

TWO-YEAR DELAY IN PLUMAGE MATURATION OF MALE AND FEMALE 'ELEPAIO

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Abstract. I studied molt and plumage in the 'Elepaio (*Chasiempis sandwichensis*), a monarch flycatcher endemic to the Hawaiian Islands, at Hakalau Forest National Wildlife Refuge on the island of Hawai'i from 1994–1997. I captured birds in mist nets, examined them for molt, measured their plumage color with Munsell color chips, and followed them for several years to document plumage changes. Male and female Hawai'i 'Elepaio exhibited three distinct post-juvénal plumages, first basic, second basic, and definitive basic, and thus have a two-year delay in plumage maturation. 'Elepaio have a single annual molt, so there are no alternate plumages. The first prebasic molt is partial, but all subsequent molts are complete. The first basic plumage is juvenile-like and sexually monochromatic. The second basic and definitive basic plumages are sexually dimorphic in throat color. In each sex the second basic plumage resembles definitive plumage. Age-related plumage changes include increases in the whiteness, number, and length of contrasting tips to feathers on the throat, rump, wing coverts, and tail. Subadults do not molt fewer body feathers than adults and produce many feathers that are not adult in coloration, indicating the subadult plumages are not caused by a molt constraint. Appearance of the subadult plumages is consistent in some respects with juvenile mimicry, but the subadult plumages are unlikely to function in sexual mimicry.

Key words: *Chasiempis sandwichensis*, color, delayed plumage maturation, 'Elepaio, molt, molt constraint.

Desfase de Dos Años en la Maduración del Plumaje del Macho y la Hembra de *Chasiempis sandwichensis*

Resumen. Entre 1994–1997 estudié la muda y el plumaje de *Chasiempis sandwichensis*, un monarca atrapamoscas endémico de las Islas de Hawai, en el Refugio Forestal Nacional de Vida Silvestre Hakalau en la Isla de Hawai'i. Capturé aves empleando redes de niebla, las examiné para establecer la muda, medí el color de sus plumajes con fichas de colores Munsell, y las seguí durante varios años para documentar cambios en el plumaje. El macho y la hembra de *C. sandwichensis* exhibieron tres plumajes post-juveniles diferentes, básico primero, básico segundo, y básico definitivo, mostrando así un desfase de dos años en la maduración del plumaje. La primera muda pre-básica es parcial, pero todas las mudas subsecuentes son completas. El primer plumaje básico se asemeja al del juvenil y es similar para ambos sexos. El segundo plumaje básico y el básico definitivo presentan dimorfismo sexual en el color de la garganta. En ambos sexos el color del plumaje básico se asemeja al del plumaje definitivo. Los cambios en el plumaje relacionados a la edad incluyen un incremento en blancura, número, y largo de la punta contrastada de las plumas de la garganta, rabadilla, cubiertas alares y cola. Los subadultos no mudan menos plumas corporales que los adultos y producen muchas plumas que no son como la de los adultos en coloración, indicando que el plumaje de los subadultos no responde a una limitante de la muda. La apariencia del plumaje de subadultos es consistente en cierto sentido con la imitación de juveniles, pero el plumaje de subadultos es improbable que funcione como imitación sexual.

INTRODUCTION

The 'Elepaio (*Chasiempis sandwichensis*) is a small, territorial, nonmigratory monarch fly-

catcher (Monarchidae) that comprises a genus endemic to the Hawaiian Islands of Hawai'i, O'ahu, and Kaua'i (Conant 1977, Pratt 1980, VanderWerf 1998). Male and female 'Elepaio exhibit a great deal of plumage color variation both among and within islands, and this variation caused considerable confusion and disagreement among early taxonomists of Hawaiian birds about the number of 'Elepaio taxa and their distribution and nomenclature (Sclater

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1888, Newton 1892, Rothschild 1893, Pratt 1980, Olson 1989). The subadult and adult plumages are so different that at times they were erroneously described as different sexes (Sclater 1885) or even different species (Stejneger 1887, Wilson 1891). Various early authors recognized anywhere from one to five or six different species of 'Elepaio. Later studies recognized that much of the plumage variation within islands is age related, that there is only moderate sexual dichromatism, and that birds of both sexes sometimes breed in subadult plumage (Henshaw 1902, MacCaughey 1919, Conant 1977, Pratt 1980). The 'Elepaio comprises three subspecies (AOU 1957, 1998), the Hawai'i 'Elepaio (*C. s. sandwichensis*), the O'ahu 'Elepaio (*C. s. ibidis*), and the Kaua'i 'Elepaio (*C. s. sclateri*), which earlier authors treated as species (Perkins 1903, MacCaughey 1919).

Previous studies of 'Elepaio have focused on ecology, breeding biology, and geographic plumage variation (Conant 1977, Pratt 1980, van Riper 1995), but molt patterns and plumage sequence have not been investigated previously. Information in the literature on plumages of 'Elepaio is partially correct, but incomplete; some plumages have not been described previously and molt patterns have not been determined. In this paper I describe the complete sequence of plumages and molts in the Hawai'i 'Elepaio based on repeated observations of banded individuals over four years, and I discuss the implications of this information for hypotheses of the evolution of delayed plumage maturation.

METHODS

STUDY SITE AND POPULATION

I studied 'Elepaio from 1994–1997 at Hakalau Forest National Wildlife Refuge, on the east slope of Mauna Kea volcano on the island of Hawai'i. The habitat at Hakalau is montane rainforest dominated by 'ōhi'a (*Metrosideros polymorpha*) and koa (*Acacia koa*) trees, with a variable amount of human disturbance from past cattle ranching and logging. For a more detailed description of the study site, see VanderWerf (1993, 1994). The form of 'Elepaio occurring in wet forests on the eastern side of Hawai'i Island, including Hakalau, is recognized by some authors as a separate subspecies, *C. s. ridgwayi*, distinguished by its darker coloration and heavier ventral streaking (Henshaw 1902, Pratt 1980).

I captured 'Elepaio in aerial and pole-mounted mist nets, sometimes using playbacks of recorded songs to target particular birds and lure them into a net. Each bird was marked with a unique combination of an aluminum U.S. Fish and Wildlife Service leg band and three plastic color bands, then weighed, measured, inspected for molt and breeding condition, measured for plumage color, photographed, and released unharmed at the site of capture within one hour. A small blood sample was collected from the brachial vein of each bird for use in genetic and disease research.

Age and sex of each bird were provisionally determined using plumage criteria based on examination of museum specimens, information in the literature, and birds captured during the first year of this study. Provisional ages were verified by following banded individuals over several years and observing the changes in plumage as each bird aged. Ageing criteria proved to be reliable, and the provisional age was correct in every case. Provisional sex classifications based on plumage were confirmed with behavioral observations (singing, copulations), and were correct for second-year subadults and adults in all but two cases, both of which occurred in the first year of the study. The sex of first-year subadults and juveniles was difficult to determine because the plumages of males and females proved to be very similar at these ages. I therefore used measurements only from first-year subadults whose sex was determined behaviorally, or that were recaptured or resighted in subsequent years when their sex could be determined by plumage. Juveniles were not sexed because they rarely exhibited sex-specific behavior and relatively few of them were resighted.

MOLT

To quantify molt, I counted the number of remiges and rectrices either sheathed or recently grown, and I estimated to the nearest 10% the proportion of body feathers either sheathed or recently grown. Recently grown feathers were recognized by their lack of wear and, in subadult plumages, by their different coloration. Molt of only one or two isolated feathers in any one body area was regarded as adventitious and not counted in the proportion of birds molting (Pyle et al. 1987). Molt and plumage terminology follow Humphrey and Parkes (1959).

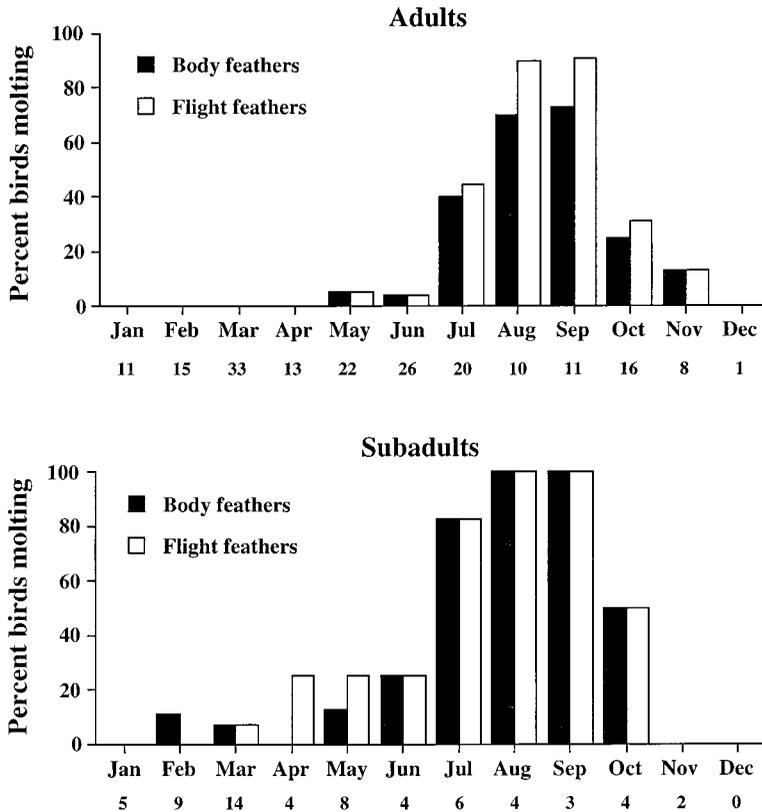


FIGURE 1. Monthly proportions of adult and subadult 'Elepaio molting body and flight feathers at Hakalau Forest National Wildlife Refuge, Hawai'i. Numbers below each month are total numbers of birds caught that month, all years pooled.

PLUMAGE COLOR

I measured plumage color of the eyebrow, auricular, crown, back, rump, throat, breast, wing coverts, and rectrix tips by visually comparing live, wild 'Elepaio to Munsell color chips (Munsell Color 1994). Some of these body regions were found to be useful by Pratt (1980) for distinguishing 'Elepaio populations on the island of Hawai'i, and I chose additional body regions that seemed potentially important for distinguishing age classes. The most obvious age-related changes in 'Elepaio plumage are the acquisition of white tips to feathers on the throat, wing coverts, rump, and tail. I therefore measured the color and length of any contrasting tips on feathers in these areas, and I counted the number of feathers with contrasting tips on the wing coverts and tail. Length of the white tips varied somewhat within each body area. To reduce subjectivity and increase repeatability, I measured (1) the longest tip on the rump; (2) the

longest tip on the greater wing coverts; (3) the longest tip in the center of the throat; and (4) the length of the tip along the shaft of the outermost rectrix, which usually had the longest tip. Length of the tips likely varied seasonally depending on the degree of feather wear, with shorter tips in the summer prior to molting, and longer tips in the fall just after molting. However, the seasonal distribution of captures was similar for birds of different ages and sexes (Fig. 1), so there was no systematic bias of tip length among ages or sexes caused by feather wear. Birds with both fresh and worn plumage were included in analyses, so the values of tip lengths reported thus represent averages of birds at all seasons.

It should be noted that, since comparisons were made visually in this study and not with a spectrometer, it was possible to detect only differences in plumage color that were visible to the human eye. In several species of birds there

is intraspecific variation in reflectance of ultraviolet wavelengths that are invisible to humans, and in some cases subtle variation in visible wavelengths that are not detectable by humans, and these variations can be important in mate choice (Andersson et al. 1998, Hunt et al. 1998, Cuthill et al. 1999). It is possible that, in addition to the plumage variation described in this study, there are further differences in plumage color among age-classes, sexes, and individual 'Elepaio that are not visible to humans.

In the Munsell system a color is described by three parameters: hue (spectral color or wavelength), value (darkness), and chroma (intensity or saturation). The notation for hue consists of a letter abbreviation (Y for yellow, YR for yellow-red, R for red, etc.), preceded by a number from 0 to 10. Within each letter, higher numbers represent approximately equivalent decreases in wavelength, with 10 being equal to 0 for the next lower-wavelength letter code (i.e., 10YR = 0Y, with 5 YR approximately intermediate). Value is measured on an approximately linear scale from 0, for black, to 10, for white. Chroma is also measured on a roughly linear scale from 0, for neutral gray, to a maximum of 20, for extremely intense colors. For example, 10YR 5/8 would mean a color with a hue of 10 yellow-red, a value of 5, and a chroma of 8.

The Munsell system provides a precise, quantitative method of measuring color that is suitable for statistical treatment and can be used internationally with little translation of color names. However, the Munsell system has not been used widely yet in biology, and its notation may not be meaningful to those unfamiliar with it. In contrast, the Smithe (1975) color system has been widely used, and its English color names may be more familiar, but it does not provide quantitative measures for statistical comparison, and English names given to colors may be subjective and imply different meanings to different observers. I used Munsell chips to measure plumage color, but I also report the Smithe (1975) color (capitalized) that was closest to the observed Munsell color, because it might be more meaningful to some readers.

STATISTICAL ANALYSES

I examined variation in number and whiteness of feather tips and in color of each body region among age-sex classes with either a one-way ANOVA or a Kruskal-Wallis test, depending on

whether the data were normally distributed. If the overall test was significant, I compared values among all age-sex classes with Tukey's correction for multiple comparisons (Conover 1980, Sokal and Rohlf 1981). I treated the plumage of each bird at each age as an independent observation. Munsell measures were used directly in analyses of value and chroma, but measures of hue were first converted to a numerical scale (2.5YR = 1, 5YR = 2, 7.5YR = 3, 10YR = 4, 2.5Y = 5, 5Y = 6). I determined whether adult-like subadults or mimetic subadults were more likely to acquire a territory by comparing the plumages of territory holders and floaters with either a *t*-test or a Mann-Whitney *U*-test. All analyses were done with Minitab (1995). Values presented are means \pm SE.

RESULTS

MOLT

'Elepaio at Hakalau underwent a single, prebasic (postbreeding) molt each year, with a single peak in proportion of birds molting in August and September (Fig. 1). The first prebasic molt, in which birds lost their juvenal plumage, began within about four weeks of fledging and was only partial. All body feathers were replaced, but the remiges and rectrices were retained. The second prebasic molt and all subsequent molts were complete; all body and flight feathers were replaced. There was no evidence of a bimodal distribution of molt, which would be expected if there were also a prealternate (pre-breeding) molt. There are thus no alternate (breeding) plumages in 'Elepaio. Molt of body and flight feathers occurred simultaneously. No differences were found in patterns or extent of molt between males and females, so data from both sexes were combined.

Timing and extent of molt were similar in adults and subadults. Peak of molt was the same for adults and subadults, but a larger proportion of subadults than adults began molting in April–June (Fig. 1). This likely is because birds that did not attempt to nest tended to molt earlier, and more subadults than adults did not attempt to nest because they had no territory or mate. The small number of subadults molting in February and March were birds still replacing feathers from the previous plumage, which could be recognized by their coloration and extreme wear. Almost all birds replaced all body feathers each

year; subadults did not molt fewer body feathers than adults.

PLUMAGE SEQUENCE AND DESCRIPTION

Both male and female 'Elepaio exhibited three distinct postjuvinal plumages; first basic, second basic, and definitive basic (adult). There were no alternate plumages because there was only one molt per year. A total of 39 birds was observed in different years, all of which went through the expected transitions from one plumage class to the next, including four that were observed in juvenal and first basic plumages, 17 that were observed in first basic and second basic plumages, and 35 that were observed in second basic and definitive basic plumages. Three birds were captured during the first prebasic molt; all were producing body feathers typical of first basic plumage, but none were replacing flight feathers. All nine birds captured during the second prebasic molt and all 11 birds captured during the third prebasic molt were growing body and flight feathers typical of second basic and definitive basic plumages, respectively.

There was some variation within each age class (Fig. 2), but plumage did not differ between individuals of high (territorial) and low (floater) social status. Subadults with territories were neither more adultlike nor more mimetic than floaters of the same age in any of 17 plumage characters found to differ among age-classes (*t*-test or Mann-Whitney *U*-test, $P > 0.05$).

Juvenal plumage. Juvenal plumage was held for only a few weeks after fledging and was very similar to first basic plumage, but in juvenal plumage the eyebrow was slightly darker (Fig. 3c). Juvenal plumage also differed from all later plumages by its loose, fluffy appearance, caused by fewer barbs and interlocking barbules (Pyle et al. 1987, Thompson 1991).

First basic plumage. First basic plumage of males and females was similar in all respects. Both sexes were dull brown above, pale gray below, with only a few mildly contrasting markings (Table 1). The tips of feathers on the rump and wing coverts were Cinnamon, the latter forming two narrow wingbars. The outer two or three rectrices had small pale-gray tips (Fig. 2g, h). The upper mandible and distal portion of the lower mandible were Blackish Neutral-Gray, and the proximal one-half to two-thirds of the lower mandible, the tomia, and the mouth lining were Buff-Yellow (2.5Y8/8).

Second basic plumage. In second basic plumage, the tips of feathers on the throat, rump, wing coverts, and tail were white mixed with a variable amount of Tawny or Cinnamon, forming a moderately contrasting pattern (Table 1, Fig. 2). Crown and back color were similar to those in juvenal and first basic plumages, but the breast was white instead of gray and had light brown streaks (Table 1, Fig. 3d, f). The sexes could be distinguished in this and later plumages by the length of the white or Cinnamon tips on the throat feathers (Fig. 2b). The throat feathers of both sexes were black with white tips, but in females the tips were longer and overlapped, obscuring the black base of feathers below and causing the throat to appear mostly white. In males the tips were shorter and many did not overlap, revealing a variable amount of black. The distal portion of the lower mandible and the entire upper mandible were Blackish Neutral-Gray, and the proximal one-third to one-half of the lower mandible and the mouth lining were Plumbeous (Table 1).

Definitive basic (adult) plumage. In definitive basic plumage, the tips of feathers on the throat, rump, wing coverts, and tail were completely white, forming a very contrasting pattern (Table 1, Fig. 2a, c, e, g). The breast was white with moderate to heavy brown streaks (Fig. 3). Sexes still could be distinguished by the length of white tips on the throat feathers. Crown, back, and bill color were unchanged from second basic plumage.

Comparison of plumages. With each molt the plumage of each sex became progressively brighter, more adultlike, and had more contrasting markings, up to the third prebasic molt when definitive plumage was acquired. The most obvious age-related plumage changes were increases in the amount of white in several body areas. With increasing age, tips of feathers on the throat, wing coverts, rump, and tail became more white, feathers on the wing coverts, rump, and tail had longer white tips, and the number of feathers with white tips increased on the wing coverts and tail (Fig. 2; all $T_6 > 68$, all $F > 9$, $df = 6, 96-107$, all $P < 0.001$). Plumage brightness, as measured by the chroma or saturation of a color, increased with age on the eyebrow and breast (Fig. 3e, f; $F_{6,103} = 51.2$, $T_6 = 51.8$, respectively, both $P < 0.001$), but did not change on the crown or back (both $T_6 \leq 6.73$, both $P > 0.2$). The eyebrow and breast also de-

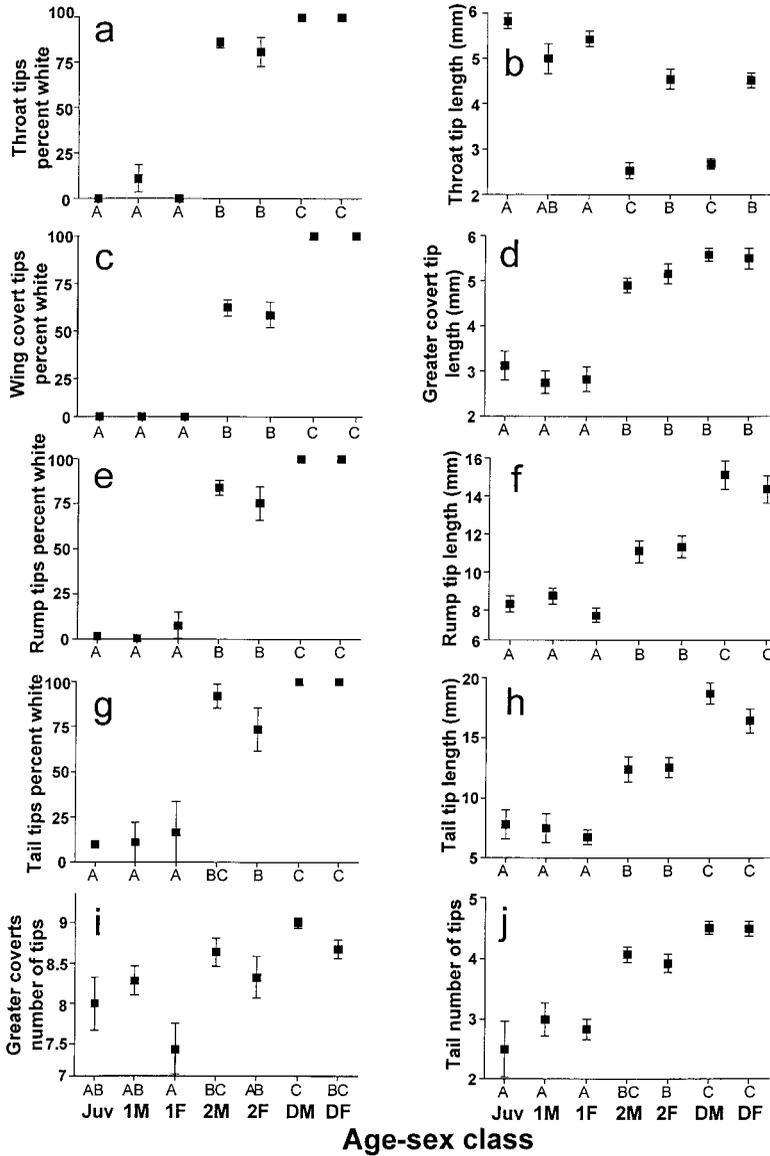


FIGURE 2. Comparisons among 'Elepaio age-sex classes of length, whiteness, and number of contrasting feather tips at Hakalau Forest National Wildlife Refuge, Hawai'i. Juv = juvenal; 1 = first basic; 2 = second basic; D = definitive basic; M = male; F = female. Letters below age-sex classes indicate which classes differed; shared letters indicate classes that were not different. Sample sizes: Juv = 5; 1M = 9; 1F = 7; 2M = 17; 2F = 12; DM = 42; DF = 20. Each comparison was significant by ANOVA or Kruskal-Wallis test with $P < 0.001$.

creased in value (became darker) each year (Fig. 3c, d; $F_{6, 103} = 26.2, 53.7$, respectively, both $P < 0.001$), and their hues became more red and less yellow (Fig. 3a, b; $F_{6, 103} = 19.0, 10.5$, respectively, both $P < 0.001$). The first basic plumages of males and females were indistinguishable and both were similar to juvenal

plumage, but the second basic plumages were sexually dimorphic in throat color and were similar to adult plumage of the same sex. Neither sex's subadult plumage resembled adult plumage of the opposite sex. In particular, the throat-feather tips of second-year subadults of each sex were similar in length to those of adults of the

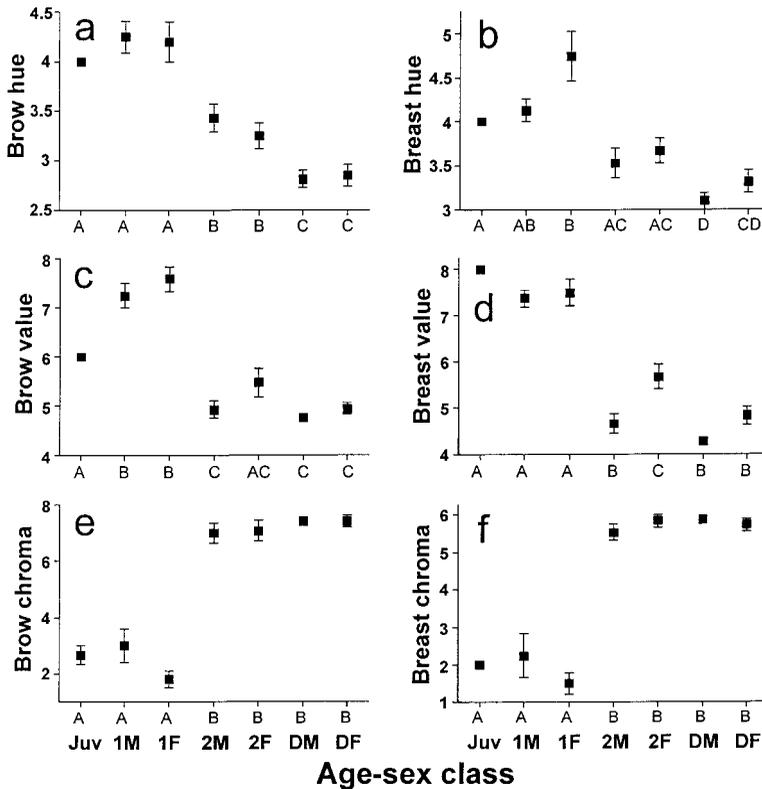


FIGURE 3. Comparisons of plumage color among 'Elepaio age-sex classes at Hakalau Forest National Wildlife Refuge, Hawai'i. Juv = juvenal; 1 = first basic; 2 = second basic; D = definitive basic; M = male; F = female. Letters below age-sex classes indicate which classes differed; shared letters indicate classes that were not different. Hue = spectral color; value = darkness; chroma = intensity. Lower values for hue represent lower (more red) wavelengths. Sample sizes: Juv = 5; 1M = 9; 1F = 7; 2M = 17; 2F = 12; DM = 42; DF = 20. Each comparison was significant by ANOVA or Kruskal-Wallis test with $P < 0.001$.

same sex, and differed in length from the throat feather tips of adults of the opposite sex (Fig. 2b; $F_{6, 103} = 46.5$, $P < 0.001$), providing a clear and consistent distinction between subadults and adults of the opposite sex.

DISCUSSION

DELAYED PLUMAGE MATURATION

'Elepaio at Hakalau exhibited a two-year delay in plumage maturation in both sexes. Males and females sometimes bred when one year old, but did not acquire definitive plumage until they were three years old. The first basic and second basic plumages were distinct from each other and from definitive plumage. The first basic plumage was dull in color, similar to juvenal plumage, and showed no sexual dichromatism. The second basic plumage was intermediate in brightness, sexually dimorphic in throat color,

and strongly resembled definitive plumage of the same sex. The definitive plumage was brighter still, more sexually dimorphic in throat color, and had highly contrasting white markings on the rump, wings, and tail that formed a conspicuous pattern. Another somatic character that showed delayed maturation in 'Elepaio was bill color. In both sexes the proximal part of the lower mandible, the tomia, and the mouth lining were Buff-Yellow in juveniles and first-year subadults, and Plumbeous in second-year subadults and adults. Delayed somatic maturation occurs in males of many bird species (Lawton and Lawton 1986, Lyon and Montgomerie 1986, Rohwer and Butcher 1988), but it is relatively rare in females (Thompson and Leu 1995), and rarer still in both sexes.

Delayed plumage maturation appears to be relatively common in Hawaiian birds (Freed et

TABLE 1. Coloration of 'Elepaio plumages from Hakalau Forest National Wildlife Refuge, Hawai'i. Sexes are the same color unless otherwise noted. Capitalized color names and numbers follow Smithe (1975).

Body region	Juvenal	First basic	Second basic	Definitive basic (adult)
Eye-brow	Dark Drab (119B)	Drab Gray (119D)	yellowish Tawny-Cinnamon	Tawny-Cinnamon to Amber, some with white
Crown	Olive-Brown	Olive-Brown	Olive-Brown	Olive-Brown
Back	Olive-Brown	Dark Drab (119B) to light Cinnamon-Brown	Cinnamon-Brown	Cinnamon-Brown
Throat	Drab Gray (119D)	Drab Gray (119D)	like adult, but approx. 80% white, rest Cinnamon	male black with white tips, female mostly white
Breast streaking	Drab Gray (119D), no streaks	Drab Gray (119D), no streaks	white, light streaks of light Antique Brown	white, moderate to heavy streaks of Antique Brown
Wing-covert tips	Tawny	Cinnamon	approx. 60% white, rest Cinnamon	white
Rump	Cinnamon-Brown	Tawny-Cinnamon	approx. 80% white, rest Tawny-Cinnamon	white
Bill color	base of lower mandible low, rest Blackish	Buff-Yel-Neutral-Gray	base of lower mandible Plumbeous, rest Blackish Neutral-Gray	same as second basic

al. 1987), and some form of postjuvenal sub-adult plumage has been found in virtually all Hawaiian passerine species that have been carefully examined. In sexually monochromatic Hawaiian species both sexes generally have a first basic plumage, including the 'Apapane (*Himatione sanguinea*; Fancy et al. 1993), 'I'iwi (*Vestiaria coccinea*; Fancy et al. 1993), 'Ākohekohe (*Palmeria dolei*; Simon et al. 1998), 'Ōma'ō (*Myadestes obscurus*; Fancy et al. 1994), and Puaiohi (*Myadestes palmeri*; Perkins 1903). In most sexually dichromatic Hawaiian species only males have a first basic plumage, including the Palila (*Loxioides bailleui*; Jeffrey et al. 1993), Laysan Finch (*Telespiza cantans*; Banks and Laybourne 1977), Hawai'i 'Amakihi (*Hemignathus v. virens*; van Riper 1987), 'Akiapō-lā'au (*Hemignathus munroi*; Pratt et al. 1994), and Maui Parrotbill (*Pseudonestor xanthophrys*; Berlin et al. 2001). In the Hawai'i 'Ākepa (*Loxops c. coccineus*) males have first basic and second basic plumages (Lepson and Freed 1995).

Other birds in which males are known to have delays in plumage maturation longer than one year include the Swallow-tailed Manakin (*Chiroxiphia caudata*; 2 years, Foster 1987), the Long-tailed Manakin (*C. linearis*; 3 years, McDonald 1993), Darwin's finches (*Geospiza* spp.; up to 6 years, Grant 1990), and many species of bowerbirds and birds of paradise (Ptilonorhynchidae and Paradisaeidae; four or more years, Cooper and Forshaw 1977, Frith and Beehler 1998). In several species of corvids and bowerbirds, bill color takes up to 6 years to mature in both sexes (Lawton and Lawton 1986). It is perhaps no coincidence that all bird species thus far reported to have delays in somatic maturation longer than one year are residents of tropical areas, often islands. Many tropical and resident birds are long-lived, particularly those on islands (Faaborg and Arendt 1995, Johnston et al. 1997, but see Karr et al. 1990), and delayed plumage maturation often is associated with a long lifespan, strong intrasexual competition, and delayed recruitment (Studd and Robertson 1985, Grant 1990, but see Montgomerie and Lyon 1986). It seems likely that lengthy delays in somatic maturation will prove to be more common and widespread in birds than is currently realized as more tropical resident species are studied.

IMPLICATIONS FOR HYPOTHESES OF DELAYED PLUMAGE MATURATION

Numerous hypotheses have been proposed for the evolution of plumage maturation, some of which can be addressed using information on molt and plumage patterns (Thompson 1991). For example, the molt constraint hypothesis proposes that subadult plumage is not necessarily adaptive, and that young birds retain some immature feathers because they are energetically limited and unable to produce a complete set of new feathers (Rohwer 1986, Rohwer and Butcher 1988). If subadult plumage is caused by an energetic constraint, one would expect subadults to molt fewer feathers than adults, and that all new feathers produced by subadults be adult in coloration (Rohwer et al. 1983, Hill 1992). However, in 'Elepaio subadults did not molt fewer feathers than adults and a large proportion of new feathers produced by subadults were not adult in coloration, indicating the subadult plumages are not caused by a molt constraint. 'Elepaio have two opportunities to acquire adult plumage before they actually do so. The first prebasic molt is only partial, but all body feathers are replaced, and many feathers in the resulting first basic plumage are differently colored than those in definitive plumage. The second prebasic molt is complete, but still does not produce definitive plumage. The presence of two subadult plumages distinct from each other and distinct from adult plumage indicates they are not caused by a molt constraint and suggests each plumage has a function.

The female mimicry hypothesis contends that subadult plumage reduces aggression by serving as a deceptive symbol of sex. Young males that resemble adult females are not recognized by rival males and therefore are not attacked (Rohwer et al. 1980, 1983). For species in which females have delayed plumage maturation an analogous argument can be applied to the subadult plumage of females, in which case this hypothesis more generally could be termed "sexual mimicry." Similarly, the juvenile mimicry hypothesis states that subadult plumage reduces aggression by functioning as a deceptive symbol of sexual maturity (Foster 1987). Young birds of either sex that resemble sexually immature juveniles are not viewed by adults as potential rivals and therefore are not attacked. In 'Elepaio from Hakalau, neither subadult plumage resembles definitive plumage of the opposite sex,

which presumably would make them poor sexual mimics. First basic plumage is similar to juvenal plumage, but second basic plumage is not, providing only partial support for juvenile mimicry.

DELAYED PLUMAGE MATURATION IN RELATED TAXA

The O'ahu 'Elepaio also has a two-year delay in somatic maturation in both sexes, but is less sexually dichromatic than the Hawai'i 'Elepaio, and both the first basic and second basic plumages are juvenile-like (VanderWerf 1998). The Kaua'i 'Elepaio has at least a distinct first basic plumage, but the complete sequence of plumages and molts has not been examined (VanderWerf 1998). The closest relatives of the 'Elepaio are other members of the Monarchidae from the Pacific and Australasian regions (Pratt et al. 1987, Sibley and Ahlquist 1990). Many monarch flycatchers are reported to have distinct subadult plumages, sometimes in both sexes (Pratt et al. 1987, Simpson et al. 1996), but in most species the sequence of plumages and molts is poorly known. Two of the better-known monarchs are the Grey Fantail (*Rhipidura fuliginosa*) and Rufous Fantail (*R. rufifrons*) from Australia, both of which have a single prebasic molt per year and first basic plumages in both sexes, resulting in a one-year delay in plumage maturation (Rogers et al. 1986).

It is not clear whether delayed plumage maturation is ancestral in the Monarchidae or has evolved independently more than once because generic relationships in this group are poorly known (Boles 1979, Sibley and Ahlquist 1990). Investigation of demography, mating system, and phylogeographic patterns of plumage maturation in monarch flycatchers on different Pacific islands would help increase our understanding of delayed plumage maturation and the conditions under which it is favored in each sex.

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