

VARIATION IN MALE PLUMAGE AND BEHAVIOR OF THE HAWAII AKEPA

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ABSTRACT.—The sexually dichromatic and endangered Island of Hawaii subspecies of Akepa (*Loxops coccineus coccineus*) is a 10- to 12-g Hawaiian honeycreeper that shows remarkable variation in male plumage coloration, ranging from dull gray to bright orange. We found that this variation is primarily due to a two-year delay in plumage maturation by young males. Second-year males possess a mainly grayish-green plumage that is similar to that of females, and rarely try to breed. Third-year males have a partially orange plumage that is intermediate between that of females and adult males, and competently breed in small numbers. In addition, there are variations within age classes that reflect alternative life histories and perhaps diet. The existence of both femalelike and malelike subadult plumage in a population is unlike North American passerines with delayed plumage maturation, especially cardueline finches, which are considered to be the closest relatives of the Hawaiian honeycreepers. The extreme delay is associated with high survivorship, strong philopatry, and a varied prebreeding competition among males that includes group displays and which lasts for six months or more each year. These characteristics are common in lekking or cooperatively breeding species, but are unusual for a small, monogamous passerine with biparental care. Received 1 October 1993, accepted 11 January 1994.

FEW PHENOTYPIC CHARACTERS so closely track the life history and social system of birds as do color and brightness of plumage (Baker and Parker 1979, Rohwer and Butcher 1988, Butcher and Rohwer 1989). Plumage can make an individual more or less conspicuous to predators, ecological competitors, sexual rivals, and potential mates, and may reflect a genotype that has superior tolerance of or resistance to diseases and parasites (Hamilton and Zuk 1982). The relation between plumage and reproductive maturity also has been identified as an example of paedomorphosis or heterochrony in birds (Lawton and Lawton 1986). Whereas birds typically reach adult size within a year after fledging, individuals may become sexually mature before acquiring terminal adult plumage. Delayed maturation of plumage, appropriately identified as a neotenic character, has been documented in numerous avian orders and families and has been shown to be related to complexity of social organization (Lawton and Lawton 1986) and to intensity of sexual selection (Selander 1965, Rohwer et al. 1980, Studd and Robertson 1985).

Delayed plumage maturation has received considerable attention in sexually dichromatic passerines where adult males have brighter and more colorful plumage than females (Selander 1972, Rohwer 1978, Rohwer et al. 1980, Studd

and Robertson 1985, Lyon and Montgomerie 1986). Studies of North American sexually dichromatic passerine species reveal a distinctive subadult plumage of males during their first potential breeding season that tends to be malelike in territorial species and femalelike in non-territorial species (Lyon and Montgomerie 1986). Highly seasonal breeding makes variation among males in a population largely age specific over time. More lengthy delays in plumage maturation, that range over time from femalelike to malelike coloration in individual males, are known from tropical passerines with leks (Foster 1987) or other promiscuous mating displays (Gilliard 1969, Vellenga 1981, Collis and Borgia 1992).

Additional sources of plumage variation exist among males that are not necessarily linear functions of age. Male coloration can be genetically polymorphic in some taxa, as indicated by brown and black plumage in male Pied Flycatchers (*Ficedula hypoleuca*; Huhta and Alatalo 1993). Male coloration can also become deeper with age (Darwin's ground finches [*Geospiza*], Grant 1986; Pied Flycatcher, Huhta and Alatalo 1993). Nongenetic causes of variation within cohorts at a point in time includes nutritional condition (Grant 1990) and composition of the diet with respect to pigments and their precursors (Hill 1992). Total variability among males

can be extensive when these additional sources of variation are added to age-specific variation associated with delayed plumage maturation.

The Akepa (*Loxops coccineus*) is a 10- to 12-g sexually dichromatic Hawaiian honeycreeper (Drepanidinae) with extraordinary variation in the color and brightness of male plumage both within and among populations (Freed et al. 1987a, Pratt 1989). On the island of Oahu (subspecies *L. c. wolstenholmei*), males were brick red. On the island of Maui (subspecies *L. c. ochraceus*), males range from mustard yellow to a rufous orange color, which has prompted some workers to hypothesize the existence of two morphs within the population that may not be a simple function of age (Amadon 1950, Pratt 1989). On the island of Hawaii (subspecies *L. c. coccineus*), males range from the gray-green of females to bright international orange. Males with differing amounts and brightness of orange plumage have been seen or collected during each month of the year (Perkins 1903, Amadon 1950). This year-round variability in the Hawaii Akepa (i.e. the island of Hawaii subspecies) has not been observed in Temperate Zone sexually dichromatic birds with delayed plumage maturation, especially in cardueline finches, which are believed to share the most recent common ancestors with the drepanidines (Raikow 1976, Sibley and Ahlquist 1982). The variation manifested by the Hawaii Akepa requires either aseasonal breeding, a delay in plumage maturation that extends for more than a year, and/or variation within age classes that is related to genetic polymorphism or physical condition.

In this study we investigate male plumage variability in the Hawaii Akepa. First, we establish age- and time-specific patterns of plumage and molt, and document variations within age classes. We then relate male variability to breeding biology, social organization, social behavior, and demography. The combination of plumage, behavior, and life history reveals unexpected social complexity for nonterritorial passerines with biparental care.

METHODS

Our study was conducted at the Pua Akala Tract of the Hakalau Forest National Wildlife Refuge at an elevation of 1,900 m on the eastern slope of Mauna Kea, island of Hawaii. Annual rainfall averaged 270 cm during the study period, and temperatures ranged

from -10° to 19° C. The study site is an approximately 20-ha area of meadows and open forest dominated by ohia (*Metrosideros polymorpha*) and koa (*Acacia koa*). Over a century of use as a cattle ranch has resulted in an understory dominated by introduced grasses, native ferns, shrubs (primarily *Vaccinium calycinum* and *Rubus hawaiiensis*), and scattered small trees (most commonly *Cheirodendron trigynum* and *Myrsine lessertiana*). The Hawaii Akepa exists in four discontinuous populations in high-elevation rainforest habitat such as this on the island of Hawaii (Scott et al. 1986), and was federally listed as endangered in 1970 because of its reduction in range, discontinuous distribution, and general rarity (U.S. Fish and Wildlife Service 1983). However, the Hawaii Forest Bird Survey (Scott et al. 1986) found that the Hawaii Akepa is fairly common in parts of its range, and it exists at densities of over 200 birds/km² at the study site.

We used a system of aerial mist nets to capture 158 Akepa (69 hatch-year, 3 unsexed second-year, 19 subadult males, 28 adult males, and 39 adult females) between May 1987 and September 1993. All individuals were extensively measured, examined for molt and breeding condition, and given a unique combination of one aluminum U.S. Fish and Wildlife Service band and three colored plastic leg bands for identification in the field. Birds were observed in 12 body regions (wing, tail, abdomen and undertail coverts, flanks and thighs, breast, throat, forehead, face, crown, nape, back, and rump and uppertail coverts), and color was matched to reference colors in Smithe (1975; color numbers indicated). Plumage changes were monitored in birds by recapture and by observations with 10 \times 40 binoculars.

Adult males and females were identified by plumage and by presence of cloacal protuberance or brood patch during the breeding season. Fledglings and hatch-year birds (less than nine months old) were identified by: presence of unossified or partially ossified skulls; bill size, shape, and color; presence of large flanges on the bill; plumage color; distinctive calls; and feeding by adults during the dependent period. Birds intermediate in plumage between hatch-year and adult males were classified as subadult males. Knowledge of plumage sequence gained during our study has allowed us to identify further the age of subadult males when initially captured. Data obtained from recaptured birds indicates that full skull ossification may not occur until at least 10 months after fledging, with partial ossification present in second-year birds. We have not yet been able to sex fledglings or juveniles.

We located nests by following females gathering nest material and during incubation, and both sexes while feeding nestlings. Nests were observed with binoculars and/or 15–60 \times spotting scope; blinds were not necessary. Behavioral observations were conducted throughout the year with binoculars.

Survival estimates were calculated following the

examples of McDonald (1993), and involved constructing a detection (recapture or resighting) matrix with years as columns and individuals as rows. We used a number of different methods for comparisons that differed in number of age classes or approach. Program SURVIV (White and Garrett 1990) estimated age-specific survival for one to four age classes, incorporating constant or variable capture probabilities for each age class or year of the study. For this, one-half of the hatch-year individuals of unknown sex were randomly selected as males. Enumeration was employed for weighted estimates over the study (total number of individuals recaptured or resighted relative to total number available for detection) and for unweighted estimates for each year. Program JOLLY (Brownie et al. 1986, Pollock et al. 1990) was used to estimate survival rates for adult males and females. We used goodness-of-fit and likelihood-ratio tests between models to determine which model was most appropriate (Karr et al. 1990).

The sex ratio was estimated by comparing the mean population sizes of males and females calculated by program JOLLY run for each sex. Annual population estimates provided the basis for a paired *t*-test with a sample size of six years for each sex.

RESULTS

Molt and plumage characteristics.—Variation in male plumage is not related to aseasonal breeding. Active nests ($n = 74$) were found from early March to late June, with a nesting peak in April and May (Table 1). While the beginning and end of nesting varied among years, there were no years in which nesting extended over more than the same four-month period. The Hawaii Akepa has the most restricted nesting season of the six species of Hawaiian honeycreeper at our study site (pers. obs.).

Based on plumage changes followed in 11 males of known age, originally banded as hatch-year individuals (Fig. 1), we have determined that the Hawaii Akepa undergoes a two-year delay in male plumage maturation. Plumage changes in three additional males originally captured in femalelike subadult plumage (Fig. 1) and five others captured in malelike subadult plumage also conform to this pattern.

Juveniles are dull gray-green (similar to, but paler than #42) dorsally. They are paler and yellower ventrally (#54, 118), with an extensive darker gray wash or mottling on the breast. We have found the gray mottling on the breast to be one of the most distinctive features of juvenile plumage of Akepa and the related insectivorous honeycreepers at our site. This

TABLE 1. Distribution of Akepa nests (incubation) by month and year. Dates determined by onset of mate-feeding or by counting back 15 days from hatching or 35 days from fledging. Hatching indicated by males entering nest to feed chicks or brooding female. Incubation was assumed to be seven days from discovery of construction for nests that failed early. Low numbers of nests for 1987 and 1988 were due to less observer time and experience in the field.

Year	Month			
	March	April	May	June
1987		1	2	
1988			1	
1989	1	3	9	2
1990		12	4	
1991	2	5	3	1
1992	1	4	8	
1993		9	6	
Total	4	34	33	3

plumage is replaced in the first prebasic molt, which begins by early June, while the birds are still dependent on their parents, and which lasts at least through the end of October (Fig. 2). The first basic plumage is similar to the juvenile plumage, but includes green (#50) on the wings, tail, and rump/upper tail coverts and (#52) on the sides of breast and flanks, and the gray mottling on the breast is reduced. The first basic plumage is held through the start of the birds' first potential breeding season in their second year, and allows us to determine the age of birds in the spring of their second year.

Second-year males are not distinguishable from second-year females until they begin to grow small amounts of dull orange (#18, 132C, 132D) on the face, sides of breast, and flanks as early as March (Fig. 2). During their first potential breeding season, this orange plumage covers less than 25% of their body, and gray-green feathers have been seen molting on a male of this age (bird 2 in Fig. 1). Subadult males of this stage resemble second-year and dull older females in general appearance in the field. Aside from lacking the gray mottling on the breast, they actually look more like hatch-year birds, and are duller than most older females, which have a yellow or yellow-orange breast band acquired sometime after their second year.

The second prebasic molt continues over the next seven months to result in a more malelike subadult plumage by the end of October (Figs.

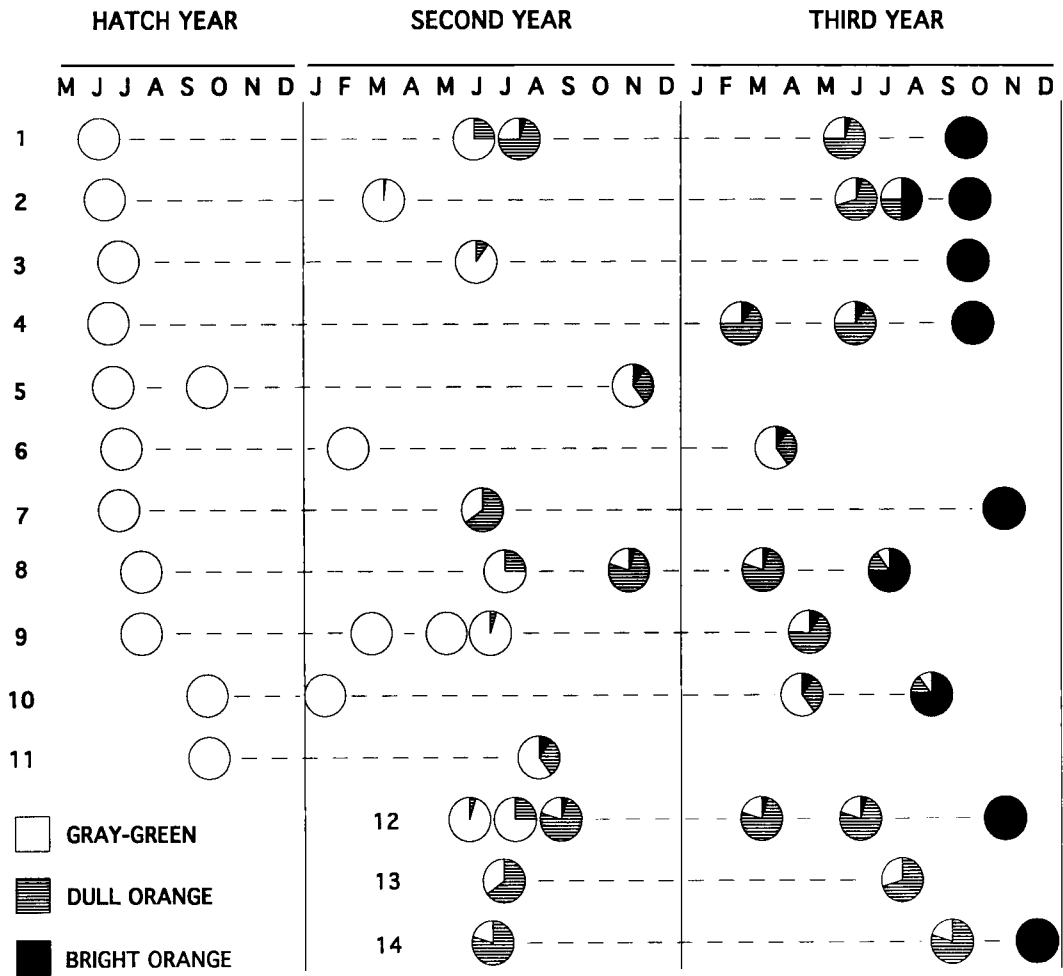


Fig. 1. Plumage sequences in male Hawaii Akepa demonstrate acquisition of terminal adult plumage after second potential breeding season. Pie diagrams along a horizontal line represent proportion of gray-green, dull orange, and bright orange feathers in an individual male each time he was captured or resighted. Center of each diagram is located at appropriate month of year. White circles (birds 1-11) are from juvenile males of known age that fledged during breeding season (March-June) of that year. Black circles represent full adult plumage that is then maintained both within and between breeding seasons. Bird 2 was molting dull orange plumage when captured in March, indicating that acquisition of second year subadult plumage can occur during first potential breeding months when birds of this age fail to breed. Bird 9 attempted to breed during April and May of his second year, and was not seen to acquire any orange plumage until June. Acquisition of third-year subadult plumage occurs after first and before second potential breeding season. Ages of males initially captured as second-year subadults (birds 12-14) were estimated by comparison of plumage with males 1-11. Variability of plumage is evident among males within this cohort, but temporal sequence is consistent with males of known age. One potential exception is bird 13, which maintained subadult plumage without change for more than one year, but was not recaptured or resighted after the second prebasic molt.

1 and 2). Individual birds may be in molt for over five months. This plumage is retained through their second potential breeding season. Young males of this stage are readily distin-

guishable from males in both first basic and adult plumages, and also from females of all brightness. These third-year males are 40 to 90% orange, the color of which is usually duller and

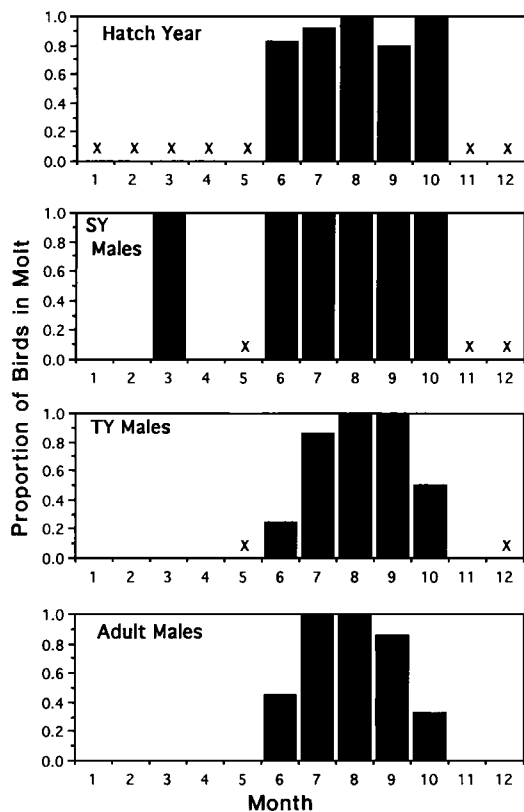


Fig. 2. Molt patterns in Hawaii Akepa demonstrate single annual molt. "X" indicates months in which no birds were captured. Hatch-year individuals undergo first prebasic molt from June at least through October (latest date 31 October; no birds captured later). Second-year (SY) males may start second prebasic molt as early as March, rather than attempt to breed, and continue through October. Third-year (TY) and adult males undergo postbreeding molt between June and October that also is shared by females (not shown).

browner (#17, 18, 40, 94, 116, 132C, 132D, 140) than that of adult males. They are brightest on the face and breast, which may be similar in color and brightness to adult males and are duller on the nape and back, which may remain pale gray-green.

Males acquire full adult plumage during a molt between June and October (Figs. 1 and 2), after their second potential breeding season. This brilliant orange plumage (close to #16) shows negligible variation between males and is retained without change within or between seasons. Adult males (and females) then undergo a single annual postbreeding molt be-

tween June and October (Fig. 2). Hawaii Akepa males thus acquire their full adult plumage only in time for their third potential breeding season.

Molt and plumage variation.—Second-year males (femalelike subadult plumage) exhibit variation in plumage color and timing of molt. This variation appears to be related to their breeding status. Second-year males that were not known to pair with females began to molt in orange feathers by the start of the nesting season in March. These males acquire extensive amounts of orange by June, when older birds only begin to molt, as seen by mist-net operations ($n = 3$) and through binoculars ($n = 2$). In contrast, two second-year males in 1992 formed pair bonds with females and were seen through binoculars to retain first basic plumage into May without signs of molt. These birds did not have the femalelike subadult plumage typical of most males in their first breeding season. One bird was seen to copulate, and the other's nesting attempt progressed to the nestling stage. The latter male had been color-banded as a juvenile (bird 9 in Fig. 1) in the previous year, and was identified as male by behavior (singing, feeding incubating female and nestlings). He was seen in normal third-year (malelike) subadult plumage the following year.

Third-year males (malelike subadult plumage) also exhibit considerable variation in amount and brightness of orange. Some subadult males are largely dull brownish orange, whereas others are a harlequin patchwork of bright orange and pale gray-green. This gray-green plumage is often extremely worn and faded, leading us to believe that some of it may be retained first basic plumage from the autumn of their hatch year. Third-year males from across the spectrum of plumage brightness have been observed to mate and successfully raise young, so unlike the case of second-year males, this variation does not seem to be related to breeding status.

There were cases of birds that manifested additional variability. Two birds appeared to retain their subadult plumage for over a year. Bird 13 in Figure 1 appeared not to have changed its plumage 13 months after banding, but it may not yet have initiated its third pre-basic molt. It may have molted normally into adult plumage later in the year as did bird 14. Another bird (not illustrated) that was captured in October with over 75% bright adult plumage molt-

ed into full adult plumage during the next summer. Based on the timing of acquisition of adult plumage, this appeared to be a second-year male, but one that was much brighter than any other bird of this stage.

The extensive variation in plumage colors among subadult males within age classes may result from dietary differences, as has been documented with the House Finch (*Carpodacus mexicanus*), a cardueline finch (Hill 1992). The orange coloration in the Hawaii Akepa is likely to be due to carotenoids (Brush 1978), which are obtained in the diet, as is the case with the House Finch. Introduced House Finches exhibit a range of color from pale yellow to bright red at our study site, indicating that dietary differences in this floristically simple habitat are possible. However, the variation in Hawaii Akepa plumage within age classes is minor compared with variation among age classes. In addition, there is essentially no variation among adult males observed repeatedly over the study, suggesting that, in the Hawaii Akepa, dietary differences have only a limited if any effect on plumage.

Annual cycle.—The annual cycle of the Hawaii Akepa is comprised of three major segments: a lengthy prebreeding competition (August–April); nesting (March–June); and care of dependent offspring within mixed species flocks (June–October). Nest construction lasts a week or less, and is followed shortly by egg laying and incubation, although in one instance incubation did not begin until a month after construction. Incubation lasts about two weeks, and nestlings fledge nearly three weeks after hatching.

Fledglings are fed by the parents for as long as 10 weeks after leaving the nest. Family groups form the nuclei of mixed-species flocks. These flocks were noted 159 times during the study during the fledgling period, with numbers of flocks peaking in July through September. Two or more flocks usually can be found within the study area on any given day, and few Akepa are found outside of these flocks during this time. These mixed-species flocks may number over 50 individuals, and are shared with large numbers of endangered Hawaii Creepers (*Orcomystis mana*), a few Common Amakihi (*Hemignathus virens*), occasional endangered Akiapolaau (*H. munroi*), and introduced Japanese White-eyes (*Zosterops japonicus*). The flocks may contain over 40 Akepa of all ages and both sexes.

Nonbreeders and failed breeders also join. The extent of flocking behavior varied among years, and flock size was not entirely dependent on breeding success of adults.

The mixed species flocks begin to dissipate in September after offspring become independent. Males then start a prolonged prebreeding competition (detailed below) that lasts six months or more until the start of the next nesting season in March or April.

Mating system.—Hawaii Akepa are apparently monogamous and form long-term pair bonds with biparental care of offspring. One pair has nested together at least five consecutive years, and six have nested together at least three consecutive years. Only one clutch is usually raised, but in 1992 a male renested, and was concurrently feeding an incubating female and a dependent fledgling. Due to the height of the nest and the rapidity with which the female entered and left the cavity, she was not positively identified. However, color bands seen were consistent with those on the female with whom he had nested earlier in the season and in the previous four years, indicating that this was probably a case of sequential nesting.

Only the female builds the nest ($n = 14$ nests during construction) and incubates the eggs ($n = 65$), but males feed the incubating females outside of the nest ($n = 65$). Both sexes participate in feeding and care of nestlings and fledglings ($n = 40$). The clutch size was two in the two nests we were able to inspect, but a report exists of a three-egg clutch (Sincock and Scott 1980). No more than two nestlings were seen in the nest or at the entrance ($n = 18$), nor were more than two fledglings noted with any pair. Frequently, only one fledgling is observed with both parents in flocks.

Although a strongly skewed sex ratio in favor of males (approximately two males per female) has been suggested by museum collections (Amadon 1950, Hatch 1985), mist-netting data suggest otherwise. The sex ratio obtained from the mean population estimates calculated by program JOLLY was 1.14 males per female. The six annual estimates ranged from 0.88 to 1.39, and the numbers of males and females did not differ significantly (paired t -test, $t_5 = 1.86$, $P = 0.12$). Although we are not yet able to sex juveniles ($n = 69$), a nearly equal number of birds originally banded as juveniles, and later seen or captured in our study area, grew up to be males and females (12 males and 10 females).

males. Our field observations of banded birds also may be biased by conspicuous males, but if so, the true sex ratio would be closer to 1:1.

Mating behavior.—Hawaii Akepa are not territorial. Many different males have been captured in the same net, even on the same day. Home ranges are not exclusive, and males often will feed within close proximity to each other. They do not sing from display perches, and rarely sing more than once or twice at a time. Thus, they do not defend all-purpose territories, as do some coexisting Hawaiian honeycreepers such as the Common Amakihi (van Riper 1987), but appear to practice roving mate defense in the manner of the Palila (*Loxioides bailleui*; van Riper 1980).

Males do not even defend specialized nest sites. All nests ($n = 74$) were located in cavities in large, old-growth ohias or koas 1 to 20 m above the ground, as were the seven nests previously known for the species from other locations on the island (Freed et al. 1987b, Scott et al. 1980). The Hawaii Akepa is thus an obligate cavity nester and the only forest-dwelling Hawaiian honeycreeper to nest exclusively in cavities (Freed et al. 1987b). Since there are no cavity-excavating birds in Hawaii, Akepa are dependent on naturally formed cavities in large, old-growth ohias and koas. These cavities are a potentially limiting and defendable resource attractive to females. Males, however, have not been seen to defend cavities in order to attract females. Instead, pair bonds are formed independent of cavities, and potential nest sites are explored by males and females both before and after pairing.

Mating behavior begins six months before the onset of nesting. As postbreeding flocks dissipate in September and October, more active social interactions become apparent as males begin a lengthy period of prebreeding competition. Males engage in long bouts of countersinging, often with more than two individuals involved. Chases involving small groups or pairs of males are frequent, often covering paths over 50 m long. Males also will physically fight each other and, occasionally, fall to the ground while grappling with their opponents. Chases, fights, and song bouts were observed from August through April ($n = 121$), peaking as flocks dissipate in October (0.52 observations per day) and in February (0.63 observations per day) just before the onset of nesting.

More impressive are arboreal and aerial group displays. Arboreal displays consist of up to six

males vocalizing and hopping back and forth in the outer branches of a tree, often with a duller bird visible near them. Those birds that were seen well enough to identify have been females rather than young males. The movements are similar to those used in courtship, in which a male hops back and forth near a female while giving short, buzzy chipping calls. This courtship movement is similar to that used by male Common Amakihi to prospective mates (van Riper 1987), but the amakihi display does not involve groups. The group displays of Hawaii Akepa often are followed by chases between males. Although these displays are usually short (<1 min), a similar display between two adult males, but with slower and more deliberate movements, was seen to continue for over 30 min late one afternoon, and again the next morning, after which one of the males disappeared. The female with whom he had nested in the previous year then paired with the other male. On two occasions groups of males (once 8 and once 12) were seen to fly sequentially out of a single tree, sing in flight, and return. No other honeycreeper is known to have these complex group displays.

Aerial displays consist of up to eight males rising over the canopy to form a loose group, with some males travelling over 200 m to join the fray. Males call, sing, and chase each other in spectacular "dogfights" in these groups, sometimes rising as high as 100 m before breaking up and returning to the trees, often in chases. Perkins (1903) described what may have been a similar towering flight in the now nearly extinct Maui Akepa (*L. c. ochraceus*).

This intense competition lasts up to seven months, until nesting resumes in the spring. Arboreal and aerial displays were seen from August through April ($n = 77$), and also peaked in February (0.40 observations per day), shortly before the onset of nesting.

Second-year subadult males (femalelike plumage) have not been seen to participate in this competition. These young males are inconspicuous, however, and are infrequently seen. Thus, it is possible that their participation may have been overlooked. They have been observed to possess cloacal protuberances similar in size to adult males during the breeding season, indicating reproductive maturity, and they have been observed to sing. Once, a second-year male actually nested, but the attempt failed, and another was seen to copulate with a female, but breeding did not progress any further. We

TABLE 2. Akepa survival and recapture estimates with standard errors. Dashes indicate estimates not attempted or obtained.

Estimate	Age class				
	All hatch-year birds (<i>n</i> = 57)	Second-year males (<i>n</i> = 18)	Third-year males (<i>n</i> = 23)	Adult males (<i>n</i> = 36)	Adult females (<i>n</i> = 46)
SURVIV (MODD)					
Survival	0.43 ± 0.10	0.85 ± 0.13	0.57 ± 0.12	0.82 ± 0.04	—
Recapture	—	0.70 ± 0.14	0.88 ± 0.56	0.82 ± 0.05	—
SURVIV (MODD2)					
Survival	0.42 ± 0.10	0.79 ± 0.04	0.79 ± 0.04	0.79 ± 0.04	—
Recapture	—	0.81 ± 0.04	0.81 ± 0.04	0.81 ± 0.04	—
JOLLY (model D)					
Survival	—	—	—	0.83 ± 0.04	0.80 ± 0.04
Recapture	—	—	—	0.82 ± 0.05	0.77 ± 0.05
ENUMERATION (weighted)					
	0.39	0.78	0.55	0.81	0.77
ENUMERATION (unweighted)					
	0.54 ± 0.26	0.70 ± 0.40	0.61 ± 0.25	0.79 ± 0.15	0.76 ± 0.10

have observed only five copulations in over five years of fieldwork on the Hawaii Akepa, so it may be significant that one of these was by a second-year male.

In contrast, third-year subadult males (male-like plumage) have been seen to take part in all aspects of this competition. They have frequently been observed to pair with females and to successfully breed. Five of six (83.4%) subadult nests fledged as least one young, as opposed to 37 of 47 (78.7%) adult nests whose fates were known. Nesting success thus is comparable to that of adult males (Fisher exact test, $P = 0.7$) indicating that these males are competent parents. In addition, feeding rates of incubating females and nestlings by these males do not significantly differ from males in full adult plumage. Subadult males fed incubating females every 33.40 min ($n = 5$ males), compared to 32.84 min for adults ($n = 16$; two-way t -test, $t = 0.08$, $P = 0.94$), and fed nestlings every 53.90 min ($n = 3$), compared to 47.96 min for adults ($n = 12$; $t = 0.28$, $P = 0.81$). Both duller and brighter males of this stage nest successfully.

Possible higher social status of brighter birds is suggested by observations of adults chasing subadults, but not vice versa. In addition, the mates of these subadult males have been young females, of the same age or younger than these males, based on females banded as juveniles ($n = 4$) and females whose age was inferred from plumage ($n = 3$; one female was not identified).

Demography and philopatry.—All demographic models indicate that Hawaii Akepa are unusually long-lived for small passerines, with annual survival varying from 0.43 for hatch-year birds to 0.83 for adult males and 0.80 for adult females (Table 2). Model-evaluation procedures for SURVIV, based on goodness-of-fit and Akaike information criterion (White and Garrett 1990), suggest that the two-age-class (MODD2) and four-age-class (MODD) models for males are most appropriate. These models have the lowest Akaike information criterion and are within two units of each other (141.95 and 143.81, respectively). Likelihood-ratio tests do not distinguish the two models ($P = 0.19$).

The common features of MODD and MODD2 are lowest survival of hatch-year birds and high survival of second-year subadult and adult males. The major difference is in the survival of third-year subadults, which is lower than the contiguous age classes in MODD (Table 2). Because the recapture probabilities are high, the enumeration estimates are similar to the SURVIV models, especially MODD for third-year subadults (Table 2). On this basis, we prefer MODD over MODD2.

The Hawaii Akepa is a year-round resident on the study site, based on recaptures and resightings of banded individuals during each month of the year. The high recapture and resighting rate for hatch-year birds and adults in our study site constitutes evidence of not only

Skewed collections doubtless reflect the much more conspicuous plumage and behavior of high survivorship, but also strong philopatry, since only a few of these individuals were recovered outside of our study area. Both males and females commonly enter the breeding population and nest within the study area where they were initially captured as juveniles. However, the apparent lower survival of third-year subadults in MODD raises an issue of possible age-specific dispersal.

Most dispersal appears to occur after young males begin to acquire their subadult plumage. Juveniles and hatch-year birds were never seen more than 250 m from the study site. Several males, banded as juveniles, disappeared after being seen while molting into malelike subadult plumage in the summer of their second year. One of these males was later found as an adult approximately 1 km from the study area, where it has remained for at least four years. Two other subadults with malelike plumage were found over 500 m from where they were banded as juveniles, but were not subsequently resighted. One male, banded as a third-year subadult, was found in adult plumage approximately 1 km from the study area. Actual survivorship of subadult males, thus, is likely to be higher than estimated because of the effects of dispersal. However, the data are too limited to determine if the relatively low survival of third-year males is due to greater dispersal, sampling error, or a high cost of breeding.

Dispersal also contributes to the estimated survival of adult birds. One adult male was found 500 m away from where it had been banded, and two adult females have been seen that far. One other female was found 4 km away. More extensive studies of dispersal may reveal higher survival rates for all classes, since we probably missed some dispersing individuals.

DISCUSSION

The major source of variation in male plumage in the Hawaii Akepa is associated with stepwise acquisition of adult plumage over two years. The two-year delay in plumage maturation exhibited by this biparental species does not readily fit existing paradigms, and poses problems for issues associated with delayed plumage maturation. Here we consider the extended delay in plumage maturation in relation to sexual competition and aspects of life history.

Temperate passerines that exhibit delayed plumage maturation typically have subadult males with plumage that resembles either adult males or adult females, but not both (Rohwer et al. 1980, Lyon and Montgomerie 1986). Only rarely do species have subadults with plumage intermediate between the two extremes (Hill 1988). The distinctly bimodal distribution of subadult male plumage types has been linked to social system and to territory type (Lyon and Montgomerie 1986). Malelike subadult plumage is found more in polygynous, territorial species, where females choose mates on the basis of resources controlled by males. Femalelike subadult plumage is found more in monogamous, nonterritorial species where females choose mates on the basis of male attributes. The Hawaii Akepa is monogamous and nonterritorial, and yet has both types of subadult plumage in the population at all times.

Comparisons between the Hawaii Akepa and its nearest nondrepanidine relatives, the cardueline finches (Raikow 1976, Sibley and Ahlquist 1982), reveal additional differences. The femalelike plumage of subadult cardueline finches, in which males do not defend all-purpose territories, has been attributed to strong competition for females associated with a highly skewed sex ratio (Rohwer et al. 1980). However, while Hawaii Akepa males may be slightly more numerous than females because of marginally higher adult survivorship (Table 2), there is no evidence of a highly skewed sex ratio. Neither is there evidence in cardueline finches, or in other temperate passerines with delayed plumage maturation, of prebreeding competition of the length and variety seen in the Hawaii Akepa.

Lengthy delays in male plumage maturation and group displays are found more in tropical passerines, such as bowerbirds (Ptilonorhynchidae; Vellenga 1981, Collis and Borgia 1992), birds-of-paradise (Paradisaeidae; Gilliard 1969), and manakins (Pipridae; Foster 1987, McDonald 1989), with leks or other elaborate displays associated with mate choice. None of these groups have monogamous mating systems, and males do not perform parental care. However, the group displays of Akepa males in the presence of females are leklike, despite the presence of biparental care. Sexual selection is widely seen as being more extreme in lekking and other polygynous species than in monogamous birds (Wade and Arnold 1980, West-Eberhard 1983,

Payne 1984), yet fully one-half of the annual cycle of the Hawaii Akepa can be taken up by prebreeding competition, which involves a diversity of group agonistic behaviors. As in lekking systems, female choice of male characters may shape male behavior. In this case, females may lead consorting males into situations where they must compete with several additional males at the same time.

The only other reported instance of such a delay in a monogamous passerine involves some of Darwin's ground finches (*Geospizinae*) in the Galapagos Islands in which males take two to six years to acquire full adult plumage (Grant 1986). This situation is related to male condition in the extreme and unpredictable environment inhabited by these birds (Grant 1990). The Hawaii Akepa differs in having a consistent and predictable plumage change that permits potential mates and competitors to accurately assess the age of a young male in his first two potential breeding seasons.

The extreme delay in plumage maturation in the Hawaii Akepa reveals the problems encountered by young males in acquiring mates in a rigorous social environment with long-lived adults. The variety of prebreeding displays and physical aspects of competition indicate that young males have much to learn in order to compete effectively for females. Competition is largely among adult males that have previous experience with one another, and age and experience may be crucial to success in the competition for mates (Collis and Borgia 1992). Avoidance of this intense competition is to be expected of a young and inexperienced bird who is unlikely to prevail in competition against older and more experienced males (Studd and Robertson 1985, Lyon and Montgomerie 1986), and who may be avoided by older females that make up the bulk of potential mates. Although third-year males in brighter subadult plumage take part in these struggles and successfully breed, their patterns of coloration, with brightest patches on the face and breast and duller plumage elsewhere, may indicate a trade-off between conflicting selective pressures for crypsis and signalling (Butcher and Rohwer 1989).

The rarity and episodic nature of breeding attempts by second-year males suggest that breeding positions are opportunistic for young birds. In this light, alternative tactics with respect to molt and breeding appear to have evolved. Second-year males, which have fem-

alelike plumage, were only seen to attempt to nest or to pair with females during one of the five years of the study. Instead of breeding, most second-year males begin their molt into brighter plumage several months before older birds start their postbreeding molt. In contrast, the two second-year subadults that attempted to breed did not show signs of early molt. Thus there appear to be two alternative tactics for young male Akepa: attempt to breed; or molt into brighter plumage. It remains to be determined if the delay in molt of breeding second-year males is to separate the cost of molting and reproduction (Payne 1972, Walsberg 1983), or to maintain greater crypsis while breeding.

Why should such a competitive mating behavior evolve in a system with biparental care and an approximately equal sex ratio? The survival and philopatry of the Hawaii Akepa are similar to those reported for cooperatively breeding birds (Brown 1987, Skutch 1987, Smith 1990), but there is no indication of cooperative breeding by this species. However, the apparently higher survival of males (Table 2), and direct defense of females by males may cause females to be a limiting resource even more than suggested by the slightly skewed 1.14 sex ratio. With an average of one out of eight males unable to obtain a female, even adult males would frequently experience intense competition for mates. Breeding opportunities may open up only rarely for young males. Young males that remain may take advantage of occasional dips in adult male survival or peaks in adult female survival in order to enter the local breeding population. Those that disperse may be investigating breeding opportunities elsewhere.

Although the details of mate choice by female Akepa remain to be elucidated, the lack of territoriality indicates that females choose males based on evaluations of male characters. Females have diverse situations during which they can observe males. During the lengthy prebreeding competition, females can observe males in group displays. The large postbreeding flocks are another opportunity. Although these occur primarily in the context of parents feeding dependent fledglings, nonbreeders and other birds without offspring also join the flocks. The existence of large numbers of adult and subadult birds provides an opportunity for females to evaluate a wide selection of individuals as potential mates, as well as to judge parental skills. Sexual selection acts on a variety of sig-

nals (West-Eberhard 1983), and variation in both plumage color and the ability of males to participate in group displays is likely to be used by females in their evaluations of potential mates. Plumage color has been found to be a sexually selected character that accurately reflects male condition in the cardueline House Finch (Hill 1990), but male displays may be a more honest signal of competitive ability than is plumage alone because displays are harder to mimic deceptively and, therefore, false advertising is more difficult (Kodric-Brown and Brown 1984).

Lengthy delays in plumage maturation may be more widespread in the Hawaiian avifauna than previously realized (Freed et al. 1987a). Conventional delayed plumage maturation (one year, confined to males) exists in at least two populations of the territorial Common Amakihi (van Riper 1987; pers. obs.) and in those large finch-billed honeycreepers that have been studied; both sexes take more than one year to acquire full adult plumage (Palila, van Riper 1980; Laysan Finch [*Telespiza cantans*], Banks and Laybourne 1977, Morin 1991; Nihoa Finch [*T. ultima*], Banks and Laybourne 1977). There also is evidence of breeding in subadult plumage in the Elepaio (*Chasiempis sandwichensis*; Perkins 1903, Conant 1977), a monarchine flycatcher (Pachycephalidae). In addition, Perkins (1903) collected a male and a female Puaiohi (*Myadestes palmeri*, Turdinae) in breeding condition that still retained their distinctive spotted juvenile plumage. Studies that focus on delayed plumage maturation in the species that still survive can elucidate the strength of social and sexual selection that might have been associated with the differentiation of Hawaiian passerines on different islands.

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