flight and body feathers occurred after the breeding season for most individuals, we documented molt-breeding overlap for individuals of all six species. Overlap of molting and breeding effectively prolongs the breeding season for an individual and could increase its probability of producing offspring (Foster 1974). Foster's (1975) third scenario for explaining molt-breeding overlap, by which an individual is able to reduce energy requirements for molt or reproduction so that both activities can occur simultaneously, is the only one of her

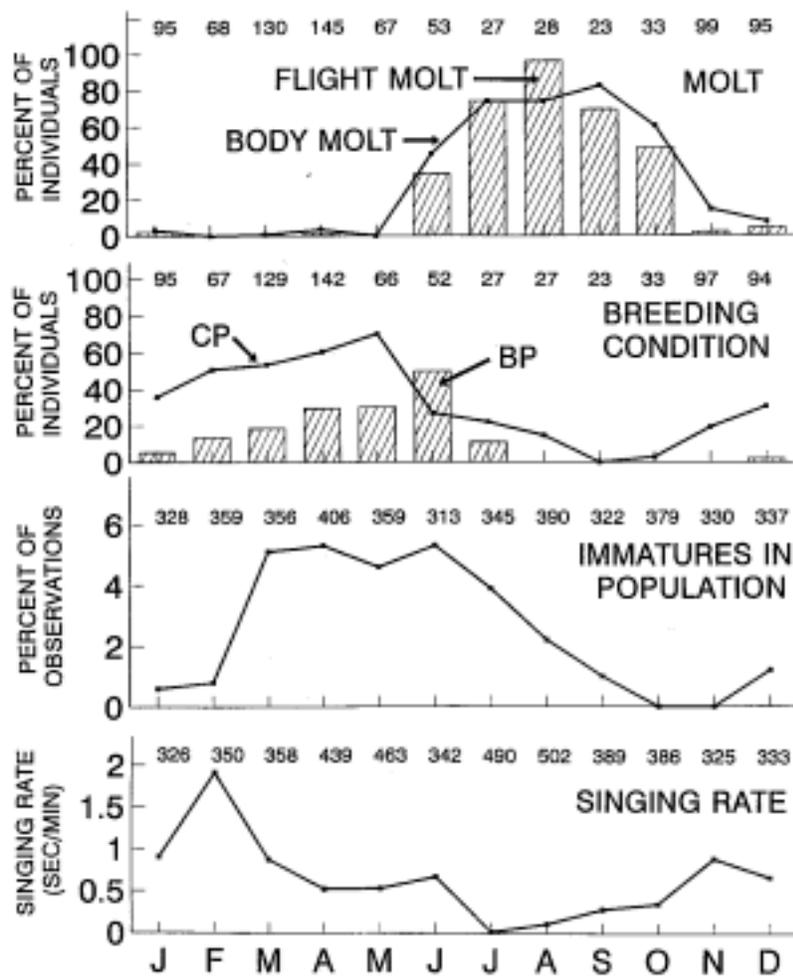


FIGURE 3. Timing of molt and breeding for adult Apapane. Numbers above bars or lines are sample sizes.

three scenarios that applies in our study. Most of the 88 individuals we captured with molt-breeding overlap were caught after the peak of the breeding season. Conceivably, these could have been birds that lost their young and were able to allocate energy reserves immediately to molting. Alternatively, small clutch size and an extended brooding period (Berger 1981), and slow rate of molt (Baldwin 1953; C. J. Ralph, unpubl. data), could reduce energy expenditures for both breeding and molt and allow both activities to occur simultaneously in some individuals.

Breeding and molting periods of insectivorous species, for which food availability was more constant throughout the year, were longer and less defined than those for Apapane and Iiwi, for

which food availability was seasonal. Relative constant availability of insects throughout the year is common in tropical areas (Baldwin 1953, Buskirk and Buskirk 1976, Lefebvre et al. 1992). The timing of breeding and molting for Hawaii Creeper, Akepa, and Akiapolaau apparently was not constrained by seasonal variation in resources or the need to migrate because of relatively constant food availability and climate (Bridges 1981). However, we did not sample insects on and under the bark of koa and ohia trees, where Akiapolaau and Hawaii Creeper spend most of their time foraging (Ralph, unpubl. data), and we recognize that additional research is needed to determine seasonal availability of insects for those two species.

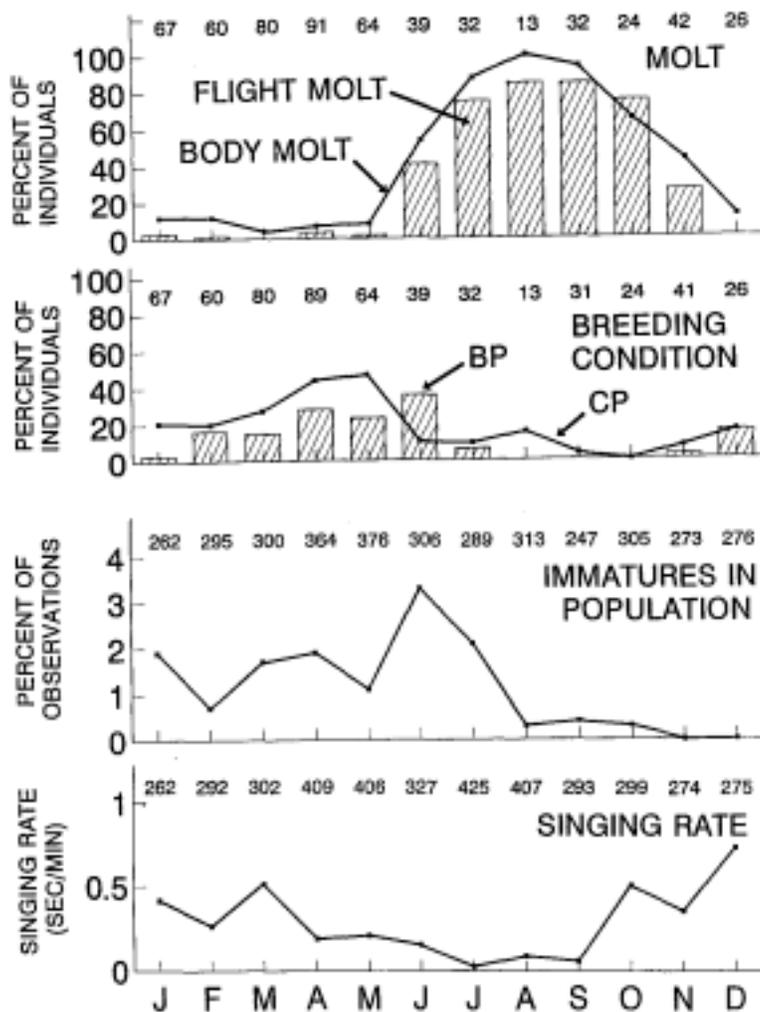


FIGURE 4. Timing of molt and breeding for adult Iiwi. Numbers above bars or lines are sample sizes.

The breeding season for Apapane and Iiwi coincides with the seasonal availability of ohia nectar. Flowering of *Metrosideros* is regulated internally rather than in response to some environmental cue (Bridges et al. 1981). Ohia patches at the peak of flowering can be found at any time of year in different areas (Bridges et al. 1981, Pimm and Pimm 1982). Apapane and Iiwi are strong fliers that can reach nectar blooms in distant areas (MacMillen and Carpenter 1980). Nevertheless, several observations suggest that the distribution of these species during the breeding season may be limited by their ability to thermoregulate and their susceptibilities to disease (Warner 1968, MacMillen and Carpenter

1980, van Riper et al. 1986) as well as by competition for feeding and nesting sites. For example, Apapane and Iiwi are not found at lower elevation sites during peak nectar availability, and most individuals that emigrate to high-elevation mamane forests during peak flowering of *Sophora* in fall are immature birds that presumably are less able to compete for limited food resources in the best areas (Pimm and Pimm 1982; USFWS, unpubl. data). C. J. Ralph (unpubl. data) identified the same color-banded Apapane and Iiwi repeatedly at the same locations both during and after peak flowering of ohia, suggesting that individuals may compete for high-quality feeding or nesting areas that they

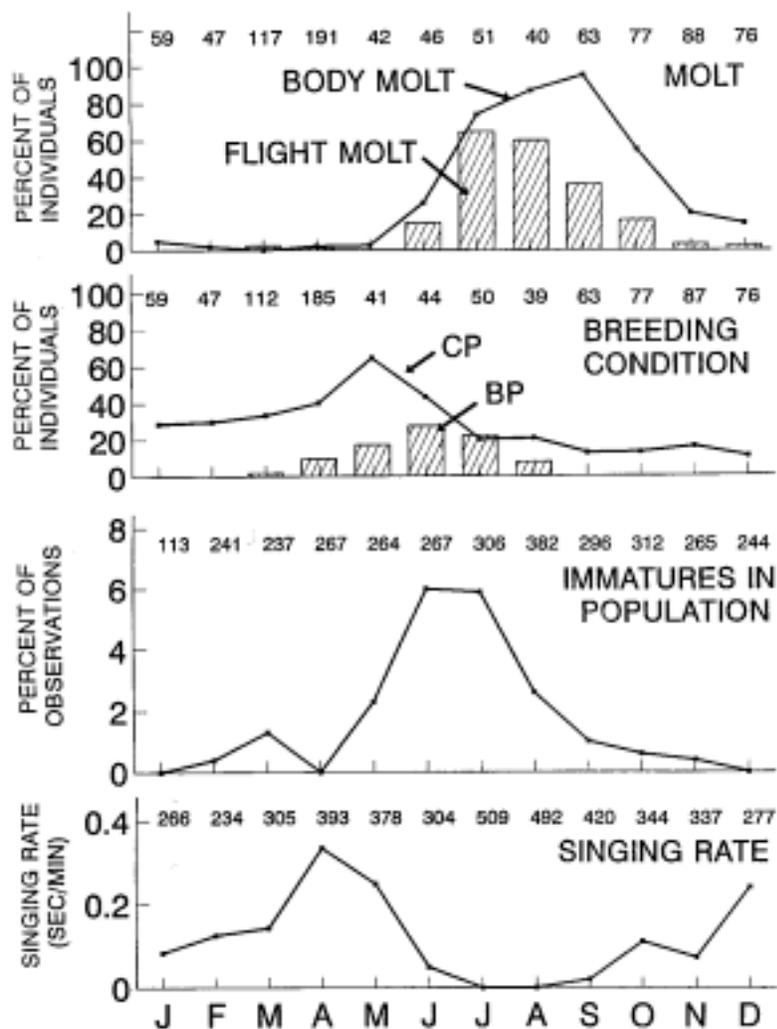


FIGURE 5. Timing of molt and breeding for adult Common Amakihi. Numbers above bars or lines are sample sizes.

use throughout the year. Thus, although ohia stands in peak bloom may be available in many areas at any given time, high-quality breeding habitat may be more limited and have a highly seasonal food supply.

Our results and Baldwin's (1953) indicate that Apapane and Iiwi have similar breeding and molting cycles, with breeding activity beginning in October and November and reaching a peak during February through June. Baldwin (1953) found increased testicular development from November through July for Apapane and from October through June for Iiwi, whereas females were found in breeding condition as early as Oc-

tober and November for Iiwi and Apapane, respectively. Berger (1981) found an Apapane nest under construction on 9 December, and another nest contained a fledgling on 21 December. On Kauai, Eddinger (1970) noted increasing singing by Apapane and Iiwi in association with the breeding season, with peak singing for Iiwi in March and April.

From June through November, we captured Apapane and Iiwi that were molting flight feathers; the greatest proportion of birds with flight feathers in molt was recorded in August and September. Baldwin (1953) collected Apapane that were molting flight feathers from July to Novem-

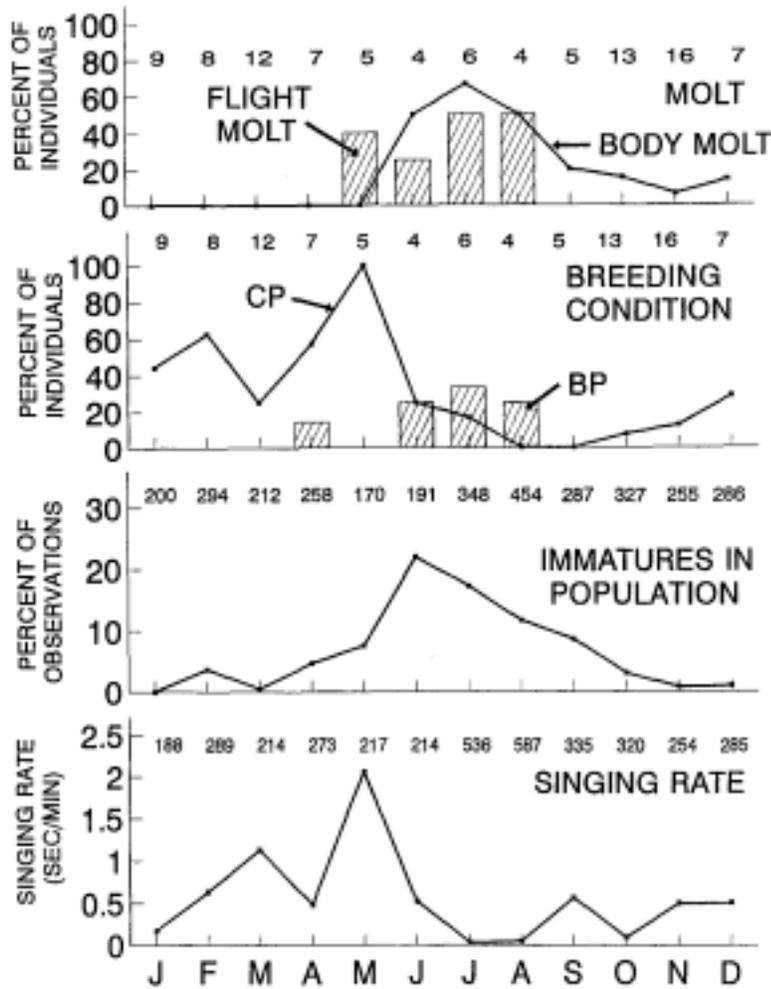


FIGURE 6. Timing of molt and breeding for adult Hawaii Creeper. Numbers above bars or lines are sample sizes.

her, and Iiwi that were molting flight feathers from July through October.

The Common Amakihi is the best studied of the six species. In our study area, breeding activity occurred primarily between December and July, with peak activity in April through July, although we captured males in breeding condition during all months. We found molting of flight feathers from June to December, with a peak in July. In nearby Hawaii National Park, Baldwin (1953) noted increased testicular development in Common Amakihi between October and July, with peak development during March-June. In mamane-naio forest on Mauna

Kea, Berger (1969) reported a breeding season of mid-October to May through June for Common Amakihi, and van Riper (1987) reported a nine-month breeding season from November to July with peak breeding activity in March through May. On Kauai, Eddinger (1970) found that breeding occurred mostly in March, but noted an increase in singing during March through May in association with the breeding season.

The greatest proportion of Common Amakihi with molting flight feathers was found during July through September in both high-elevation mamane-naio forests on Mauna Kea and mid-elevation ohia forests. Van Riper (1987) cap-

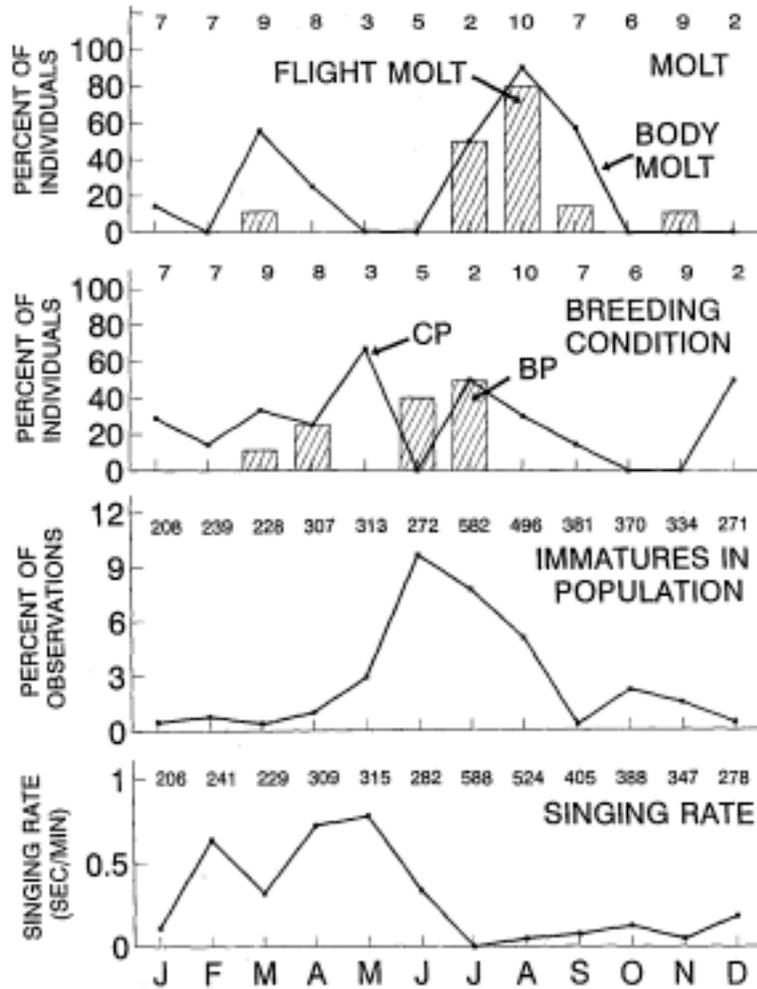


FIGURE 7. Timing of molt and breeding for adult Akepa. Numbers above bars or lines are sample sizes.

tured Common Amakihi with molting flight feathers from May to August, with a peak in July. More recent work on Mauna Kea ($n = 4,909$; G. Lindsey, unpubl. data) also indicated peak molting of flight feathers in July, although birds with missing or growing flight feathers were captured in every month.

Very little is known of the breeding biology of the Hawaii Creeper (Sakai and Johanos 1983). Five of the nine nests that have been described were discovered in January and February, and one each was found in March, April, May and August (Sakai and Johanos 1983). We captured male creepers in breeding condition from October to July, with a peak in May, and females

with brood patches in April, June, July and August (Fig. 6). Our results indicate that the Hawaii Creeper has an extended breeding season from November through September, with peak breeding activity in May. Two males with enlarged cloacal protuberances that we captured in May were molting flight feathers, as was one male captured in July. We also captured one female in August with a receding brood patch that was molting flight feathers.

We captured only 77 adult Akepa, but seasonal patterns of molt, breeding condition, observations of immature Akepa, and singing rates indicate that Akepa also have an extended breeding season from December through July. Freed (1988)

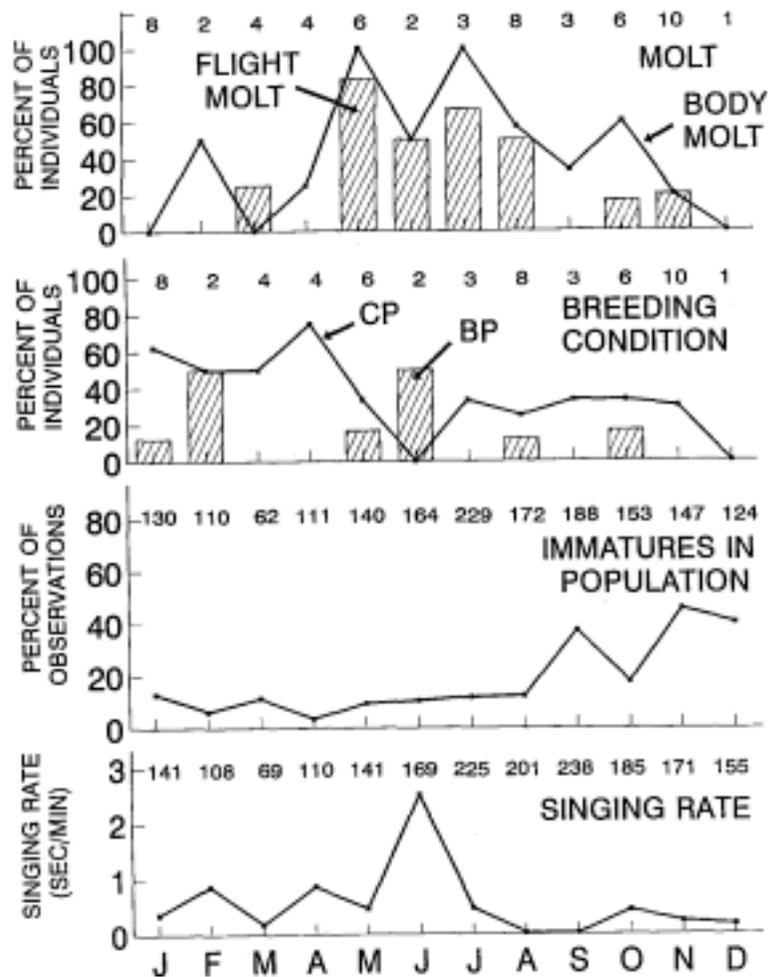


FIGURE 8. Timing of molt and breeding for adult Akiapolaau. Numbers above bars or lines are sample sizes.

reported that courtship and mate defense occurred as early as January, and Akepa nests, all of which have been found in cavities, have been located from March to May (Sincock and Scott 1980, Collins 1984, Freed et al. 1987, Freed 1988). As part of their ongoing study of the Akepa, L. Freed and J. Lepson (pers. comm.) have found molting of flight feathers after the breeding season, as our limited sample suggests. Akepa that were molting body feathers in January, March and April, and the one bird that was also growing a new tail feather in March, could have been second-year birds completing their first pre-basic molt.

The Akiapolaau, the rarest of the six species (Scott et al. 1986), appears to breed and molt

throughout the year (Fig. 8). Akiapolaau nests have been discovered in January, February, July and October (reviewed by Banko and Williams 1993). We captured seven Akiapolaau in breeding condition that were simultaneously molting flight feathers. One was a female with an active brood patch in May that was molting primary and tail feathers, and the remaining six were males captured in March, May, July, August, October and November.

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