The effects of delayed plumage maturation on aggression and survival in male red-backed fairy-wrens

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The occurrence of multiple phenotypes within a sex of a single species has long puzzled behavioral ecologists. Male red-backed fairy-wrens *Malurus melanocephalus* exhibit 3 behaviorally distinct types in their first breeding season: breed in bright nuptial plumage, breed in dull plumage, or remain as an unpaired auxiliary (helper) with dull plumage. The retention of dull plumage by auxiliaries and dull breeders is an example of delayed plumage maturation (DPM), a widespread phenomenon in birds whose costs and benefits are not well understood. At a mechanistic level, DPM might allow dull males either to deceptively mimic females (female mimicry hypothesis) or to honestly signal their subordinate status (status-signaling hypothesis). DPM might function via either mechanism to provide ultimate benefits relative to developing nuptial plumage by increasing reproductive success, survival, or both. In this study, we tested the hypothesis that DPM is related to increased male survival in the red-backed fairy-wren via either female mimicry or status signaling. Aviary-based experiments revealed that dull males were perceived as male, which is consistent with the status-signaling hypothesis but contradicts the female mimicry hypothesis. Further aviary and field-based experiments also revealed that dull males were socially subordinate to bright males and received less aggression than bright males, further evidence for status signaling. However, male survival was not related to plumage coloration or breeding status. These findings indicate that male plumage coloration signals social status but that dull plumage does not afford a net survival advantage, perhaps because plumage color is a conditional strategy. *Key words:* alternative breeding strategies, delayed plumage maturation, fairy-wren, *Malurus melanocephalus*, plumage coloration, survival. *[Behav Ecol 19:508–516 (2008)]*

A mong vertebrates, it is common for individuals of the same sex to exhibit behavioral or morphological variation in relation to age, social status, or environmental conditions. Yet, a general understanding of such intraspecific variation has remained elusive. Delayed plumage maturation (DPM), or the delayed acquisition of nuptial breeding plumage by reproductively capable individuals until after their first potential breeding season, is a common source of intrasexual phenotypic variation in birds (Lawton SM and Lawton SO 1986). DPM has been recorded in 33 avian families, has evolved independently several times (Chu 1994; Hill 1996), and varies both within and between species in intensity and duration (e.g., Slagsvold and Sætre 1991; Rowley and Russell 1997; Doucet et al. 2007). Perhaps because of the tremendous diversity of species exhibiting DPM, a robust and general explanation for the adaptive benefits of DPM has continued to elude researchers (Cucco and Malacarne 2000). Indeed, the fitness benefits of DPM have been identified for only a few species (e.g., Conover et al. 2000; Greene et al. 2000; Berggren et al. 2004), and in many cases, DPM appears to be selectively neutral or even maladaptive (e.g., Stutchbury 1991; Landmann and Kollinsky 1995a, 1995b).

A full understanding of DPM requires an examination of both proximate effects and ultimate benefits (Lyon and Montgomerie 1986). Several proximate effects of DPM have been proposed, but 2 in particular have received considerable attention and are most applicable to our study system (see below). The "female mimicry hypothesis" (Rohwer et al. 1980) proposes that dull plumage is a deceptive signal that allows young males to mimic females. The key prediction of the female mimicry hypothesis is that dull males will be perceived as female and treated as such by conspecifics, at least during certain times of the year when such mimicry would be useful. Conversely, the "status-signaling hypothesis" (Lyon and Montgomerie 1986) proposes that retention of dull plumage is an honest signal of male sex and subordinate status. This hypothesis argues that if some males (e.g., younger males) are subordinate to others (e.g., older males), and therefore do not pose much of a reproductive threat, an honest signal of sex and social status by subordinate males should reduce aggression from dominant males. Three key predictions of this hypothesis are that dull males are perceived as adult males (not females), receive less aggression than bright males, and are socially subordinate to bright males.

Regardless of the proximate effects of DPM, there are only 2 possible, but not mutually exclusive, direct fitness benefits: increased survival or increased reproduction. That is, both female mimicry and status signaling may result in dull (younger) males enjoying increased survival, for example, through reduced aggression and predation risk or increased access to resources, or either mechanism might lead to increased reproductive success via increased access to breeding opportunities. However, it is important to note that these ultimate

benefits for DPM are relative to what these same males might experience if they had developed nuptial plumage, not relative to other males that have developed nuptial plumage. The delayed acquisition of nuptial plumage often appears to be a conditional strategy (Gross 1996), and as such the fitness of dull and bright males is not necessarily expected to be equal. Thus, both the "decision" to retain dull plumage as well as the relative fitness benefits of DPM may depend on a range of factors including individual quality or condition, season, and social context. For example, males in poor condition with limited breeding opportunities may gain higher relative fitness by retaining dull plumage coloration and perhaps increasing survival probability relative to what they might encounter in bright plumage (i.e., making the "best of a bad job"), whereas males in good condition may be better able to bear increased aggression and other costs and therefore do better with bright plumage. It may also be the case that DPM has fitness benefits during a particular phase of life but is maladaptive or selectively neutral in other phases. For example, many species that exhibit DPM undergo only one full body molt per year, which links breeding and nonbreeding plumage; a selective advantage of DPM in one of these seasons may be neutral or even costly in the other (Rohwer and Butcher 1988). Similarly, fitness consequences of DPM may be related to social context; for example, in species where not all males breed, it is possible that DPM is adaptive for nonbreeding males but not for males who acquire mates. Because of these complications, it has proved challenging to make clear predictions about the expected fitness of one plumage type versus another and to gather the data needed to fully examine fitness consequences of DPM (but see Conover et al. 2000; Greene et al. 2000; Berggren et al. 2004). For these reasons, studies of the ultimate benefits of DPM have lagged behind those addressing proximate effects.

Red-backed fairy-wrens (Maluridae: *Malurus melanocephalus*) are small, Australian passerine birds in which DPM appears to be a derived trait (Rowley and Russell 1997). Although all male red-backed fairy-wrens reach reproductive maturity at 1 year of age (Karubian 2002), males exhibit 3 distinct behavioral types in their first potential breeding season (Figure 1): "bright breeders" molt into black and red nuptial plumage, attract mates, hold territories, and raise young; "dull breeders" molt into dull brown plumage similar to that of females and juveniles but also attract mates, hold territories, and raise young; and "auxiliary males" retain dull plumage and remain on their natal territories to assist parents with subsequent reproductive efforts (i.e., cooperative breeding). In our study population, male plumage color is strongly bimodally distributed, with a very low number of intermediate males (see Figure 1 in Webster et al. forthcoming). Plumage color is also related to age in our study population. Most 1-year-old males retain dull plumage (becoming either dull breeders or auxiliary males), but a smaller proportion (~15%) develops nuptial plumage (becoming bright breeders). By their second breeding season, however, nearly all males become bright breeders. Auxiliary males in nuptial plumage are exceedingly rare (Webster et al. forthcoming), though in other populations acquisition of bright plumage may take up to 4 years (Rowley and Russell 1997). Both dull breeders and auxiliaries have dull, female-like plumage, but they often have darker bills and/or spots of bright plumage that distinguish them from females to the human eye (Karubian 2008). Red-backed fairy-wrens live in socially monogamous groups in which adult males and females form multiyear social pair bonds, yet exhibit high levels of sexual promiscuity (Karubian 2002; Webster et al. forthcoming).

Red-backed fairy-wrens are unusual among species studied for DPM in that they undergo 2 full body molts per year

Figure 1
DPM in red-backed fairy-wrens. Shown are pictures taken during the breeding season of (a) a breeding female (left) and bright breeding male (right), (b) a bright breeding male, (c) a dull breeding male, and (d) an auxiliary male. Dull breeding males and auxiliary males retain a female-like plumage during the breeding season and exhibit DPM (auxiliary males are always dull). Bright breeding males and dull breeding males (b and c) have dark bills, whereas females and auxiliary males (a and d) do not.

(Schodde 1982 and references therein). Adults in our study population (including 1-year-old males and females) undergo a full body molt before or during the breeding season (a prealternate or prebreeding season molt) and then another complete body molt at the end of the breeding season (a prebasic or postbreeding season molt) (Karubian J, Webster MS, unpublished data). Because most or all males pass the winter in identical (dull) plumage and winter plumage is unlinked from breeding season plumage by the prebreeding season molt, potential adaptive benefits of dull coloration during the nonbreeding season cannot explain DPM during the breeding season (see Rohwer and Butcher 1988). In this paper, we examine the proximate consequences of DPM in the breeding season by testing the female mimicry and status-signaling hypotheses and also test whether DPM affects male survival. In a companion paper (Webster et al. forthcoming), we address the reproductive consequences of DPM in this study system.

METHODS

General field methods

The red-backed fairy-wren is a small insectivorous passerine that inhabits open woodlands and grasslands in northern Australia (Schodde 1982; Rowley and Russell 1997). We studied a population of red-backed fairy-wrens resident in the open forests surrounding the Herberton Shire Reservoirs (Moomin Road) on the Atherton Tablelands in Queensland, Australia (145°25′E, 17°22′S). We monitored this focal population for every breeding season (typically early October to early February, depending on rains) from 1998 to 2000 and 2003 to 2007 (breeding seasons are designated by the year that breeding ended; i.e., the 1998 season began October 1997 and extended to February 1998), for a total of 8 field seasons. Beginning in 2003, we also monitored a second population resident at Kalinvale Farm, approximately 10 km from the focal population.

During each field season, we captured most adults and marked them with individually specific combinations of colored leg bands and an Australian Bird and Bat Banding

Scheme numbered aluminum band. At the time of capture, we scored molt, measured several morphological traits, and collected a small (ca., 20–50 μL) blood sample. We scored plumage coloration of captured birds using the system described in Karubian (2002). Briefly, each bird's body was divided visually into 5 parts (head, back, belly, chest, and tail), and each area was scored on a scale of 1–10 for the proportion of that area that was in bright (jet black or crimson red) or dull (brown) plumage. We did not use a photospectrometer to measure color differences because the relevant trait for this study is the extent of nuptial plumage rather than the color characteristics of the plumage per se. These scores were then summed and multiplied by 2 to produce an overall brightness score ranging from 0 (completely dull) to 100 (completely bright). For analyses reported in this paper, we placed each male into a plumage class based on plumage color score: dull males had brightness scores less than 33, intermediate males had plumage scores between 33 and 66, and bright males had plumage scores of 67 or greater. Male color categories were unambiguous because few males had intermediate plumage scores (see Webster et al., forthcoming), and these few males were excluded from analyses (i.e., for all analyses we contrast dull with bright males).

We were able to determine social groupings of banded individuals unambiguously through daily observations of behavioral interactions. For groups with more than one male, we defined the dominant breeding male as the male who spent the most time with and sang with the group's breeding female; other group males were defined as auxiliary helpers. In all cases, these designations were consistent with known pedigree information (i.e., the auxiliary was typically a male offspring from the previous season).

General experimental methods

Birds used in experiments were captured 3–15 km from the focal study site in qualitatively similar habitat. Although we could not do so in all cases, we were able to ascertain social status prior to capture for a subset of dull males used as stimulus birds in the experiments and therefore know that the dull males were a combination of auxiliaries and dull breeders. We were able to distinguish dull males from females in all cases by observations of breeding behavior and/or phenotypic cues such as the presence of a cloacal protuberance, small spots of bright plumage, and/or slight darkening of the bill. Some dull males used in experiments were experiencing moderate body molt, but no change in plumage brightness occurred during captivity, and there were no qualitative differences in experiment outcomes in relation to molt, plumage brightness, or bill color of dull stimulus males. Most males used as stimulus birds in the experiments were known to be 1 year of age (because they were banded as nestlings in the previous year), but the age of some stimulus bright males was unknown and may have been greater than one. Sample sizes precluded distinguishing the effects of age and plumage statistically, but outcomes of experiments including known-aged bright stimulus males were qualitatively similar to those with males of unknown age. Most birds were captured as family groups and housed as such in the aviaries. Aviaries were located outdoors at our field camp but were protected from wind and rain by a roof. Captive birds were provided with mealworms and water ad lib and were released at their point of capture after the experiments. Birds trapped within 2 km of each other were never paired in the same trial, making it likely that birds used in experiments had no prior exposure to each other. Captive birds from different family groups were in auditory but not visual contact with each other.

Male choice aviary experiments

We used "male choice" aviary experiments to test if bright males distinguish between dull males and females. We conducted these experiments in a choice apparatus (see Figure 1 in Karubian and Alvarado 2003), measuring 1.5 × 0.75 × 0.75 m and built of wire mesh through which birds could see and interact but not pass. The choice apparatus consisted of 2 side chambers on either side of a central "neutral" chamber. Each side chamber had a smaller cage measuring 0.25 × 0.25 × 0.75 m within the larger apparatus that contained single stimulus bird. Partitions within the cage prevented birds in the side chambers from seeing each other. The choice apparatus was located in habitat in which red-backed fairy-wrens occur and was shaded from the sun.

Each trial involved 3 birds: a bright male in the central chamber, a stimulus female in the small cage in one side chamber, and a stimulus dull male in the small cage in the other side chamber. Mean plumage score of dull males used as stimulus birds in these experiments was 3.38 ± 0.47 (mean ± standard error [SE]), which was similar to but slightly lower than the average plumage score of dull males in our study population (6.12 ± 0.72, $n = 156$ males). The time each focal bright male spent associating with each of the 2 stimulus birds was recorded by an observer hidden in a blind 6 m from the cage, where "associating" was defined as being in the side chamber of 1 of the 2 stimulus birds while moving and/or vocalizing at least once every 5 s. Time spent on a stimulus bird's side of the cage searching for insects, preening, or bill wiping was not recorded as associating. No food or water was provided to the birds during the trials.

Trials lasted 60 min, with a 5-min acclimation period at the onset of the trial. We observed no consistent side preferences associated with the habitat or stimuli from outside the apparatus, but to control for this possibility, we rotated the entire apparatus 180° after the first 30 min followed by another 5-min acclimation period. To control for possible side preferences associated with the apparatus itself, we randomly selected the side on which stimulus birds were placed.

Each trial of the male choice experiment involved a different bright male (i.e., no bright male was used in more than one trial), but due to limited numbers, we did reuse some dull males and females as stimulus birds in multiple trials ($n = 5$ dull males and 3 females used as a stimulus bird in 2 trials each). To minimize pseudoreplication, the same 2 stimulus birds were never paired in the same trial more than once. Bright focal males spent approximately one half of each trial (26 ± 3 min per 60 min trial) associating with 1 of the 2 stimulus birds. In our analysis of these data, we attempted to control for the fact that total time associating varied between trials and also that time spent associating with 1 stimulus bird in each trial was not independent of time spent associating with the other. We therefore conducted our analyses on the proportion of time each bright male spent associating with the stimulus dull male relative to the total time spent associating with both stimulus birds combined (i.e., dull male/[dull male + female]). After confirming that the data were normally distributed (Shapiro–Wilk goodness-of-fit test, $W = 0.93$, $P < W = 0.3832$), we conducted a 1-sample t-test comparing the proportion of time associating with stimulus dull males to a predetermined mean of 0.5 (as expected under the null model of no preference). We also recorded all displays and vocalizations by all 3 birds in each trial, but these behaviors were too rare to permit statistical analyses.

Social dominance trials

Dominance trials were conducted in a small (0.5 × 0.25 × 0.25 m) wire cage that contained 2 perches and a dish of

mealworms on the floor of the cage. Two males, one bright and one dull, were food deprived for 60 min prior to the trials, then placed in the cage simultaneously. Among the males used in the trials ($n = 22$), bright males were significantly brighter than dull males (plumage scores: 88.20 ± 3.98 vs. 5.38 ± 1.78, Wilcoxon signed-rank $Z = -3.94$, $P < 0.0001$) but did not differ in tarsus length (22.28 ± 0.13 vs. 22.01 ± 0.19 mm, $t_{19} = -1.16$, $P = 0.2572$) or weight (7.75 ± 0.54 vs. 7.90 ± 0.43 g, $t_{18} = 0.58$, $P = 0.5651$). An observer hidden in a blind 5 m from the cage recorded all interactions between the birds for 15 min. A bird was considered to have scored a "win" if it displaced the other bird from a perch or stole a food item from the other bird's bill. Number of wins per trial was analyzed using nonparametric Wilcoxon signed-rank tests. We also recorded vocalizations and aggressive displays, but these were too infrequent to be analyzed statistically. Each trial featured 2 different birds, and no individual bird was used in more than one trial.

Presentation experiments

We used presentation experiments to quantify the response of free-flying pairs to live, caged stimulus birds. These experiments were conducted to determine if dull plumage is associated with reduced aggression relative to bright plumage. In each replicate of the experiment, each of 3 types of stimulus bird—a bright male, a female, and a dull male—was presented in a randomized sequence to a free-flying pair on the study site. Among the males used as stimulus birds in the trials ($n = 21$), bright males were significantly brighter than dull males (plumage scores: 93.64 ± 1.63 vs. 3.21 ± 1.99, Wilcoxon signed-rank $Z = -3.67$, $P = 0.0002$) but did not differ in tarsus length (22.28 ± 0.16 vs. 22.05 ± 0.19 mm, $t_{17} = -0.89$, $P = 0.3843$) or weight (7.79 ± 0.24 vs. 7.91 ± 0.24 g, $t_{16} = 0.36$, $P = 0.7245$). Each free-flying pair used in the experiment consisted of a bright male and a female with no helpers. All free-flying pairs were in nest construction phase, and stimulus birds were always placed 25–50 m from the nest site. A different free-flying pair was used for each replicate of the experiment.

Stimulus birds were placed in a small (0.5 × 0.25 × 0.25 m) wire cage on top of a tripod, at a height of 1.5 m from the ground. The cage was covered until the free-flying pair was located, at which point we removed the cover from the cage and revealed the stimulus bird, and we waited until the free-flying birds approached the stimulus bird. In most cases, at least one member of the free-flying pair responded in the form of a vocalization and/or a rapid advance toward the caged bird within 60 s of the cage being uncovered. If no response was recorded within 5 min, we covered the cage and repositioned the tripod. If after 3 attempts the caged bird did not elicit any response, we canceled the experiment on that free-flying pair. There was no relationship between the type of the stimulus bird and the likelihood of the response ($n = 2$ cases of no response for stimulus bright males, 1 for stimulus dull males, and 3 for stimulus females; Fisher's Exact test, degrees of freedom = 2, $P > 0.4$). Only experiments in which free-flying pairs responded to all 3 types of stimulus birds were included in the analysis.

We recorded all behaviors of the free-flying pair and the stimulus bird for 15 min after the response, a time period similar to the average length of intrusions by neighboring birds (Karubian J, Webster MS, unpublished data). In addition to time elapsed between uncovering the caged bird and response by the free-flying pair (latency), we recorded the following aggressive displays by the free-flying pair: "puffbacks," in which bright males raised the red feathers on their backs (Schodde 1982; Rowley and Russell 1997); "flybys," in

which free-flying males and females flew within 3 m of the cage; "swoops," in which free-flying males and females flew directly at the caged bird before pulling up sharply <0.5 m of the cage; and "trills," a song type associated with territory defense sung by both males and females. These displays were recorded on a continuous basis during the 15-min trials. We also recorded whether the free-flying birds were <2 m from the cage at 1-min intervals. After 15 min of observation, we covered and removed the cage. We made presentations of different stimulus birds to each free-flying group on consecutive days or sometimes twice per day, but presentations were always separated by >30 min.

We used generalized multiple mixed models with individual ID of the stimulus bird as a random factor (see below) to test the effect of type of stimulus bird (i.e., dull male, bright male, or female—the independent variable) on intensity of response (e.g., number of puffbacks, flybys, swoops, trills, and minutes <2 m from cage—dependent variables). We first analyzed the overall effect of stimulus bird type on each of the response variables separately for free-flying females and males (the relatively small sample size prohibited using principal component analysis to reduce the number of response variables). When these overall models were statistically significant, we then conducted pairwise, post hoc tests comparing response to stimulus dull males versus stimulus bright males and stimulus dull males versus stimulus females. We used a total of 32 stimulus birds in the experiments (12 bright males, 9 dull males, and 11 females), with 1 female and 1 dull male each used as a stimulus bird in 3 replicates of the experiment and 1 female, 3 dull males, and 2 bright males used as a stimulus bird in 2 replicates. To control for the fact that some individual stimulus birds were used in multiple trials, we treated individual identity as a random factor nested within status in our analyses. All statistical tests presented below were 2 tailed, and all data are presented as mean ± SE unless otherwise stated. Data distributed nonnormally were analyzed using nonparametric tests.

Survival analysis

We conducted frequent searches of the study sites and adjoining areas during our 5-month field seasons each year to assess the presence/absence of males. Adult male red-backed fairy-wrens are strongly philopatric (Schodde 1982; Rowley and Russell 1997) and long-distance adult dispersal appears to be rare (Karubian J, Webster MS, unpublished data; see also Mulder 1995; Double et al. 2005). Therefore, we are confident that we observed most or all adult males on the study sites each season.

We used Cormack–Jolly–Seber (CJS) models (Pollock et al. 1990; Lebreton et al. 1992) and model selection methods based on second-order Akaike's information criterion values, or AIC_c (Burnham and Anderson 2002), to estimate annual survival (φ) and resighting (P) probabilities from capture histories of 393 males (58 initially captured as dull helpers, 128 as dull breeders, and 207 as bright breeders). All CJS analyses were conducted with program MARK (White and Burnham 1999). Models were constructed using a sine link function. We verified fit of the global model with the program RELEASE goodness-of-fit procedure (Tests 2 and 3; Burnham et al. 1987) implemented in program MARK. The relative likelihood of each model in the candidate set was estimated with AIC_c weights (Burnham and Anderson 2002).

We hypothesized that both breeding status and plumage color could influence survival of fairy-wrens at our 2 study sites (Moomin Reservoirs and Kalinvale Farm). Annual survival probability was modeled in 4 ways: as "constant" among plumage and breeding classes, as a function of "plumage" (dull or

bright) and of "breeding status" (breeder or auxiliary), and as a "combination of these 2 factors" (i.e., dull auxiliary, dull breeder, or bright breeder). At our study site, the majority of males became bright breeders in their second year, and all males included in survival analyses fit this pattern. Therefore, estimates of φ for dull helpers and breeders represent the survival probabilities of these individuals from year 1 to year 2. To test for a survival cost in 1-year-old males, we reran our candidate model set with only 1-year-old males included. We did not model φ as a function of study site because we had no biological reason to expect that annual survival patterns of male classes would differ between our 2 study sites. Although φ could be dependent on other factors (e.g., rainfall), sample size limitations within years precluded the inclusion of annual covariates in this analysis. We always modeled P as a function of year and site due to differences in field season duration and effort among study sites and years. However, P was not modeled as a function of male status because male red-backed fairy-wrens that do not permanently emigrate from our study area are highly sedentary and detectable regardless of breeding and plumage class.

We used program MARK's model averaging procedure to compute average annual estimates and 95% confidence interval (CI) of φ for dull auxiliaries, dull breeders, and bright breeders from all 4 models in the candidate set. Model-averaged estimates include model selection uncertainty and typically have better precision and reduced bias compared with parameter estimates based only on the AIC-selected best model (Anderson et al. 2000).

RESULTS

Male choice and social dominance aviary experiments

In 12 replicates of the male choice aviary experiment, bright males spent significantly more time associating with females than with dull males (Figure 2; 1-sample $t_{11} = -3.54$, $P = 0.0046$). Vocalizations and displays were relatively infrequent during the trials, precluding statistical analyses, but bright males tended to direct puffback displays toward dull stimulus males more frequently than toward stimulus females (0.75 ± 0.39 per trial vs. 0.33 ± 0.18, respectively), and there was no indication of a trend for trills and other displays.

In social dominance trials, bright males had significantly more "wins" per trial than did dull males (Figure 3; Wilcoxon signed-rank matched-pairs test, $Z = -33.00$, $P = 0.001$, $n = 11$ trials). Again, vocalizations and displays were too infrequent to permit statistical analysis, but bright males tended to give more puffback displays than did dull males (3.54 ± 2.68 per trial vs. 0.09 ± 0.09, respectively), and there was no indication of a trend for trills or other displays.

Presentation experiments

We conducted 14 presentation experiments, each consisting of 3 separate presentations with a different stimulus bird—a bright male, a dull male, or a female—for a total of 42 trials. Latency to respond to the caged birds was brief (mean = 36.73 ± 6.61 s) and did not differ in relation to type of stimulus bird (Table 1). The response of free-flying males differed in relation to type of stimulus bird for most aggressive displays (Figure 4a, Table 1). Post hoc pairwise comparisons show that, relative to dull stimulus males, bright stimulus males elicited a significantly higher rate of puffbacks, flybys, and time <2 m from the cage by free-flying males (Table 1). Stimulus bright males also elicited more swoops than did stimulus dull males, though this difference was not statistically significant. There were no significant differences in the aggressive displays of
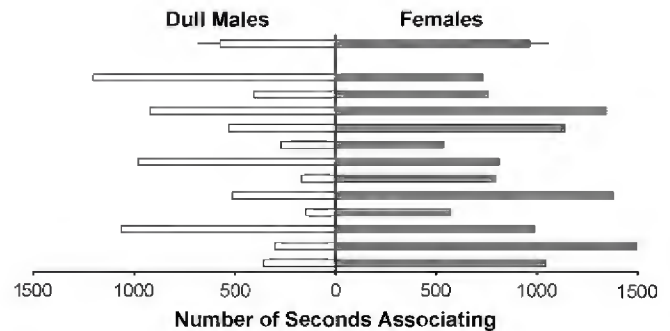

Figure 2
Time bright males spent associating with stimulus dull male (white bars on the left) and female (gray bars on the right) red-backed fairy-wrens in aviary-based "male choice" trials ($n = 12$ trials). The first pair of bars (above) shows the average amount of time (±1 SE) spent with dull males and females across all trials, and the bars below show the outcome of each individual trial.

free-flying bright males toward stimulus dull males and stimulus females (Table 1). Free-flying females appeared to exhibit a qualitatively different pattern of response than did free-flying bright males, with most aggression toward stimulus females and the least aggression toward stimulus bright males (Figure 4b), though these differences were significant only for flybys (Table 1).

Survival analysis

We found little statistical support for differences in annual survival probability among male plumage and breeding classes. Based on model averaging, dull auxiliary males had an estimated φ of 0.578 (95% CI: 0.468–0.681), dull breeding males had an estimated φ of 0.572 (95% CI: 0.497–0.643), and bright breeding males had an estimated φ of 0.568 (95% CI: 0.510–0.623). This pattern was similar for known 1-year-old males ($n = 175$): $\varphi_{dull\ auxiliaries} = 0.594$ (95% CI: 0.420–0.747), $\varphi_{dull\ breeders} = 0.576$ (95% CI: 0.457–0.687), and $\varphi_{bright\ breeders} = 0.565$ (95% CI: 0.505–0.624). Thus, our data indicate that male survival is not affected by plumage color (dull vs. bright) or breeding status (auxiliary vs. breeder) at our study sites.

DISCUSSION

Male red-backed fairy-wrens exhibit 3 behaviorally distinct types in their first breeding season: breed in bright nuptial
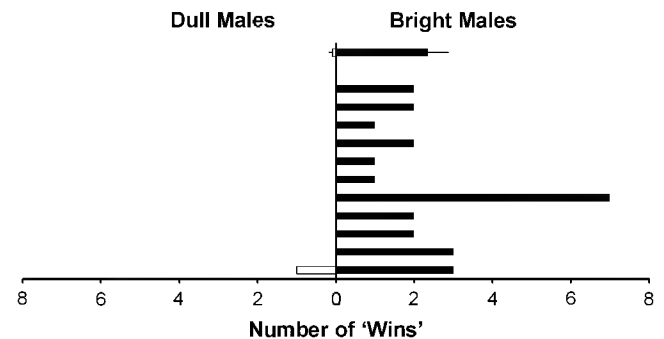

Figure 3
Number of "wins" for bright (black bars to the right) and dull (white bars to the left) male red-backed fairy-wrens in aviary-based social dominance trials ($n = 11$ trials). The first pair of bars (above) shows the average number of wins per trial (±1 SE), and the bars below show the outcome of each individual trial.

Table 1

Response of territorial pairs of red-backed fairy-wrens to 3 types of caged stimulus birds: dull males, bright males, and females

	Overall model		Dull male versus bright male		Dull male versus female	
	F (df)	P value	F (df)	P value	F (df)	P value
Male responses						
Latency	1.11 (2, 25.7)	0.3447	—	—	—	—
Male puffback	**4.99 (2, 30.4)**	**0.0134***	**4.19 (1, 19.7)**	**0.0543**	0.99 (1, 20.5)	0.3313
Male flyby	**3.21 (2, 30.1)**	**0.0545**	**4.51 (1, 19.2)**	**0.0469***	2.98 (1, 14.0)	0.1063
Male swoop	**4.62 (2, 28.6)**	**0.0182***	3.31 (1, 18.7)	0.0849	0.93 (1, 26.0)	0.3440
Male < 2 m cage	**6.46 (2, 23.8)**	**0.0057****	**8.82 (1, 28)**	**0.0097****	0.00 (1, 3.6)	0.9607
Male trills	2.75 (2, 26.9)	0.0820	0.95 (1, 18.9)	0.3421	1.46 (1, 16.3)	0.2442
Female responses						
Female fly-by	**5.65 (2, 29.4)**	**0.0084****	2.00 (1, 15.8)	0.1764	**3.93 (1, 17.0)**	**0.0638**
Female swoop	0.95 (2, 23.6)	0.4020	—	—	—	—
Female < 2 m cage	0.30 (2, 28.5)	0.7425	—	—	—	—
Female trills	2.40 (2, 23.7)	0.1123	0.46 (1, 1.6)	0.5839	1.45 (1, 14.1)	0.2487

The results of generalized multiple mixed models for each response type are shown for both the overall model (including all 3 types of stimulus bird) and for post hoc pairwise tests comparing dull males with bright males and with females, respectively. Bold font highlights results that are statistically significant or borderline; statistically significant differences are further denoted with $*P < 0.05$ or $**P < 0.01$. Identities of stimulus birds were controlled statistically as random effects in the model. df, degrees of freedom.

plumage, breed in dull plumage, or remain as an unpaired auxiliary (helper) with dull plumage. The retention of dull plumage by auxiliaries and dull breeders is an example of DPM, a widespread phenomenon in birds whose proximate and ultimate costs and benefits are not well understood. The twice-annual molt pattern of the red-backed fairy-wren excludes several hypotheses for the proximate consequences of DPM a priori and permits a focus on 2 relevant hypotheses, the status-signaling hypothesis and the female mimicry hypothesis. Experimental tests supported the status-signaling hypothesis by confirming 3 key predictions: 1) aviary-based male choice trials affirmed that bright males distinguish between dull males and females; 2) aviary-based social dominance trials confirmed that bright males are socially dominant to dull males; and 3) field-based presentation experiments demonstrated that dull males receive less aggression from conspecific males than do bright males.

In contrast, the male choice experiment contradicted the key central prediction of the female mimicry hypothesis in that adult males were able to discriminate between dull males and females. At first glance, this finding appears to be somewhat at odds with the lack of significant differences in aggres-

sive displays by free-flying bright males toward stimulus dull males and females in the presentation trials. This potential contradiction is explained by the fact that the male choice trials were designed to test ability to distinguish between dull males and females, whereas the presentation trials were designed to test aggressive response rather than ability to discriminate per se. Thus, the lack of differential male response in the presentation trials does not necessarily mean that bright males are unable to distinguish between stimulus females and dull males. A differential response, however, does signify that the responding bird is able to distinguish between stimulus birds, and it is therefore noteworthy that free-flying females in these trials exhibited borderline significant variation in an aggressive display toward stimulus females and dull males. The results from both the aviary (male choice trials) and the field (presentation trials) therefore indicate that both adult males and females were able to distinguish between stimulus females and dull males. The results of the social dominance trials were not directly relevant to the female mimicry hypothesis because this hypothesis makes no specific predictions about social dominance (Rohwer et al. 1980; Brown MB and Brown CR 1988).
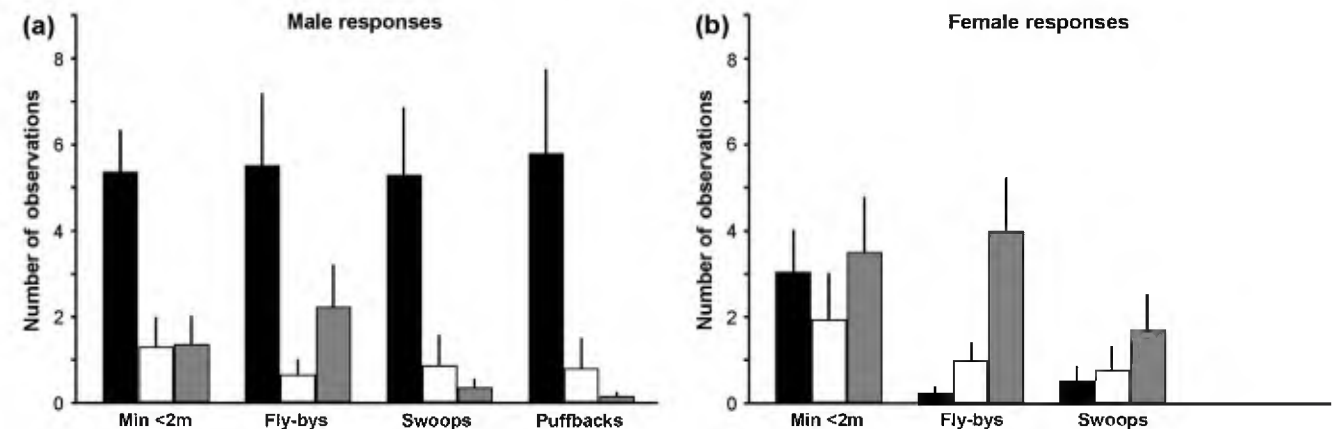

Figure 4

Response of free-flying male (a) and female (b) red-backed fairy-wrens to caged stimulus birds during field-based presentation experiments ($n = 13$ replicates). In each replicate of the experiment, a dull male, female, and bright male were presented individually in random order for 15 min each and aggressive displays by free-flying birds were recorded (see Methods for a description of each display type). Shading of bars indicates identity of stimulus bird (black = bright males, white = dull males, gray = females). Females do not perform puffback displays.

Although there is evidence for female mimicry from some species (e.g., Slagsvold and Sætre 1991; Hakkarainen et al. 1993), the status-signaling hypothesis is currently the most widely supported proximate explanation for DPM. Status signaling via plumage coloration has been shown to operate across a range of mating systems, ecological zones, taxonomic affinities, and life histories (e.g., Rohwer 1978; Flood 1984; Hill 1988a, 1988b; McDonald 1993; Muether et al. 1997; Conover et al. 2000; Greene et al. 2000; VanderWerf and Freed 2003; Berggren et al. 2004), and the red-backed fairy-wren is the latest species for which status signaling appears to apply. These results make sense biologically for the red-backed fairy-wren: because adults live in sedentary, stable social groups, deceptive signaling is less probable than it would be for migratory species for which the female mimicry hypothesis was originally formulated (Rohwer et al. 1980; Rohwer 1983). Moreover, many dull breeding males and some auxiliaries have spots of nuptial plumage and relatively dark bills compared with females (Karubian 2008, Figure 1) making female mimicry unlikely.

Although many studies have demonstrated a proximate benefit from DPM—that is, reduced aggression through status signaling—it is often unclear what the ultimate fitness benefits, if any, of this reduced aggression might be. At the ultimate level of analysis, there are 2 possible fitness benefits of DPM, increased survival and/or increased reproductive success, and to date, only a small handful of studies have examined these. In the mute swan (*Cygnus olor*), dull males had higher survival and received more parental care than did same-aged bright males, but bred later in life (Conover et al. 2000). In the North Island robin (*Petroica longipes*), dull males whose plumage was experimentally brightened suffered a marked decrease in survival during the nonbreeding season relative to unmanipulated controls (Berggren et al. 2004). In the lazuli bunting (*Passerina amoena*), conversely, dull plumage was associated with increased access to high-quality territories and higher reproductive success relative to same-aged males with intermediate plumage (Greene et al. 2000). Other studies have examined fitness consequences indirectly without identifying any benefits. For example, although dull plumage was associated with reduced aggression in the black-headed grosbeak (*Pheucticus melanocephalus*), this did not translate into increased access to higher quality territories (Hill 1988a, 1988b, 1989). Thus, despite relatively widespread support for status signaling as a proximate effect of DPM, our understanding of the how this in turn affects survival or reproductive success remains quite limited.

In this study, we found no statistical evidence for a survival advantage for DPM in the red-backed fairy-wren. Instead, our estimates of survival probability for dull auxiliary males, dull breeding males, and bright breeding males were nearly identical. This result also held when analyses were limited to 1-year-old males. These findings appear to suggest that bright plumage coloration does not carry a large survival cost in the red-backed fairy-wren, which is somewhat surprising given that bright plumage is often associated with increased aggression and may also carry ecological costs such as increased predation (Huhta et al. 2003). Moreover, in the red-backed fairy-wren bright plumage color is associated with high androgen levels (Webster MS, unpublished data), and androgens themselves may be costly (e.g., Peters 2000; Buchanan et al. 2001; Redpath et al. 2006).

There are several possible explanations for why we did not find an effect of plumage color, or male breeding status, on survival. First, the costs of bright coloration may indeed be low, for example, if the current suite of predators differs from those present in the recent past. A second possibility is that dull plumage may in fact be associated with increased risk of depredation, perhaps because bright plumage is a signal of unprofitable prey to potential predators (Götmark 1992, 1993). For example, in the pied flycatcher (*Ficedula hypoleuca*), a species which exhibits DPM, sparrowhawks (*Accipiter nisus*) were more likely to attack mounts of birds in dull plumage than in bright plumage, leading Götmark (1995) to conclude that bright plumage may serve to reduce predation risk (but see Slagsvold et al. 1995).

However, in species where DPM is a conditional strategy (Gross 1996), the fitness benefits of DPM are expected to accrue relative to what the same individual would experience in nuptial plumage and thus there are no clear a priori predictions about relative survival of different plumage classes. In the red-backed fairy-wren, plumage color in the first year is likely a conditional strategy in which coloration may be associated with male quality, such that "low-quality" males develop dull plumage and "high-quality" males develop bright plumage (Studd and Robertson 1985). Under this scenario, dull males may simply be making the best of a bad job, with DPM serving to increase survival (via increased access to resources and/or reduced aggression; see below) for males whose chances of reproductive success are already low regardless of what plumage they develop. Related to this idea is the possibility that bright plumage may carry survival costs but (high quality) bright males are able to absorb the costs, whereas (low quality) dull males are more likely to succumb to disease or predation. In support of this possibility, during molt male red-backed fairy-wrens acquiring dull plumage were in poorer body condition than were males acquiring bright coloration (Webster MS, unpublished data). Consequently, underlying differences in male quality may be masking the costs (and benefits) associated with each plumage type. Accordingly, experimental manipulation of plumage color may be needed to determine the costs of plumage color per se while controlling for male quality effects (e.g., Berggren et al. 2004). Nevertheless, our results indicate that any survival benefits associated with dull plumage coloration are likely to be relatively subtle and counterbalanced by variation in male quality.

Additionally, although our results argue against a strong effect of plumage color and breeding status on male survival, subtle yet biologically meaningful effects are possible. In this study, the confidence limits on φ were tightest for bright breeding males but somewhat broader for dull breeders and auxiliaries. Thus, it is possible that auxiliary males have somewhat higher survival than do dull breeders. In our study population, dull breeding males have higher reproductive success than do auxiliary males (Webster et al., forthcoming), and auxiliaries rapidly switch to breeding whenever an opportunity arises (Karubian 2008). This suggests that any survival advantage associated with delayed breeding for auxiliaries is likely to be slight and outweighed by the higher reproductive success of independent breeding. Nevertheless, males with poor prospects for breeding may benefit somewhat from remaining as auxiliaries on their natal territory.

These considerations lead us to hypothesize that, in the red-backed fairy-wren, DPM may be adaptive for auxiliary males, but not for dull breeders. We propose that DPM may function as an honest signal of subordinate social status (i.e., status signaling) that reduces the probability that an auxiliary will be expelled from its natal group. By remaining in the natal group, an auxiliary can bide its time until an opportunity for independent breeding presents itself. This may be especially true for young males in poor condition with relatively low prospects of successful reproduction (Studd and Robertson 1985), as suggested by the association between plumage color and male condition during molt (Webster MS, unpublished data). One-year-old males who are in better physiological condition and have good prospects of breeding, conversely,

are expected to develop nuptial plumage in the prebreeding season molt. The relative importance of physiological constraints and social mediation in determining the plumage color a male develops in his first breeding season is presently unclear but could be resolved by experiments involving independent manipulation of plumage and physiological state.

Many auxiliary males become dull breeders during their first breeding season by filling a breeding vacancy on a territory near the natal group (Karubian 2008) and therefore begin breeding relatively late in the season (Karubian 2002). Once an auxiliary male obtains a breeding territory, DPM may be maladaptive because of reproductive advantages associated with bright plumage: in a companion paper (Webster et al., forthcoming), we demonstrate age-independent reproductive benefits for bright males relative to dull males in the form of increased extrapair paternity. Thus, dull breeding males may be constrained to retain a plumage type that was advantageous at the time of molt (i.e., when an auxiliary) but not later in the breeding season once a breeding territory has been obtained. Interestingly, a switch in status from auxiliary to dull breeder is often accompanied by a rapid darkening of the bill, suggesting that dull males take advantage of a trait (bill color) that is more labile than plumage color to signal a change in status within a breeding season (Karubian 2008). The present study in combination with Webster et al. (forthcoming) emphasize the need to analyze ultimate as well as proximate effects of DPM in order to gain a full appreciation of this complex phenomenon.

FUNDING

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