

'Elepaio subadult plumages reduce aggression through graded status-signaling, not mimicry

Authors: VanderWerf, Eric A., and Freed, Leonard A.

Source: Journal of Field Ornithology, 74(4) : 406-415

Published By: Association of Field Ornithologists

URL: <https://doi.org/10.1648/0273-8570-74.4.406>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

‘Elepaio subadult plumages reduce aggression through graded status-signaling, not mimicry

Eric A. VanderWerf¹ and Leonard A. Freed

University of Hawaii, Department of Zoology, Edmondson Hall, 2538 The Mall,
Honolulu, Hawaii 96822 USA

Received 21 October 2002; accepted 27 January 2003

ABSTRACT. The ‘Elepaio (*Chasiempis sandwichensis*) is a monarch flycatcher endemic to the Hawaiian Islands. Both sexes have a two-year delay in plumage maturation, with distinct first-year and second-year subadult plumages. This study tested hypotheses for the evolution of delayed plumage maturation in ‘Elepaio by presenting adult males with models representing different ages and sexes in the breeding and nonbreeding seasons. The subadult plumages of ‘Elepaio appeared to serve as honest, graded signals of status that reduced aggression from dominant adults. Both first-year and second-year subadult male models were attacked less than adult male models, and aggression increased linearly with age of male models. Neither subadult plumage appeared to function in sexual mimicry or juvenile mimicry. Second-year male models were attacked more than adult female models; neither subadult plumage resembles adult plumage of the opposite sex. First-year male models, which are juvenile-like, were not attacked more than adult female models, but juvenile mimicry cannot account for the behavior toward second-year male models and is a less parsimonious explanation. Aggression toward models was much higher in the breeding season, and all models were treated similarly in the nonbreeding season, suggesting competition for mates has been the primary selective force shaping the evolution of the ‘Elepaio’s plumage coloration. Models made from color photocopies can be a useful alternative to museum specimens in behavioral studies of rare species or those in which damage to specimens during model presentation would occur.

SINOPSIS. Los plumajes subadultos de *Chasiempis sandwichensis* reducen la agresión mediante la gradación de señales de estatus, no por mimetismo

Chasiempis sandwichensis es un Passeriforme (Tyrannidae) endémico a las islas de Hawaii. Ambos sexos tardan dos años en la maduración del plumaje, con plumajes, subadultos distintivos de primer y segundo año. El estudio examinó las hipótesis para la evolución de la tardanza en la maduración del plumaje en esta especie al presentar (a machos adultos) modelos representando diferentes edades y sexos en las temporadas reproductivas y no reproductivas. Los plumajes subadultos de la especie parecieron servir como señales honestas, graduadas de señales de estatus que redujeron la agresión de los adultos dominantes. Tanto los modelos de machos subadultos de primer y de segundo año fueron atacados menos que modelos de machos adultos, y la agresión incrementó linealmente con la edad del modelo de macho. Ningún plumaje subadulto pareció servir para mimetismo sexual o mimetismo juvenil. Modelos de machos de segundo año fueron atacados más que los modelos de adultos femeninos; y ningún plumaje subadulto se aparece al plumaje adulto del sexo opuesto. Los modelos de machos de primer año, que parecen juveniles, no fueron atacados más que los modelos de hembras adultas, pero el mimetismo juvenil no puede la conducta hacia modelos de machos de segundo año y es una explicación de menos parsimonia. La agresión hacia los modelos fué mucho mayor durante la época reproductiva, y todos los modelos se trataron similarmente en la época no-reproductiva, sugiriendo que una competencia por machos ha sido la principal fuerza selectiva moldeando la evolución del color del plumaje en *Chasiempis sandwichensis*. Modelos hechos de fotocopias a color pueden ser una alternativa útil al uso de especímenes de museo en estudios de conducta de especies raras o de aquellas en que pueden ocurrir daños a especímenes al presentar modelos.

Key words: *Chasiempis sandwichensis*, delayed plumage maturation, ‘Elepaio, Hawaii, model presentations, status signaling, subadult plumage

In many species of sexually dimorphic passerine birds, males do not acquire definitive (adult) plumage until after their first potential breeding season, even though they are sexually

mature and sometimes breed in predefinitive (subadult) plumage (Rohwer et al. 1980; Lyon and Montgomerie 1986). This pattern is often termed delayed plumage maturation (DPM; Rohwer et al. 1980), and is a form of neoteny in which sexually mature individuals possess an immature somatic character, the color of their plumage (Lawton and Lawton 1986). Often, birds with subadult plumage are less likely to

¹ Corresponding author. Current address: U.S. Fish and Wildlife Service, 300 Ala Moana Boulevard, Room 3-122, Box 50088, Honolulu, Hawaii 96850 USA. Email: eric.vanderwerf@fws.gov

obtain a mate and breed (Rohwer et al. 1980; Procter-Gray and Holmes 1981; Flood 1984), raising the questions of why this delayed plumage maturation has evolved, and what function, if any, is served by subadult plumage. Several hypotheses have been proposed for the evolution of DPM, all of which assume young birds are subordinate and cannot compete directly with adults (Rohwer et al. 1980; Procter-Gray and Holmes 1981; Studd and Robertson 1985; Lyon and Montgomerie 1986; Foster 1987; Rohwer and Butcher 1988).

Some of these hypotheses propose that subadult plumage evolved, or at least functions, to communicate information about social status, sex, or sexual maturity in order to reduce aggression from dominant adults. The status-signaling hypothesis proposes that subadult plumage is an honest symbol of subordination that allows young birds to avoid fights with dominant adults, which they likely would lose (Rohwer 1975; Lyon and Montgomerie 1986). The female mimicry hypothesis proposes that subadult plumage is a dishonest signal of sex that reduces aggression by deceiving adults of the opposite sex, thereby increasing access to potential mates or food resources (Rohwer et al. 1980). The juvenile mimicry hypothesis proposes that subadult plumage is a dishonest signal of sexual maturity that prevents adults from distinguishing subadults and sexually immature juveniles (Foster 1987). An alternative view is that, although subadult plumage may be juvenile-like, it is not necessarily mimetic, and rather than being a deceptive signal of sexual maturity, subadult plumage is an honest advertisement of subordination (Geist 1971; Lawton and Lawton 1986). The latter view can be regarded as a form of status-signaling in which subadult plumage is necessarily juvenile-like, not simply distinct from adult plumage. The proximate function of a juvenile-like subadult plumage is the same in both cases, reduced aggression, but the mechanism by which the reduction occurs is different. In practice these may be difficult to distinguish.

Each hypothesis could apply in the breeding season, in the nonbreeding season, or in both. Subadult plumage could serve as a symbol of subordination in the breeding season, in which case it presumably would reduce aggression in competition for mates (summer status signaling; Lyon and Montgomerie 1986), or in the

nonbreeding season, when it presumably would reduce aggression in competition for food (winter status-signaling; Rohwer and Butcher 1988). Similarly, a mimetic plumage could provide a mating advantage for young birds in the breeding season (Rohwer et al. 1983), and it could be beneficial in the nonbreeding season if dominant individuals, usually males, control food resources and preferentially allow access to potential mates (Geist 1971; Brown and Brown 1988).

A powerful method of testing the various hypotheses for the evolution of DPM is an experimental approach that uses either model presentations or phenotypic modifications, such as plumage dyeing, to test predictions about how subadults are treated by adults. By presenting adult birds with pairs of models representing a subadult and either an adult of the same sex or an adult of the opposite sex, it should be possible to determine whether subadult plumage reduces aggression and the mechanism by which the reduction occurs. By presenting models at different times of year, it also should be possible to determine the season when subadult plumage is adaptive, if any. The null hypothesis is that plumage does not provide information about social status, sex, or sexual maturity, and thus predicts that responses to models should be independent of the plumage they represent. In this study models were presented with recordings of male territorial songs to attract subjects to the models. Thus, if all models were viewed similarly and the response was based only on the auditory stimulus of the recorded song, then under the null hypothesis one might expect all models to be viewed as potential competitors by adult males and therefore treated aggressively (Enstrom 1992a).

Most previous studies investigating the function of subadult plumages have involved north temperate, migratory passerines, which typically have a one-year delay in plumage maturation in males only (for exceptions see Grant 1990; McDonald 1993; and Lepson and Freed 1995). We studied DPM in a tropical bird endemic to the Hawaiian Islands, the 'Elepaio (*Chasiempis sandwichensis*). 'Elepaio provide an interesting system in which to study DPM because both sexes exhibit a two-year delay in plumage maturation and each sex has two distinct subadult plumages (VanderWerf 2001a). Both first year and second year subadult 'Elepaio are sexually

mature and sometimes breed, but subadults are subordinate to adults and must act as floaters until a breeding opportunity becomes available (VanderWerf 2001b). 'Elepaio are relatively small (average mass of males, 16 g; VanderWerf 1998), but they are long-lived; annual survival of adults is often over 85% (VanderWerf 2001b), and the maximum known lifespan is at least 16 yr (E. VanderWerf and L. Freed, unpubl. data). 'Elepaio are nonmigratory and socially monogamous, and males defend a territory year-round with assistance from the female (van Riper 1995; VanderWerf 1998).

The appearance of subadult plumages and the pattern of molts in 'Elepaio are consistent with status-signaling but are not consistent with sexual mimicry or juvenile mimicry (VanderWerf 2001a). The next step is to test whether the subadult plumages do indeed reduce aggression, and whether they do so by serving as honest signals of status. In addition, 'Elepaio provide an opportunity to test whether distinct first-year and second-year subadult plumages cause birds to be treated differently by adults (McDonald 1993). Lastly, because 'Elepaio are nonmigratory and defend territories year-round, it is possible to present models to the same individuals at different times of year to determine the season(s) when subadult plumage is adaptive, which is more difficult with migratory species (Enstrom 1992b).

METHODS

Study species and site. The 'Elepaio comprises a genus of monarch flycatchers (Monarchidae) endemic to the Hawaiian Islands of Hawai'i, O'ahu, and Kaua'i (Pratt et al. 1987; VanderWerf 1998). Both sexes have a two-year delay in plumage maturation and do not acquire definitive plumage until they are three years old, resulting in three distinct postjuvenile plumages: first basic, second basic, and definitive basic (VanderWerf 2001a). 'Elepaio have a single prebasic (post-breeding) molt per year, so there are no alternate (breeding) plumages (VanderWerf 2001a). We refer to the three age-classes that are recognizable by plumage as first-year subadult, second-year subadult, and adult.

On Hawai'i, where this study was conducted, adult plumage is dark brown above, white with brown streaks below, and has conspicuous white wings bars, white rump, and white tail

tips. Adult males have a mostly black throat and adult females have a mostly white throat, but in other respects the sexes are similar. The first-year subadult plumages are not sexually dichromatic, and both are very similar to juvenile plumage: dull gray-brown above, pale gray below, with narrow cinnamon-colored wing bars, rufous rump, and pale gray tail tips (VanderWerf 2001a). The second-year subadult plumages are intermediate in appearance between adult and first-year plumages: the wing bars, rump, and tail tips are partly white, as in the adult plumage, and partly cinnamon or rufous, as in the first-year plumage. In second-year subadults the throat shows intermediate sexual dichromatism, partly cinnamon, as in first-year plumage, and partly black (males) or white (females), as in adult plumage (VanderWerf 2001a).

This study was conducted at Hakalau Forest National Wildlife Refuge, on the east slope of Mauna Kea volcano on the island of Hawai'i. Habitat on the refuge is montane rainforest dominated by 'ohi'a (*Metrosideros polymorpha*) and koa (*Acacia koa*) trees, with varying degrees of human disturbance from prior cattle ranching and logging. 'Elepaio are fairly common permanent residents, occurring in contiguous territories throughout most of the refuge. The breeding season of the 'Elepaio at Hakalau is usually April–July, with most nests initiated in April and early May (E. VanderWerf, unpubl. data). Male 'Elepaio defend territories year-round, but aggression peaks just prior to and during nest construction and declines rapidly once incubation begins (E. VanderWerf, unpubl. data). Nonbreeding season model presentations were conducted from 9–15 November 1995, and breeding season model presentations were conducted from 14–18 March 1997. We attempted to conduct breeding season presentations in early April 1996, but were unable to complete the presentations before most birds began incubating because nesting began unusually early that year.

Models and presentations. Models were made from color photocopies of photographic slides of live, hand-held 'Elepaio captured in mist nets. Each side of a model was a mirror-image of the same slide, and models were stuffed with cotton to make them three-dimensional. Two models of each age-sex class were made from photographs of different birds, and

Table 1. Response scores toward models during presentations, in order of increasing aggression. The highest score toward each model in a pair was used for analysis.

Response	Score
No reaction	0
Distant approach (>2.5 m) and undirected display	1
Close approach (<2.5 m)	2
Spend much time close (>30 s) or directed display (<2.5 m)	3
Swoop at model	4
Physical attack of model (peck, scratch, hit)	5

they were used alternately in presentations to reduce pseudoreplication (Catchpole 1989; Kroodsma 1989). Photocopies were scaled to be life-size when stuffed (15 cm in length), and birds in all photographs were in the same neutral, non-aggressive posture. Models were treated with a clear, non-shiny plastic spray-coating to make them more durable and water-resistant. Coloration of models was compared to coloration of live birds using Munsell color chips (Munsell 1994), and in all cases appeared similar, as judged by the human eye. It was not possible to use 'Elepaio museum specimens as models because they are too valuable and could not be replaced if damaged. Photocopied models elicited strong responses, and specimens probably would have been damaged had they been used.

Two sets of model presentation experiments were conducted, using different sets of birds as subjects for each experiment to reduce habituation, which may reduce intensity of response in later trials (Falls 1992). The first experiment used three pairs of models: an adult male (AM) with a second-year male (2M); an adult male with a first-year male (1M); and a second-year male with a first-year male. These pairings were designed to test whether intrasexual aggression was related to age. Each of 12 territorial adult male 'Elepaio was presented with all three combinations, with one rest day between presentations. The order of presentation was varied systematically to control for habituation, so that equal numbers of subjects were presented with each treatment on each day. The second experiment used two pairs of models: an adult female (AF) with a second-year male, and an adult female with a first-year male. Pairings in the second experiment were designed to test whether 'Elepaio could distinguish male subadult plumages from adult female plumage. Both combi-

nations were presented to each of 10 territorial adult male 'Elepaio using the same methods as in the first experiment. Each experiment was conducted during both the breeding and non-breeding seasons, for a total of four sets of trials.

Models were mounted on 1.5-m tall sticks of 'akala (*Rubus hawaiiensis*) placed 5 m apart, and were attached to the sticks with brown clay. Models were positioned so they were equidistant from the nearest vegetation and as close as possible to the known geometric center of each 'Elepaio territory, because aggressiveness of response often declines toward territory margins (Patterson 1980; Melemis and Falls 1982). To attract 'Elepaio to the models, recorded male territorial songs were played through a speaker placed on the ground mid-way between the models. Observations were made and recordings were played from a remotely-connected cassette recorder 10 m from the speaker. Presentations lasted five minutes, and began when the recorder was started. The response of each subject toward each model in a pair was scored on a scale from 0 to 5 (Table 1). The distinction between "distant" and "close" approaches and "undirected" and "directed" displays was set at 2.5 m because this was half the distance between the models, making it more likely that the bird was deliberately responding to one of the two models.

It has been suggested that some species of birds have delayed song maturation in addition to delayed plumage maturation (Cucco and Malacarne 2000), and ages of birds used to make recordings played during model presentations can influence the response to models (Procter-Gray 1991; Enstrom 1992a). Songs of subadult male 'Elepaio are distinguishable from those of adult males (VanderWerf 1998). We therefore conducted trial presentations in Oc-

tober 1995 in which adult male and first-year subadult male models were presented together while songs of each age were played. Song age did not affect response to adult or first-year male models (Wilcoxon signed-rank tests, $P = 0.40$ and 0.61 , respectively). Furthermore, in subsequent presentations we played the song matching the model that was expected to elicit the weaker response. For example, when first-year subadult and adult male models were presented together, we played the song of a first-year male. If the adult model was then attacked more vigorously, as predicted by all but the null hypothesis, it was more likely that the response was due to the visual stimulus of the model and not to the auditory stimulus of the recorded song. If the subject arrived at the models expecting to encounter a bird of the same age as the song being played, a response resulting in rejection of the null hypothesis would require the visual stimulus to override the auditory stimulus.

Analyses. Responses to models in each pair were compared with a Wilcoxon signed-rank test. In order to further examine the overall pattern of response to all models, we combined responses to each type of model from all trials in each season. If a one-way ANOVA revealed significant overall variation within a season, we used a linear contrast of responses to male models ordered by age to test whether aggression increased with age.

We tested for habituation by comparing response strength among days with a Friedman test, using each bird as a block. We also tested whether strength of response varied among individual birds with a Friedman test, using each treatment as a block. For the latter two analyses, we used the strongest response by each bird to either model in a pair.

RESULTS

Behavior of adult male 'Elepaio toward models was variable but sometimes quite aggressive, occasionally including pecking with the bill, scratching with the feet, and hitting with the wings. On two occasions models were knocked off their stick during an attack, and one bird continued to attack the model after it fell to the ground, after which it attacked the second model. Swooping flights over or directly at the models were fairly common. Many males ap-

proached the models closely and inspected them. A threat display often was given by males perched close to the models, in which the head was held up while the feathers on the throat and crown were erected, the tail was cocked upward at 90° and fanned to display the white tips, and the wings were drooped to expose the white wing bars and rump. All these behaviors also occur in real encounters between male 'Elepaio.

During the breeding season, adult males were less aggressive toward first-year subadult male models than toward adult male models (Fig. 1b; Wilcoxon test, $P = 0.02$) and marginally less aggressive toward second-year subadult male models than toward adult male models (Fig. 1a; $P = 0.06$). Adult males were somewhat less aggressive toward first-year subadult male models than toward second-year subadult male models, but the difference was not significant (Fig. 1c; $P = 0.10$).

In tests of sexual mimicry during the breeding season, adult males were more aggressive toward second-year subadult male models than toward adult female models (Fig. 1d; $P = 0.04$), but first-year subadult male models and adult female models were treated the same (Fig. 1e; $P = 0.99$). Aggression toward second-year subadult male models was sometimes quite strong and included physical attack, but first-year subadult male models were not physically attacked.

During the nonbreeding season, all pairs of models were treated similarly in both sets of experiments, and aggression was much lower than during the breeding season (Figs. 2a–e, all P -values > 0.37). No models of any type were physically attacked during the nonbreeding season, and birds rarely spent much time close to the models.

When the results from all trials in the breeding season were combined in order to examine the overall response to all models, there was significant variation in response (ANOVA, $F_{2,89} = 4.26$, $P = 0.017$), and there was a linear pattern of increasing aggression toward older male models (Fig. 3; $F_{1,90} = 7.92$, $P = 0.006$).

Marginally significant habituation occurred in the second experiment in the breeding season (Friedman test, $P = 0.06$). During this set of trials, responses were somewhat less aggressive on the second day than on the first day. In the other three sets of trials there was no decline in

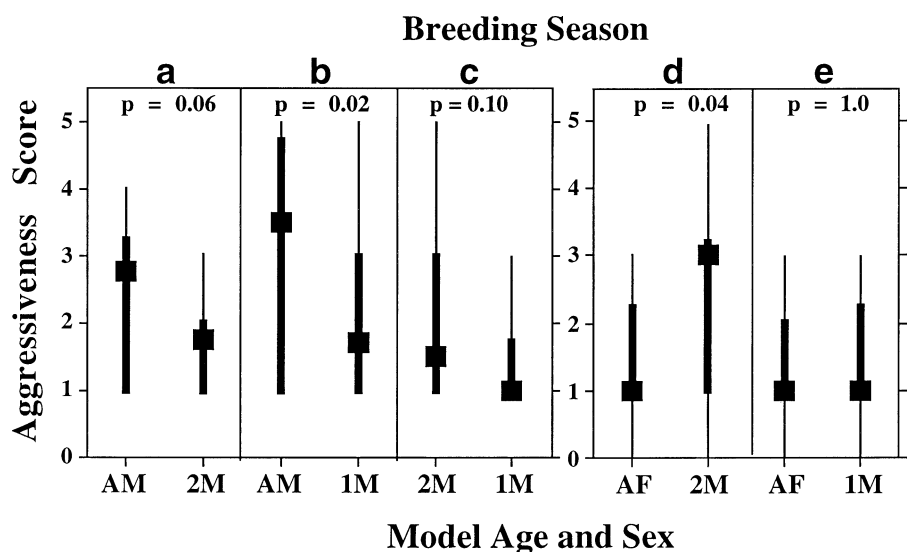


Fig. 1. Responses of adult male ‘Elepaio to pairs of models representing different ages and sexes during the breeding season. Higher scores indicate more aggression. AM, adult male; AF, adult female; 2M, second-year male; 1M, first-year male. The median, interquartile distance, and range are shown by a box, thick vertical lines, and thin vertical lines, respectively.

response, or habituation, on later days (Friedman tests, $P = 0.51\text{--}0.83$). Response strength tended to vary among individual birds in the first experiment in the breeding season. Certain birds consistently responded more strongly than other birds in this set of trials (Friedman test, $P = 0.06$), but not in other sets of trials (Friedman tests, $P = 0.42\text{--}0.90$). One bird in partic-

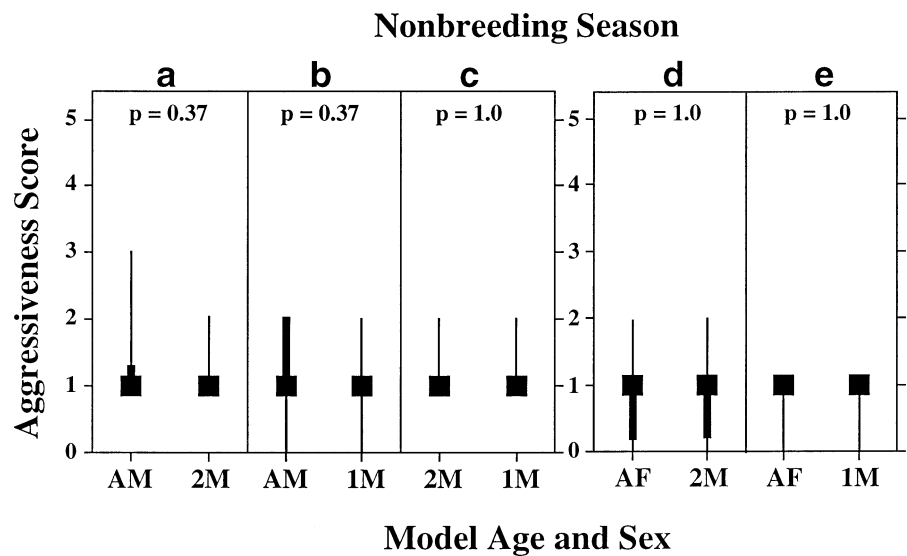


Fig. 2. Responses of adult male ‘Elepaio to pairs of models representing different ages and sexes during the nonbreeding season. Higher scores indicate more aggression. AM, adult male; AF, adult female; 2M, second-year male; 1M, first-year male. The median, interquartile distance, and range are shown by a box, thick vertical lines, and thin vertical lines, respectively.

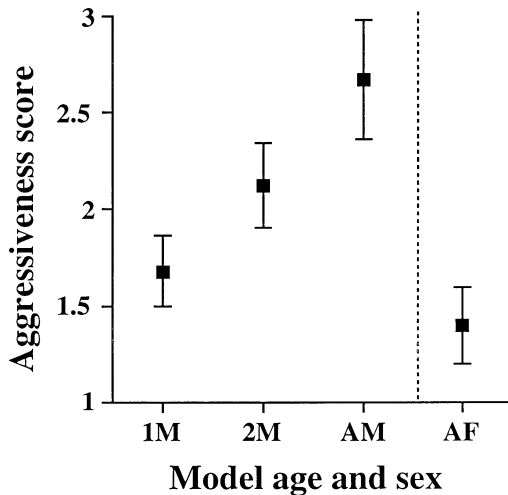


Fig. 3. Overall responses (mean \pm SE) of adult male 'Elepaio to models of different ages and sexes, compiled over all trials during the breeding season. AM, adult male; AF, adult female; 2M, second-year male; 1M, first-year male.

ular attacked all ages of male models in at least one trial, and was the only bird to physically attack a first-year subadult male model, but did so only after it had already "defeated" the adult male model by knocking it off its stick.

DISCUSSION

Responses of adult male 'Elepaio toward models representing different ages and sexes varied significantly in the breeding season, allowing rejection of the null hypothesis that plumage does not communicate information. Moreover, patterns of response indicated that the subadult plumages of male 'Elepaio reduce aggression among males. Adult males were less aggressive toward subadult male models than toward adult male models. Aggression toward models was much higher in the breeding season, and in the nonbreeding season all models were treated similarly, suggesting competition for mates during the breeding season has been the primary selective force shaping the evolution of the 'Elepaio's plumage coloration (Lyon and Montgomerie 1986), rather than competition for food, which also should be important in the nonbreeding season (Rohwer and Butcher 1988).

The subadult plumages of the 'Elepaio ap-

pear to reduce aggression by serving as honest, graded signals of subordination, and do not appear to function in sexual mimicry or juvenile mimicry. Both first-year and second-year subadult male models were treated less aggressively than adult male models, which is consistent with predictions of all three communication hypotheses, but the observed linear increase in aggression with age is expected only under status-signaling. Sexual mimicry and juvenile mimicry assume that neither subadult age class is recognized, and thus predict that first-year and second-year subadult male models should be treated similarly, which was not the case. The presence of two distinct subadult plumages cannot be explained by either mimicry hypothesis, but status-signaling can account for both subadult plumages.

Behavior toward subadult male models compared to adult female models provided more ambiguous evidence partly in support of status-signaling and partly in support of juvenile mimicry, but status-signaling provides a more parsimonious explanation for the function of both subadult plumages. Second-year male models were treated more aggressively than adult female models, which is consistent with status-signaling, but is not consistent with sexual mimicry or juvenile mimicry. This is not surprising, since the second-year plumage of males does not resemble the plumage of adult females or juveniles, and thus presumably would be a poor mimic (VanderWerf 2001a). First-year male models, however, were not treated more aggressively than adult female models, which is consistent with sexual mimicry and juvenile mimicry, but may not be consistent with status-signaling. Since first-year male plumage is similar to juvenile plumage but is not similar to adult female plumage (VanderWerf 2001a), juvenile mimicry is more likely than female mimicry. This raises the possibility that the first-year and second-year subadult plumages of 'Elepaio reduce intrasexual aggression by different mechanisms, i.e., that first-year plumage is a deceptive signal of sexual maturity, and second-year plumage is an honest signal of subordination. However, the function of both subadult plumages can be resolved more parsimoniously if the juvenile-like appearance of first-year subadult plumage is regarded as an honest signal of subordination (Lawton and Lawton 1986), rather than as a

dishonest signal of sexual maturity (Foster 1987). Retention of juvenal plumage characters does not necessarily constitute "mimicry" in the sense that it is deceptive, and may simply advertise young age and low competitive ability. The low aggression toward first-year male models does not require that they were not recognized, but instead may indicate that first-year males pose no threat to adult males and do not warrant attack. The latter interpretation is supported by behavioral and demographic observations; first-year males acquire territories and breed less often than second year males, and adult females prefer adult males as mates, and will leave a territory in search of an adult male rather than pair with a first-year male (VanderWerf 1999). First-year males thus are recognized by potential mates but are avoided, and are less able to defend territories, supporting the conclusion that they are not serious threats to adult males and are not worth attacking.

The linear increase in aggression among the three male age-classes suggests their plumages represent three levels of a graded signal that reflect a three-tiered social hierarchy based on age. First-year birds have the lowest status, breed least often, advertise their youth and subordination with a dull plumage that is very juvenile-like, and, because they pose the least threat as potential rivals, elicit the least aggression from territorial adults. Second-year birds advertise their intermediate status with a plumage that is intermediate in appearance, and therefore receive moderate aggression. Adults have the highest social status, advertise their dominance with a highly contrasting plumage that is least juvenile-like, and are treated most aggressively because they pose the greatest threat to other adults. Similar social hierarchies and graded signals have been reported in Long-tailed Manakins (*Chiroxiphia linearis*; McDonald 1993) and mountain sheep (Geist 1971). Much as male manakins and male mountain sheep resemble juveniles when they are young and slowly acquire more elaborate plumage or grow larger horns as symbols of their increasing status, 'Elepaio of both sexes signal their rise in social status over the first three years of life by acquiring progressively whiter and more contrasting markings on the wings, rump, tail, and throat. Rank within the adult age-class appears to be determined by

contests involving displays, chasing, and physical combat. These contests are serious and can result in injury or even death; we once saw an adult male 'Elepaio kill another adult male with pecks to the head during a particularly severe and lengthy contest. Larger physical size thus may be an advantage in dominance contests (Geist 1971), and the sexual size dimorphism observed in 'Elepaio, with males being approximately 10% larger (VanderWerf 1998), may be caused at least partly by the more intense aggression in contests between males (Webster 1997).

The age-based social hierarchy described above does not explain why 'Elepaio have two distinct subadult plumages, or why sexual dichromatism does not appear until the second year. Why not have the same subadult plumage for two years, and why look like a juvenile the first year? One possible explanation is that the first-year plumage is a signal of subordination that reduces aggression from the parents in particular. Fledgling 'Elepaio are tolerated by their parents and are allowed to stay on the natal territory for up to nine months, until the parents begin nesting again the following year (VanderWerf 1998). Fledglings molt and lose their juvenile body plumage when they are about two months old, but the new plumage they produce is still juvenile in appearance (VanderWerf 2001a). It is possible that if they grew a more adult-like, sexually dichromatic plumage while still on the natal territory, they might be viewed as potential rivals by their parents and immediately evicted. This hypothesis could be tested by dyeing the plumage of fledglings to resemble adult plumage. In a study of Mute Swans (*Cygnus olor*), Conover et al. (2000) found that young birds that molted into a gray subadult plumage were tolerated by their parents and had higher survival than birds that molted directly into the white adult plumage, which were attacked by the parents and driven away at the onset of molt. By continuing to look like juveniles, fledgling 'Elepaio may be allowed to stay on the natal territory, where they can forage without being harassed by other adults, and may even learn to forage by following their parents. 'Elepaio use a diverse array of foraging behaviors, forage on a wide variety of substrates, and require more than a year to fully develop their foraging skills (VanderWerf 1994). The period on the natal territory may

be important for learning the appropriate search images and developing the coordination required for complex foraging behaviors. The second-year plumage could then advertise dominance over first-year birds, but also advertise subordination to adults. The number of distinct, age-specific plumages seen in a species may depend on its potential lifespan (Studd and Robertson 1985), and on the time required to reach the highest social class. Long-lived species and those with complex social hierarchies, such as 'Elepaio, Galapagos finches (*Geospiza* spp.; Grant 1990), Long-tailed Manakins (McDonald 1993), and Hawai'i 'Akepa (*Loxops c. coccineus*; Lepson and Freed 1995), tend to exhibit three or more plumage-classes, while short-lived species, such as many north temperate migratory birds, tend to have only one or two classes.

We had hoped to conduct analogous experiments to test the function of subadult plumage in female 'Elepaio, but we were unable to because responses of females appeared to be dependent on those of males. Males usually arrived at the models before females and responded more strongly, regardless of whether male or female recordings were played. It was not clear, therefore, whether females were responding to the models or simply following males. However, the sequence of plumages and the degree of resemblance to adult plumage is the same in males and females, suggesting their functions also are the same. Females are aggressive toward each other in territorial disputes, but less so than males, and subadult females acquire territories and mates less often than adult females (VanderWerf 1999).

The results of this study are similar to those of several previous studies showing reduced aggression toward subadult-plumaged birds (Hardy 1974; Rohwer 1978; Flood 1984; Hill 1989; McDonald 1993; Conover et al. 2000). In addition, this study demonstrates that the reduction in aggression occurs through status-signaling, that plumage signals can be graded and have more than two levels (Grant 1990), and that signaling subordination is important primarily in the breeding season. These interpretations are strengthened in this study by patterns of mate choice and age structure of the breeding population.

Although it generally is preferable to use museum specimens as models in behavioral stud-

ies, in the case of rare or endangered species or those in which museum specimens are for some reason irreplaceable, it may not be possible to use specimens as models. In such cases models made from color photocopies of photographic slides or prints provide a viable alternative. The Hawai'i 'Elepaio is not endangered like its relative on O'ahu, but its distribution and abundance have declined due to human activities (VanderWerf 1998), and it is unlikely that many additional museum specimens will be collected. In this study color photocopies elicited strong responses from wild birds, and responses differed among model types, indicating they conveyed different information.

ACKNOWLEDGMENTS

This research was supported by the Ecology, Evolution, and Conservation Biology Program of the University of Hawai'i, the ARCS Foundation, Sigma Xi, the Hawai'i Audubon Society, and by a grant from the John D. and Catherine T. MacArthur Foundation (to L. Freed, R. Cann, and S. Conant). For logistical support and permission to conduct field work at Hakalau Forest National Wildlife Refuge, we thank the U.S. Fish and Wildlife Service, especially refuge manager Richard Wass and refuge biologist Jack Jeffrey. The manuscript was improved by thoughtful and constructive comments from Nancy Flood, Andy Taylor, and an anonymous reviewer.

LITERATURE CITED

- BROWN, M. B., AND C. R. BROWN. 1988. Access to winter food resources by bright- versus dull-colored House Finches. *Condor* 90: 729–731.
- CATCHPOLE, C. K. 1989. Pseudoreplication and external validity: playback experiments in avian bioacoustics. *Trends in Ecology and Evolution* 4: 286–287.
- CONOVER, M. R., J. G. REESE, AND A. D. BROWN. 2000. Costs and benefits of subadult plumage in Mute Swans: testing hypotheses for the evolution of delayed plumage maturation. *American Naturalist* 156: 193–200.
- CUCCO, M., AND G. MALACARNE. 2000. Delayed maturation in passerine birds: an examination of plumage effects and some indications of a related effect in song. *Ethology, Ecology, and Evolution* 12: 291–308.
- ENSTROM, D. A. 1992a. Breeding season communication hypotheses for delayed plumage maturation in passerines: tests in the Orchard Oriole, *Icterus spurius*. *Animal Behaviour* 43: 463–472.
- . 1992b. Delayed plumage maturation in the Orchard Oriole (*Icterus spurius*): tests of winter adaptation hypotheses. *Behavioral Ecology and Sociobiology* 30: 35–42.
- FALLS, J. B. 1992. Playback: a historical perspective. In: *Playback and studies of animal communication* (P.

- K. McGregor, ed.), pp. 11–33. Plenum Press, New York.
- FLOOD, N. 1984. The adaptive significance of delayed plumage maturation in male Northern Orioles. *Evolution* 32: 267–279.
- FOSTER, M. S. 1987. Delayed maturation, neoteny, and social system differences in two manakins of the genus *Chiroxiphia*. *Evolution* 41: 547–558.
- GEIST, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, IL.
- GRANT, B. R. 1990. The significance of subadult plumage in Darwin's finches, *Geospiza fortis*. *Behavioral Ecology* 1: 161–170.
- HARDY, J. W. 1974. Behavior and its evolution in neotropical jays (*Cissilophia*). *Bird Banding* 45: 253–268.
- HILL, G. E. 1989. Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? *Animal Behaviour* 37: 665–673.
- KROODSMA, D. E. 1989. Suggested experimental design for song playback. *Animal Behaviour* 37: 600–609.
- LAWTON, M. F., AND R. O. LAWTON. 1986. Heterochrony, deferred breeding, and avian sociality. *Current Ornithology* 3: 187–222.
- LEPSON, J. K., AND L. A. FREED. 1995. Variation in male plumage and behavior of the Hawaii Akepa. *Auk* 112: 402–414.
- LYON, B. E., AND R. D. MONTGOMERIE. 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? *Evolution* 40: 605–615.
- MCDONALD, D. B. 1993. Delayed plumage maturation and orderly queues for status: a manakin mannequin experiment. *Ethology* 94: 31–45.
- MELEMIS, S. M., AND J. B. FALLS. 1982. The defense function: a measure of territorial behavior. *Canadian Journal of Zoology* 60: 495–501.
- MUNSELL COLOR. 1994. Munsell soil color charts, revised edition. Macbeth Division of Kollmorgen Instruments Corporation, New Windsor, NY.
- PATTERSON, I. J. 1980. Territorial behaviour and the limitation of population density. *Ardea* 68: 53–62.
- PRATT, H. D., P. L. BRUNER, AND D. G. BERRETT. 1987. A field guide to the birds of Hawaii and the tropical Pacific. Princeton University Press, Princeton, NJ.
- PROCTER-GRAY, E. 1991. Female-like plumage of subadult male American Redstarts does not reduce aggression from other males. *Auk* 108: 872–879.
- , AND R. T. HOLMES. 1981. Adaptive significance of delayed attainment of plumage in male American Redstarts: tests of two hypotheses. *Evolution* 35: 742–751.
- ROHWER, S. 1975. The social significance of avian winter plumage variability. *Evolution* 29: 593–610.
- . 1978. Passerine subadult plumages and the deceptive acquisition of resources: a test of a critical assumption. *Condor* 80: 173–179.
- , AND G. BUTCHER. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. *American Naturalist* 131: 556–572.
- , S. D. FRETWELL, AND D. M. NILES. 1980. Delayed plumage maturation and the deceptive acquisition of resources. *American Naturalist* 115: 400–437.
- , W. P. KLEIN, JR., AND S. HEARD. 1983. Delayed plumage maturation and the presumed prealternate molt in American Redstarts. *Wilson Bulletin* 95: 199–208.
- STUDD, M. V., AND R. J. ROBERTSON. 1985. Life span, competition, and delayed plumage maturation in male passerines: the breeding threshold hypothesis. *American Naturalist* 126: 101–115.
- VANDERWERF, E. A. 1994. Intraspecific variation in foraging behavior of Elepaio in Hawaiian forests of different structure. *Auk* 111: 917–932.
- . 1998. 'Elepaio (*Chasiempis sandwichensis*). In: *The birds of North America* (A. Poole, and F. Gill, eds.), no. 344. The Birds of North America, Inc., Philadelphia, PA.
- . 1999. Delayed plumage maturation and demography on Hawai'i 'Elepaio. Ph.D. dissertation. University of Hawaii, Honolulu, HI.
- . 2001a. Two-year delay in plumage maturation of male and female 'Elepaio: implications for hypotheses of delayed plumage maturation. *Condor* 103: 756–766.
- . 2001b. Distribution and potential impacts of avian poxlike lesions in 'Elepaio at Hakalau Forest National Wildlife Refuge. *Studies in Avian Biology* 22: 247–253.
- VAN RIPER, C., III. 1995. Ecology and breeding biology of the Hawaii Elepaio (*Chasiempis sandwichensis bryani*). *Condor* 97: 512–527.
- WEBSTER, M. S. 1997. Extreme sexual size dimorphism, sexual selection, and the foraging ecology of Montezuma Oropendolas. *Auk* 114: 570–580.