



# Changes in breeding status are associated with rapid bill darkening in male red-backed fairy-wrens *Malurus melanocephalus*

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In many animals, an individual's social environment and status can change quickly and unpredictably, suggesting an advantage for signals capable of responding to these changes. However, many signaling traits are fixed for relatively long periods. In birds, for example, most plumage-based signals are constrained by molt and unable to respond to sudden changes in social environment. Soft parts, conversely, are vascularized and may provide an alternative signaling system that can be updated relatively quickly. In this study, the effects of changes in breeding status are documented for a putative plumage-based signal, plumage brightness, and a putative soft part signal, bill darkness, in the red-backed fairy-wren *Malurus melanocephalus*. Males that switched from unpaired helper to paired breeder within a breeding season developed significantly darker bills within three weeks of the switch relative to males that did not change status. There was no clear corresponding change in plumage brightness, though the data suggests that changes in plumage brightness are at least possible. These results suggest that bill color is a socially mediated trait capable of responding rapidly to changes in breeding status, and it is proposed that the importance of soft parts as labile signals in birds may be currently under-appreciated.

For a signal to evolve, it must benefit both the signaler and receiver (Searcy and Nowicki 2005). From the receiver's perspective, the average benefit gained by responding to a signal must outweigh the average cost of ignoring it. Working within this constraint, signalers are expected to evolve signals that maximize their own fitness. For signalers living in dynamic social environments, the optimal type or magnitude of a signal may change unpredictably from one moment to the next, suggesting an advantage for the ability to rapidly update or modify signals in relation to changing social environment or status.

However, many animal signals are fixed for relatively long periods of time and rapid change is either constrained or impossible. In birds, for example, many signals are plumage-based. Although some plumage-based signals can be covered and exposed or modified by feather wear (Searcy and Nowicki 2005), most are fixed once molt is complete until the next molt, usually an annual or semi-annual occurrence (Palmer 1972). Examples of temporally constrained signals from other taxa include antlers in male ungulates and exoskeleton-based ornaments in arthropods. Birds may therefore embody a challenge that is not uncommon in the animal world: how to overcome constraints on the speed at which a signal can be updated to respond in a timely manner to changes in social environment.

The relationship between social environment and signals is a complex one. There is ample evidence that signals affect

an individual's social environment, for example variation in the size of badges of social dominance affecting the frequency of aggressive encounters with conspecifics (Rohwer 1975, 1977). However, there is also evidence that social environment can affect signals. In fishes, for example, shifts in breeding status trigger phenotypic changes up to and including changes in sex (Warner and Swearer 1991, Munday et al. 2006). The relationship between social environment and signals is not as well worked out in most taxa as it is in fish. For birds, there are only two cases in which a clear causal link between social environment and signal has been established, both from manipulative experiments on captive birds. In the red jungle fowl *Gallus gallus*, shifts in comb size were induced by experimentally manipulating social environment (Zuk and Johnsen 2000). Similarly, in the house sparrow *Passer domesticus* experimental manipulation of social dominance during molt led to variation in size of a plumage-based badge (McGraw et al. 2003).

Here, I investigate the relationship between social environment and two putative signals, bill color and plumage color, in a small passerine bird the red-backed fairy-wren *Malurus melanocephalus*. The red-backed fairy-wren is a cooperatively breeding species in which offspring from previous breeding seasons often delay dispersal from their natal territory in order to assist their parents with subsequent reproductive efforts (Schodde 1982, Rowley and Russell 1997). In the study population, approximately

35% of breeding pairs were accompanied by one of these so-called “helpers” (groups with two helpers were very rare). Helpers were nearly always one-year-old males. As in other *Malurus* species, red-backed fairy-wren helpers are socially subordinate to the breeding male within their group but are reproductively capable (Double and Cockburn 2003, Webster et al. 2004). Red-backed fairy-wren helpers have enlarged cloacal protuberances (Karubian 2001), produce viable sperm (M. Rowe and S. Pruett-Jones, unpubl. data), and are known to sometimes sire young (M. S. Webster, unpubl. data).

One-year-old males often switch within a single breeding season from helper to breeder. This happens when the breeding male in a helper’s group or in a neighboring group dies and creates a breeding vacancy, or when a young female immigrates into the area. Males that switch from helper to breeder undergo a switch in breeding status from unpaired to paired, but not reproductive status (because they were already reproductively capable as helpers). In addition to changing breeding status, the switch from helper to breeder also liberates these males from the socially subordinate relationship helpers have to the dominant breeder in their natal group.

Although all male red-backed fairy-wrens reach reproductive maturity at one year of age, they show marked variation in plumage color and bill color (Karubian 2002). Adult fairy-wrens molt twice per year (Rowley and Russell 1997). During the pre-nuptial molt at the onset of the breeding season males develop either “dull” breeding plumage, which is dull brown and similar to that of females, or “bright” breeding plumage, which is jet black with a bright red back. In the post-nuptial molt at the end of the breeding season, nearly all males develop dull plumage that they retain throughout the non-breeding season. Most first-year males develop dull breeding plumage but approximately 25% develop bright breeding plumage in their first year. Nearly all second year and older males develop bright breeding plumage. There is no evidence of facultative molt during the breeding season or of plumage change via feather wear, so the plumage type males develop in the pre-breeding season molt is fixed for the duration of that breeding season. However, as in other fairy-wren species (Dunn and Cockburn 1999), red-backed fairy-wrens exhibit extensive variation in the onset and duration of molt (J. Karubian and M. S. Webster, unpubl. data). Among younger males in particular, pre-nuptial molt can extend into the breeding season, making it possible that male plumage color could respond to changes in status during the breeding season if the male were still molting at the time of the change in status.

Male red-backed fairy-wrens also exhibit extensive variation in bill color, which ranges from beige to black. Unlike plumage color, however, bill color is potentially capable of change for all individuals any time during the breeding season. This is because the ramphotheca (the integument of which the bill is composed) is vascularized and therefore hypothetically capable of mobilizing pigments relatively rapidly (Stettman 1972). Below, I test the effects of changes in breeding status on bill color and plumage color, and discuss the implications of the findings.

## Methods

### Study population

This study on red-backed fairy-wrens was conducted on the Atherton Tableland in Queensland Australia (145° 25′ E, 17° 23′ S) for five months (October–February) in each of three consecutive breeding seasons (1997–2000). All red-backed fairy-wrens within a contiguous area of 2.5 × 1 km were color-banded and approximately 45 groups were monitored each year. A total of 1,200 individuals were banded. Additional data on bill color and morphology was taken in the non-breeding season in March and April, 1997, and in January and February, 2003.

### Plumage brightness, age, social status, and bill color

Individuals captured in mist nets were assigned integer plumage brightness scores ranging from 0 (completely dull) to 100 (completely bright) by scoring each of five body sections for proportion of nuptial plumage (Karubian 2002). Males were classified as dull (<20), intermediate (20–80) or bright (>80). No attempt was made to score the intensity or hue of the plumage. Molt on wing, tail, and five body sections was scored at the time of capture on a four-point scale. Age was determined exactly for individuals banded in the nest as nestlings. All newly captured adults were classified as second-year birds. 1 June was used as the “birthday” each year to determine age. Breeding status was determined via repeated observation of monitored groups. Males were considered to switch breeding status when they moved from helper to breeder, either by filling a vacancy caused by the death of nearby breeding male or by pairing with a female who dispersed onto the study area. Timing of the switch was documented by sampling each group at least every third day during the breeding season, thus, there exists a potential error of two days in timing of the switch. Dates were calculated using the latest date that the switch could have occurred.

Bill color was measured for birds trapped in mist nets and for color-banded individuals observed in the field with binoculars. For birds in the hand, bill color was scored by dividing both the top and the base of the bill into four equal sized quadrants. Each of the quadrants was then scored on a scale from 0 (completely beige colored with no darkness) to 10 (completely black with no lightness) using color chips as a guide (I did not have access to a photospectrometer at the time of this study). This in-hand bill color score was collapsed to a scale from 0 (completely beige) to 3 (completely black) to make these data compatible with observations of free-flying birds made with binoculars.

Field-based observations were scored on a scale of 0–3 in increments of 0.25, making the resolution of data from birds scored in the field compatible with that of birds scored in the hand. When observations were made in the field, observers rated the quality of the data on a scale of 1 (best) to 5 (poor), based on distance from the bird, lighting conditions, and overall accuracy of observation. Only observations with quality scores of 1–3 (i.e., “good”, “very good”, and “excellent”, recorded at a distance of

Table 1. Bill darkness and plumage brightness scores for red-backed fairy-wrens in relation to season, age, sex, and status (details on scoring system and classifications in Methods). Shown are means ( $\pm$ SE), with samples sizes provided in parentheses.

Class	Bill score ( $\pm$ SE)	Plumage score ( $\pm$ SE)
Adult males, breeding season (n = 216)	2.10 $\pm$ 0.06	58.22 $\pm$ 2.85
Nuptial plumage breeders (n = 112)	2.75 $\pm$ 0.02	95.63 $\pm$ 0.50
Intermediate plumage breeders (n = 29)	2.34 $\pm$ 0.08	47.98 $\pm$ 2.93
Dull plumage breeders (n = 35)	1.47 $\pm$ 0.13	10.10 $\pm$ 1.41
Helper males (n = 40)	0.67 $\pm$ 0.12	3.01 $\pm$ 0.73
Adult males, non-breeding (n = 23)	0.53 $\pm$ 0.09	4.07 $\pm$ 2.31
Adult females, breeding season (n = 43)	0.41 $\pm$ 0.01	0.00 $\pm$ 0.00
Adult females, non-breeding (n = 16)	0.43 $\pm$ 0.08	0.00 $\pm$ 0.00
Juveniles (n = 15)	0.43 $\pm$ 0.04	0.00 $\pm$ 0.00

< 12 m with good light conditions using 10  $\times$  binoculars) were used in the analyses presented here.

A total of 674 bill color estimates on 275 individuals were analyzed, 310 (46%) from the field and 364 (54%) from birds in the hand. To compare bill scores made for birds in the hand vs. in the field, I compared a sub-set of 71 individuals for which I scored bill darkness in the hand and in the field within the same field season. There was no change in status for these individuals between the measures. Bill darkness scores for these 71 birds in the hand and from the field were correlated ( $r^2 = 0.53$ ,  $P < 0.001$ ) but when I compared the scores using a paired t-test, measures of bill darkness from the field were darker than scores in the hand ( $2.36 \pm 0.08$  vs.  $2.22 \pm 0.09$ ; paired t-test,  $t_{70} = 2.18$ ,  $P = 0.03$ ). To correct for this difference, I multiplied all field-based measures of bill color by 0.94 ( $= 2.22/2.36$ ). To ensure the validity of grouping in-hand scores with corrected field scores, I ran analyses twice, once using only in-hand scores, and once with the combined data. Analyses with in-hand measures were qualitatively identical to those obtained with the combined dataset. I therefore combined in-hand and adjusted field measures for each individual male within each breeding season.

There was no relationship between female age and female bill color (Logistic Regression,  $r = -0.12$ ,  $P = 0.41$ ), and females showed no variation in social status (all adult females on the study site were breeders) or plumage brightness (all females were dull). For this reason, analyses presented below focus on adult males in breeding condition.

## Data analysis

To determine if bill and plumage changes differed among males that did and did not switch status, I grouped males according to time (before/after) and status (switch/no switch). To do so, I first divided all helper males with multiple bill and plumage measures across a single season into two groups, those that switched to breeders and those that remained as helpers. For the males that switched ( $n = 11$ ), I calculated the mean bill and plumage scores for each individual before and after the switch. The mean switch dates in each of the three years of this study were 29 November 1997, 30 November 1998, and 2 December 1999, respectively. I therefore used 1 December as a cut-off date in each year to divide the season into “before” and “after” for males that did not switch status. This date also corresponds to the mid-point of the breeding season, which

runs from early October to late January (Karubian 2002). I obtained measures before and after 1 December for each of 11 males that did not switch and calculated mean bill and plumage scores for each of these males before and after this cut-off point. In the analyses below, therefore, time (before/after) is relative to the date of the switch for each individual that did switch status and is relative to 1 December for males that did not switch status. However, I also ran these analyses using 1 December as the before/after date for males that did switch status and obtained qualitatively identical results to those presented below.

Having grouped males in appropriate classes of time and status, I conducted the following analyses for bill color. Using paired t-tests, I compared bill color before vs. after in males that switched and bill color before vs. after in males that did not switch. Using t-tests, I compared bill color before in males that switched vs. males that did not switch, and bill color after in males that switched vs. males that did not switch. I also conducted a complementary analysis of bill color changes using a one-way repeated measures ANOVA in which the subject was bill score of each individual male, the between-subject variable was status and the within-subject variable was time. In this analysis, a significant interaction term of time  $\times$  status suggests that males that did switch status exhibit a different pattern of bill darkening in relation to time than males that did not switch.

I used the same approach to test for differences in plumage scores, but employed non-parametric tests (paired and un-paired Wilcoxon signed rank tests) because plumage scores were not normally distributed. To determine if changes in plumage brightness were associated with presence of body molt, I divided males that switched into two groups according to presence/absence of any active body molt at the time of the switch. To do, I identified whether males were molting or not when captured in the “before” or “after” time period relative to the switch. Any individuals with equivocal or missing data were excluded from analyses. I then assessed the magnitude of the change in plumage brightness (e.g., plumage score after – plumage score before) for each male in relation to molt.

For the analyses presented in Tables 1 and 2, mean values for males with multiple measures within a season were used to avoid pseudo-replication. For males with data from two or more seasons ( $n = 36$  males), I randomly excluded one year from the analyses unless the male differed in plumage type between the years, in which case each year included in because the differences associated with plumage type outweighed individual differences between years

Table 2. Determinants of bill darkness in male red-backed fairy-wrens using a general linear model. Effects of each term were calculated by holding all other terms constant while varying the term in question.

Parameter	F (df)	P
Plumage brightness	134.83 (1,213)	<0.001
Social status	31.31 (1,213)	<0.001
Age	0.12 (1,213)	0.41
Overall	220.17 (3,213)	<0.001

(Karubian 2002). All means are reported  $\pm$  SE, and all tests were two-tailed.

## Results

Bill color was recorded for 313 red-backed fairy-wrens (Table 1). Males' bills were significantly darker in the breeding season than in the non-breeding season ( $t_{237} = 162.2$ ,  $P < 0.001$ ). During the breeding season, darkness of males' bills was related to plumage brightness ( $r^2 = 0.64$ ,  $P < 0.001$ ), exact age ( $F_{2,100} = 32.6$ ,  $P < 0.001$ ), and breeding status ( $t_{214} = 182.1$ ,  $P < 0.001$ ). However, plumage brightness, age, and breeding status are inter-correlated in male red-backed fairy-wrens (Karubian 2001, 2002). A general linear model (GLM) was therefore used to determine the relative effects of each of these three parameters on bill darkness. The overall analysis was significant, and F-tests for the effect of each independent variable in the model revealed that both breeding status and plumage brightness were independently associated with bill darkness, but that age was not (Table 2). Further, there was no relationship between date and bill darkness in any of the three years ( $r^2 < 0.21$ ,  $P > 0.2$  in all three tests) among

one-year-old males, and among a subset of one-year-old males banded as nestlings, there was no relationship between bill darkness and exact age in days ( $r^2 < 0.21$ ,  $P > 0.1$  in each of two breeding seasons for which this analysis could be conducted).

Eleven males switched breeding status within a single breeding season. Bill color in these males was significantly darker after the switch than before (Fig. 1; paired  $t_{10} = 4.4$ ,  $P < 0.01$ ). There was no change in bill color over the same time period for 11 control helper males that did not switch breeding status (Fig. 1; paired  $t_{10} = 0.83$ ,  $P = 0.43$ ). Before the switch, there was no difference in bill color between males that switched and did not switch (Fig. 1,  $t_{20} = 0.27$ ,  $P = 0.8$ ) but after the switch, the males that switched had significantly darker bills (Fig. 1;  $t_{20} = 0.329$ ,  $P < 0.01$ ). Further, the interaction term of status  $\times$  time was statistically significant in a one-way repeated measures ANOVA ( $F_{1,20} = 10.18$ ,  $P < 0.01$ ), suggesting that bill color changes over time in males that switched breeding status differed from bill color changes over time in males that did not switch.

There was no difference in plumage brightness before vs. after among either the males that switched status ( $6.50 \pm 3.83$  before vs.  $7.05 \pm 3.51$  after;  $z = -2.0$ ,  $P = 0.81$ ) or the males that did not switch status ( $0.82 \pm 0.38$  vs.  $1.05 \pm 0.47$ ;  $z = -3.0$ ,  $P = 0.25$ ). There was no difference before the switch between males who switched and males that did not switch ( $z = 0.42$ ,  $P = 0.68$ ) and after the switch there was a non-significant trend toward males that switched having brighter plumage than males that did not switch ( $z = 1.58$ ,  $P = 0.12$ ).

Molt had no obvious effect on the magnitude of plumage brightness change though the small sample sizes available for these analyses preclude any definitive conclusions. Among males that switched status, there was no clear

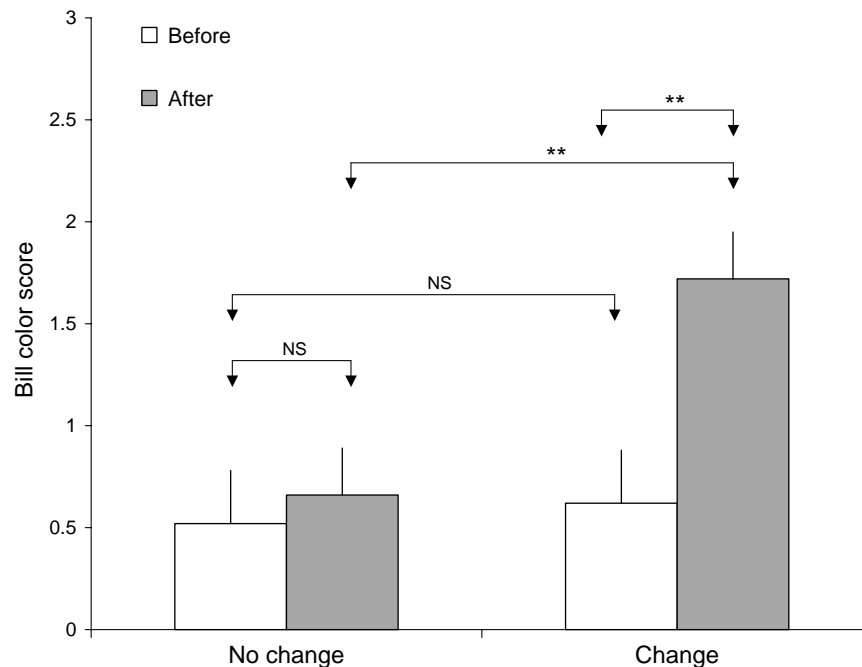


Fig. 1. Bill darkness scores for male red-backed fairy-wrens before and after a change in breeding status from helper to breeder. Males that changed breeding status developed darker bills whereas males that remained as helpers showed no change in bill darkness. Shown are mean bill darkness scores  $\pm$  SE.

difference in the magnitude of plumage change between males that were molting at the time of the switch ( $n = 3$  males, mean plumage score increase =  $2.47 \pm 3.13$ ) and males that were not molting ( $n = 5$  males, mean plumage score increase =  $0.93 \pm 0.93$ ). Males that did not switch status ( $n = 7$ ), and all males ( $n = 15$ ) combined, also showed no pattern of plumage change in relation to molt.

## Discussion

For group-living animals like the red-backed fairy-wren, breeding or social status can change from one moment to the next in an unpredictable manner. In this sense, male red-backed fairy-wrens face what may be a common challenge in the animal world: to overcome the relatively slow rate at which many signals can be updated in a dynamic social environment. This is especially relevant in social systems where an individual's status, rank or strategy is context or frequency-dependent, such as cooperative breeders or highly social species. In birds, where molt is often energetically costly and temporally constrained (Palmer 1972), other signals that can respond more rapidly to changing social conditions might play an important role as complements or alternatives to plumage-based signals. These include behaviors, vocalizations, or soft parts such as the bill, skin, and eye that are vascularized and therefore have the potential for rapid change.

Soft parts are thought to serve as signals in many species of bird for both mate attraction (Burley and Cooper-smith 1987, Omland 1996a, b, Preault et al. 2005), and dominance interactions (Miskelly 1981, Craig 1988). Examples of relatively rapid changes in the color, size, or shape of soft parts exist, though the cause or consequence of these changes is not always clear. In the red jungle fowl, comb size (but not color) of captive males whose social environment was experimentally manipulated responded within 17 d of the treatment (Zuk and Johnsen 2000). In the American goldfinch *Carduelis tristis*, bills of males held in captivity showed a significant decrease in brightness within 24 h, perhaps due to physiological stress (Rosen and Tarvin 2006). Rapid and ephemeral color changes in exposed facial skin, including "flushing" due to dilation of blood vessels, may also serve as a short-term signal in a number of avian families (Curio 2004, Negro et al. 2006).

In the current study, bill color of male red-backed fairy-wrens darkened following a switch in status from helper to breeder. This bill darkening took place within three weeks of the switch and occurred independently of age, plumage, or any population-wide trends in bill color change. In all cases the change in status and subsequent bill darkening immediately followed the death of breeding male or, more rarely, the immigration of a new female. This suggests that it is the change in social status that triggered the change in bill color, and not vice-versa, and that bill darkness may therefore be a socially mediated trait in this species. Because examples of social control of phenotype in wild birds are rare, it is worthwhile to consider what the adaptive significance, if any, of this phenomenon in red-backed fairy-wrens may be. This change in bill color was restricted to the breeding season, meaning that we can exclude non-breeding season explanations for its significance

(Rohwer and Butcher 1988). This leaves at least two adaptive explanations for the pattern documented here.

One possibility is that bill color is associated with intra-sexual dominance and aggression. Light bills may signal subordinate status, which could benefit helper males by reducing aggression from older, socially dominant breeding males in the group. This in turn could lower chances of expulsion from the group, allowing helper males to remain on their natal territory until a breeding opportunity arises nearby. Once these young males have obtained a social mate (i.e., switched from helpers to breeders), however, darker bills could become advantageous because they assist in territory defense, mate guarding, and other male:male interactions. A second, non-mutually exclusive possibility is that dark bills may be preferred by females, and that males that switch in social status develop dark bills to increase within- and extra-pair paternity. A field-based experiment in which bills of helpers and breeders are manipulated in combination with molecular analyses of paternity would test these hypotheses.

In contrast to bill darkness, plumage brightness did not show a clear response to the switch in breeding status. There is no obvious constraint why plumage could not become brighter after the switch among males that were still actively molting after the switch. Among the three males molting at the time of the switch, one male's plumage brightness score increased dramatically (from 0 to 8.7) but the other two males showed no change or even a small decrease. This suggests that males are capable of increasing plumage brightness in relation to changes in social status, but that physiological constraints or other concerns may limit their ability to do so. An experiment in which feathers are plucked (thereby inducing limited molt) concurrently with experimentally induced switches in status would further our understanding of the relationship between plumage brightness, molt, and social environment in the red-backed fairy-wren.

It is useful to consider the interplay of plumage brightness and bill darkness as signals. Does bill darkness signal the same information as plumage brightness, and if so, why are both signals needed? One hypothesis is that bill darkness and plumage brightness may in fact signal similar information, but that their expression is mediated by social environment in different ways. To the best of my knowledge, one-year-old males that have paired before or during the pre-nuptial molt develop nuptial plumage with a dark bill whereas unpaired males molt into dull plumage with a light bill in the pre-nuptial molt. Thus, breeding status at the time of the pre-nuptial molt may determine the plumage a male retains for his first breeding season, whereas changes in breeding status during the breeding season trigger within-season changes in bill darkness. However, it is interesting to note that bill color is not known to lighten in one-year-old males who have gone from paired to unpaired.

In sum, the pattern of bill darkening in male red-backed fairy-wrens suggests that soft parts in birds can respond relatively rapidly to changes in social environment. Data from a handful of other species are consistent with the idea that soft parts may function as signals that may be rapidly updated, but the possibility is currently little tested. Additional work on a range of species is needed to judge the prevalence of this phenomenon.

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