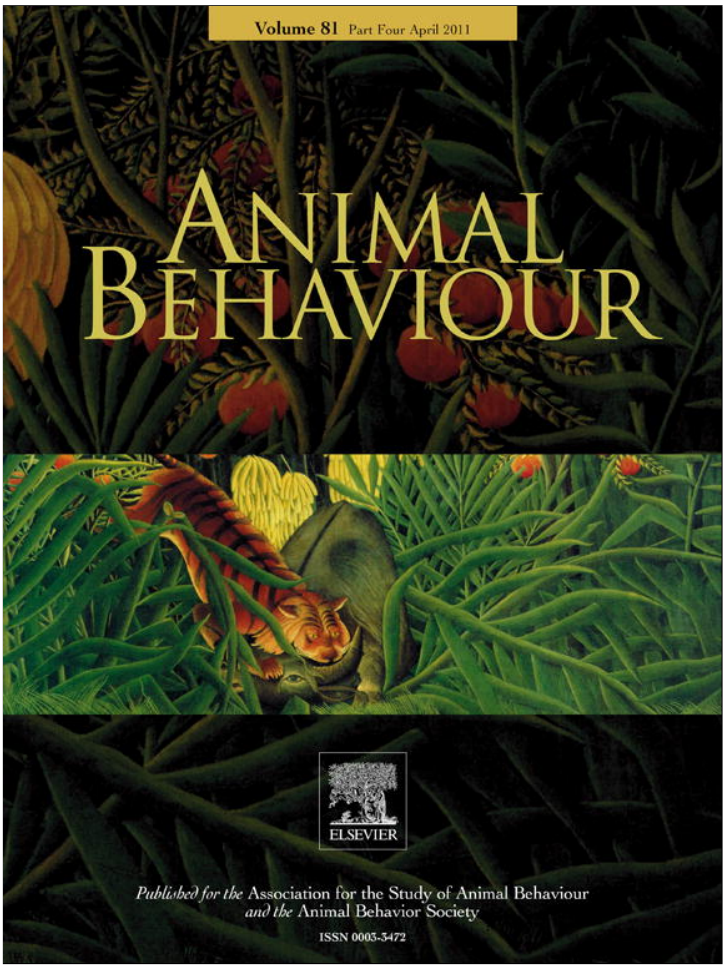

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Bill coloration, a flexible signal in a tropical passerine bird, is regulated by social environment and androgens

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Although some group-living animals dynamically modify sexual signals in response to changes in social or reproductive status, this ability is often limited by constraints inherent in the mechanism of signal production. In birds, for example, inflexible moult schedules may restrict the ability to rapidly modify plumage-based signals. In such cases, more flexible secondary signals such as skin, eye, or bill coloration (e.g. soft parts) could potentially be used to achieve dynamic signalling. We addressed the degree to which free-living red-backed fairy-wrens, *Malurus melanocephalus*, can dynamically update both plumage and soft part signals when status suddenly changes, and how this may be achieved. In this cooperatively breeding passerine, dominant breeding males are distinguished from socially subordinate nonbreeding auxiliary males by the presence of nuptial plumage, dark bills and large sperm storage organs. Following an experimentally induced shift in status from auxiliary to breeder, males showed rapid increases in excreted androgen metabolites. Although they showed no overall change in nuptial plumage colour, several experimental males developed red nuptial feathers on the back following feather plucking, indicating that they had the capacity to develop bright nuptial plumage but were constrained from doing so by the moult schedule. In contrast, experimental males showed a rapid darkening of their bills, reflecting their newly acquired breeding status. These findings (1) provide experimental evidence that status affects physiologically controlled visual signals in free-living birds, (2) suggest that this linkage is mediated by testosterone and (3) illustrate how secondary ornaments may be used in dynamic signalling when the primary signalling modality is constrained.

For species living in fluctuating or seasonal environments, the flexible expression of reproductive traits allows a timely response to changing ecological conditions (Hau 2001; Shuster & Wade 2003). Group-living animals face the added challenge of an inherently unstable social environment where breeding opportunities often occur unpredictably (e.g. when a dominant breeding individual in the group dies). Indeed, among group-living animals, reproductive success may depend as much on a timely response to changes in relative dominance and group composition as to changes in ecological conditions (Warner 1975; Munday et al. 2006; Bro-Jørgensen 2010).

In this context, socially subordinate group members often reduce investment in reproduction until a breeding opportunity presents itself. When a breeding opportunity does arise, it is important for an individual to rapidly modify reproductive functions (e.g. gamete production) and also develop appropriate sexual signals that will affect fitness through interactions with conspecifics. Yet, because of temporal or physiological limitations inherent in mechanisms of signal production, there exists wide variation within and between taxa in the ability to facultatively adjust signals. Consider, for example, ornamental coloration: whereas fish and primates may rapidly update visual signals in response to changes in status (Setchell & Dixson 2001; Burmeister et al. 2005; Munday et al. 2006), birds relying on plumage ornaments may be unable to update these signals because the timing and extent of feather replacement (i.e. moult) is often fixed by temporal, phylogenetic and/or physiological constraints (Payne 1972). The signalling constraints faced by birds embody a broad question facing many group-living animals: how can a rapid temporal signal response to unpredictable changes in social environment be achieved when the primary signal is relatively static?

Individuals might respond to this challenge by behaviourally modifying plumage-based signal expression via cosmetics (Delhey et al. 2007), feather abrasion or degradation (e.g. Møller & Erritzoe 1992; Blanco et al. 2005), or by facultatively covering and revealing

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the signal (Hansen & Rohwer 1986). In contrast, when visual signals are under physiological control (as opposed to behavioural control), relatively flexible secondary signals may provide an alternative signalling mechanism. Among birds, vascularized soft parts (e.g. exposed skin, bill, eye, or leg) may be well suited for this role. Soft parts are used as social signals (e.g. Faivre et al. 2003; Velando et al. 2006), and experiments on captive fowl, *Gallus gallus* (Zuk & Johnsen 2000) and zebra finch, *Taeniopygia guttata* (Gautier et al. 2008) demonstrate that comb size and bill colour, respectively, respond rapidly to changes in social environment, possibly via concurrent increases in levels of testosterone (Parker et al. 2002; McGraw et al. 2006). Similarly, social environment at time of moult affects subsequent size of the throat patch (a plumage-based trait) in captive house sparrows, *Passer domesticus*, probably via the effects of testosterone (McGraw et al. 2003). Yet among wild bird populations, evidence that social environment and/or status directly affects the expression of physiologically controlled visual signals is rare or absent for both plumage and soft parts. This is somewhat surprising given the large number of longitudinal field studies on marked populations, and it suggests that social determination of physiologically controlled visual signals may be uncommon or overlooked among wild birds.

We therefore investigated the effects of changes in social status on expression of visual signals in a wild population of red-backed fairy-wrens, *Malurus melanocephalus*. Red-backed fairy-wrens form cooperatively breeding groups in which male offspring often delay dispersal and assist with subsequent reproductive efforts as auxiliary males (Rowley & Russell 1997). Importantly, auxiliary status is a flexible behavioural strategy in that auxiliary males sometimes switch within a single breeding season from helping to breeding. This occurs when a breeding vacancy is created by the death of a mated male or by the immigration of a young female into the area. Auxiliary males are socially and reproductively subordinate to breeding males: they have low levels of circulating androgens (testosterone), show weak or no expression of reproductive traits and signals (in particular, they show cryptic brown female-like plumage and light bill coloration) and sire few young (Table 1 and references therein). In older adult males (after second year), breeding season plumage colour is determined during a prenuptial moult prior to the onset of reproduction (Lindsay et al. 2009), whereas in 1-year-old males, moult often extends into the breeding season, and thus, plumage coloration can change during the breeding season. Bill coloration, in contrast, has the potential to change at any point within a single breeding season because, unlike feathers, bills are vascularized (Karubian 2008). A previous correlative study (Karubian 2008) documented that switching from auxiliary to breeder status within a season was associated with development of darker bills, but the direction of causality was unclear, a proximate mechanism was not identified, and the degree to which plumage coloration might also respond to changes in status via delayed or facultative moult was ambiguous.

In the present study, we manipulated social status of free-living male red-backed fairy-wrens via a removal experiment designed to induce a switch from auxiliary to breeder status. We hypothesized that alteration of a male's behavioural phenotype would coincide with morphological changes in potentially flexible signal traits such as bill darkness, but not in plumage coloration because of moult constraints. We further hypothesized that changes in phenotype would be associated with increased levels of androgens as both male reproductive behaviour and soft part coloration have been linked to androgens in red-backed fairy-wrens (Lindsay et al. 2009) and other avian species (e.g. Wingfield et al. 2001; McGraw et al. 2006). Our results provide experimental evidence linking breeding status to expression of physiologically controlled visual signals via up-regulation of testosterone production and demonstrate the importance of secondary ornaments for dynamic signalling when production of the primary signal, in this case plumage colour, is constrained.

METHODS

Research Site, Study Species and Basic Methods

Red-backed fairy-wrens are small (ca. 8 g) insectivorous passerines that inhabit open forests and grasslands in northern Australia. Our research was conducted on the Atherton Tablelands in Queensland (145°25′E, 17°23′S), where the breeding season typically extends from October to February. Males and females form long-term socially monogamous pair bonds with high rates of sexual promiscuity (Karubian 2002; Webster et al. 2008), and pairs are commonly (ca. 25%) accompanied by a male auxiliary helper (Varian-Ramos et al. 2010).

Male red-backed fairy-wrens reach reproductive maturity in their first year of life. In their first potential breeding season, males may be either brown or red/black; they may have light or dark bills; and they may have small or large cloacal protuberances (an external sperm storage organ; Mulder & Cockburn 1993; Table 1). Variation in the expression of these traits occurs almost exclusively in the first breeding season; by the second year of age nearly all males acquire definitive bright nuptial plumage, black bills and large cloacal protuberances during the breeding season. Differences in both body condition and circulating androgen levels during prebreeding season (prenuptial) moult predict plumage coloration and, to a lesser degree, cloacal protuberance volume and bill coloration in the subsequent breeding season (Lindsay et al. 2009).

The present study is confined to 1-year-old males of known age (based on banding history or skull ossification) in brown plumage. Birds were captured in mist nets and provided with a unique combination of coloured leg bands and a numbered aluminium band. At time of capture, we measured cloacal protuberance volume and tarsus length (±0.01 mm) and weighed (±0.1 g) birds and collected faecal droppings for hormonal analyses from sterile inserts in holding bags immediately following capture. For treatment males at the initial capture (see below), we also plucked five feathers from the top of the dorsal feather tract and two central tail feathers to induce standardized feather regrowth. We calculated extent of

Table 1
Reproductive traits characteristic of three phenotypic classes of free-living male red-backed fairy-wrens from Queensland, Australia

Male type	Sexual signals			Other reproductive traits		
	Back colour*	Tail*	Bill colour*	Body condition	Cloacal protuberance*,†	Circulating androgens
Red/black breeder	Red[1,2]	Black & short[3,4]	Black[5]	High[6]	Large[1,6,7]	High[6]
Brown breeder	Brown & red[1,2]	Brown & long[3,4]	Dark/black[5]	Intermediate[6]	Moderate[1,6,7]	Moderate[6]
Auxiliary	Brown[2]	Brown & long[3,4]	Light[5]	Low[6]	Small[6,7]	Low[6]

Auxiliary males showed reduced expression of sexual signals and other reproductive traits relative to brown and red/black breeding males.
[1]Karubian (2002); [2]Karubian et al. (2008); [3]Karubian et al. (2009); [4]Swaddle et al. (2000); [5]Karubian (2008); [6]Lindsay et al. (2009); [7]Rowe et al. (2010).
* Indicates that development of this trait is positively associated with levels of circulating androgens at time of moult.
† Differences between male types in cloacal protuberance volume are mirrored by differences in total sperm number and ejaculate volume.

nuptial plumage by scoring each of five body sections for proportion of red/black plumage as in Karubian (2002), allowing scores from 0 (completely brown) to 100 (completely red/black). Bill colour was measured by dividing both the top and the base of the bill into proximal and distal halves and scoring each section on a 10-point integer scale as in Karubian (2008), allowing scores from 1 (completely beige) to 40 (completely black). We did not have access to a spectrophotometer for this study, so no attempt was made to score the reflectance spectrum across the bird visible range, or the hue of plumage or bill colour. While this may have caused us to miss subtle modifications in coloration, the differences in bill and plumage coloration between auxiliaries and breeding males are pronounced, and our scoring methods are repeatable and accurately capture these differences (see Karubian 2008; Webster et al. 2008). Cloacal protuberance volume was calculated following Mulder & Cockburn (1993). An index of body condition was computed as the standardized residuals from a linear regression of log(body mass) on $3 \times$ log(tarsus length). Residual condition is a useful measurement of body condition in red-backed fairy-wrens as it is positively correlated with measurements of fat storage (Lindsay et al. 2009).

Removal Experiment

Removal experiments were designed to change breeding status of males from auxiliary helpers to breeders by creating breeding vacancies via removal of established breeding males. We identified treatment groups consisting of a breeding pair with an auxiliary male in nest construction phase and lacking dependent young. Experimental manipulations of breeding status took place between 23 November and 24 December 2005, a period of high breeding activity. In each replicate of the experiment, we captured the entire group and processed the auxiliary male (i.e. the 'treatment' male) as described above while the breeding female was held in a bag. While birds were detained we destroyed the nest, thereby ensuring that all treatment groups began the experiment at an equivalent nesting stage. After processing, the treatment male and breeding female were released on their original territory and the former breeding male was released in suitable habitat 10–15 km distant; there were no resightings of removed males on their initial breeding territories.

Treatment males were monitored intensively for 48 h post-removal and then at 3-day intervals for the duration of the experiment to assess pair formation and to follow breeding attempts. Treatment males were recaptured from 31 December 2005 to 20 January 2006, approximately 1 month after the removal (mean $= 34 \pm 8.5$ days; range 23–46 days). We processed birds following methods above and assessed the colour of regrown plucked feathers. Of 24 total removal experiments attempted, 20 met the criteria above; of these, 13 were completed and 7 failed because treatment birds disappeared (i.e. died or moved).

To serve as controls for this experiment, we identified 1-year-old auxiliary males that were captured at least twice within a single breeding season within a similar time frame as treatment males and that did not undergo a switch in breeding status. Thirteen individuals distributed across five breeding seasons fit these criteria. Control males were initially captured between 10 November and 24 December, and were recaptured between 5 December and 28 January (mean interval between captures $= 32.5 \pm 4.0$ days; range 21–74 days).

Faecal Steroid Metabolite Radioimmunoassays

When selecting samples for analysis of faecal androgen metabolite concentrations, we included only treatment and control males sampled in similar nesting stages (nest construction, recent nest failure and mid-season prebreeding) at initial and final recaptures to avoid the confounding effects of parental behaviour on androgen metabolite concentrations (see Lindsay et al. 2009). The intersampling time period was also similar for control and treatment males (mean: 22.5 ± 3.3 days versus 26.8 ± 2.0 days; range 13–37 versus 22–33 days, respectively).

We validated the use of red-backed fairy-wren faeces for radioimmunoassay of total androgen metabolite concentration following the guidelines of Goymann (2005) and Palme (2005) (see Supplementary Material). We extracted steroid metabolites following Goymann et al. (2002) with 1 ml of 75% ethanol in double-distilled water from lyophylized, pulverized and weighed (± 1 mg) faeces. Sample dry mass was restricted to a range of 2–10 mg to offset a documented negative correlation between faecal hormone metabolite concentration and sample mass (Goymann 2005; Supplementary Material). We incubated 500 μl of ethanolic steroid supernatant for 16–18 h at 39 °C with 200 μl of sodium acetate buffer containing β-glucuronidase/arylsulfatase to hydrolyse β-glucuronides and sulfate esters. We measured total androgen metabolite concentration using radioimmunoassay following Schwabl (1993). Radioimmunoassays were conducted using tritium-labelled testosterone (PerkinElmer Life Sciences NET-553, Waltham, MA, U.S.A.) and a testosterone antibody (Wien Laboratories T-3003, Flanders, NJ, U.S.A.) that cross-reacts with closely related steroids such as 5α-dihydrotestosterone. We ran duplicate assay tubes for each sample containing 20 μl of hydrolysed extract and 80 μl of phosphate-buffered saline with gelatine, pH 7.1 (PBSg). We determined recovery using five pooled samples, to which we added 2000 cpm of tritium-labelled testosterone, with mean testosterone recovery of 74.3%. The intra-assay coefficient of variation for the single assays was 8.5% (calculated following Chard 1995). Androgen metabolite concentrations are expressed as pg/mg of dry faeces, and differences were compared as for other phenotypic traits (above).

Statistical Analyses

We used two-way repeated measures general linear mixed models using residual maximum likelihood (REML; Patterson & Thompson 1971) to conduct F tests for the effects of male type (i.e. treatment or control), time (i.e. first or second capture) and the interaction of male type $\times$ time on each of our dependent variables. A statistically significant interaction term in these models indicates that treatment and control males showed differential rates of change between the two captures; in these cases, we went on to conduct post hoc, pairwise tests to ascertain the degree and directionality of the difference between control and treatment males between captures. As androgen metabolite and plumage data exhibited mild departures from normality, we confirmed that a Scheier–Ray–Hare two-way ANOVA yielded qualitatively similar results to those presented below, and we used nonparametric post hoc tests as appropriate. Analyses were conducted using JMP software (SAS Institute, Cary, NC, U.S.A.) using two-tailed tests of significance, and data are reported as means $\pm$ SE unless otherwise stated.

Ethical Note

All animals were handled and released in a safe and humane manner, and all procedures were approved by Institutional Animal Care and Use Committee (protocol no. 3067) of Washington State University, the James Cook University Animal Ethics Review Committee (approval no. A1004) and the Queensland Government Environmental Protection Agency. Export of samples from Australia was approved by the Australian Government Department of Environment and Heritage.

RESULTS

Behavioural Response to Treatment

In 9 of 13 (69%) replicates of the experiment, treatment males assumed the breeding position on their natal territory and began mate guarding and duetting with the female within 1 h of the removal of the breeding male. Formation of social pairs between males and their genetic mothers is a relatively common phenomenon in *Malurus* fairy-wrens that may partially explain the high rates of extrapair paternity seen in this genus (Brooker et al. 1990; C. Varian-Ramos, unpublished data). In the remaining four replicates, a neighbouring breeding male paired with the treatment group female, and the treatment male moved to the neighbouring territory and formed a pair bond with the female there. These four cases resulted in stable pair bonds 4 h to 2 days postremoval. In all 13 replicates, once the initial pair bond between a treatment male and the female was established, it remained stable for the duration of the experiment.

Phenotypic Response to Treatment

Bill coloration was the only phenotypic trait measured that showed a statistically significant relationship between male type and time of measurement (Table 2, Fig. 1a). Post hoc, pairwise tests demonstrated significant increases in bill darkness between measurement periods for both treatment males (12.08 ± 1.23 versus 22.65 ± 2.28; paired t test: $t_{12} = 6.43$, $P < 0.0001$) and control males (11.20 ± 1.54 versus 14.83 ± 1.66; $t_{12} = 2.84$, $P = 0.02$). However, the relative increase in bill darkness among treatment males was greater than that of control males: at the time of the first capture, there was no significant difference between treatment and control males ($t_{24} = 0.45$, $P = 0.7$), but at the time of the second capture, treatment males had significantly darker bills ($t_{24} = 2.77$, $P = 0.01$).

There were no significant changes in the overall extent of nuptial plumage colour between measurement periods within treatment males (2.31 ± 1.50 versus 3.92 ± 2.36) and control males (1.34 ± 0.60 versus 1.37 ± 0.66), or between the two types of males (Table 2). This finding suggests no facultative moult among birds during the reproductive phase. However, of the 11 treatment males for which we induced feather regrowth by plucking, five had, upon recapture, grown in the red, carotenoid-based nuptial plumage on the back typical of red/black breeder males. This demonstrates a capacity to obtain, transport and deposit carotenoids into growing feathers at this time. In contrast, tail feathers that are typically melanin-based black in red/black breeders grew in exclusively brown, providing no evidence for the ability to produce melanin-based plumage for this portion of the body when breeding.

Cloacal protuberance volume increased between measurements for both treatment males (69.28 ± 13.90 versus 101.44 ± 11.67; paired t test: $t_{12} = 3.35$, $P = 0.006$) and control males (48.96 ± 10.53 versus 66.83 ± 11.35; $t_{12} = 1.78$, $P = 0.05$), but there was no significant difference in the relative rate of increase between male types (Table 2). There was no significant change in body condition between measurement periods within treatment males (0.00 ± 0.35 versus -0.17 ± 0.34) or control males (0.24 ± 0.20 versus 0.00 ± 0.69), nor between the two types of males (Table 2).

Hormonal Response to Treatment

Faecal androgen metabolite concentrations exhibited a significant male type × treatment term in our mixed model (Table 2, Fig. 1b). Post hoc, pairwise tests demonstrated statistically significant increases in androgen metabolite concentrations between measurement periods for treatment males (121.08 ± 36.61 versus 443.89 ± 57.07; paired t test: $Z = 10.50$, $N = 6$, $P = 0.03$) but not for control males (123.31 ± 49.46 versus 188.23 ± 50.82; $Z = 3.50$, $N = 6$, $P = 0.56$). There was no significant difference in androgen metabolite levels between treatment and control males at the time of the first sampling ($Z = 0.24$, $P = 0.81$), but at the time of the second sampling, levels of androgen metabolites were significantly higher in treatment males than in control males ($Z = 2.64$, $P = 0.008$).

DISCUSSION

Intrasexual variation in the degree of ornamental coloration is often associated with social status in birds (Senar 2006), but the causal direction of this relationship is usually unclear. In particular, the degree to which status or social interactions may affect the expression of elaborate colour traits is uncertain. The current study provides experimental evidence that social status affects the expression of sexual signals in wild birds. Specifically, among red-backed fairy-wren males whose status was experimentally shifted from nonbreeding auxiliary to breeder, we observed rapid increases in bill colour. We also observed an increase in androgens (as measured by excretion in faeces), which in turn may be the proximate mechanism linking status and morphological phenotype.

In contrast, there was no change in the overall plumage coloration of experimental males, because birds did not naturally moult during the study period. However, we experimentally induced feather regrowth by plucking feathers, and in approximately half the cases, treatment males grew red feathers, rather than brown, on their backs. Our previous work has shown that androgen levels during the prebreeding season moult determine colour of breeding plumage (Lindsay et al. 2009), and in this study, treatment males showed an increase in androgen metabolite levels. Thus, our results show that the underlying machinery for growth of carotenoid-based bright plumage is in place for males that change status during the breeding season, but that the time window during which status can affect development of plumage colour signals is constrained by the annual moult schedule. In contrast, these same treatment males grew in brown rather than black tail feathers, suggesting that mechanistic limitations (e.g. prevalence of melanosome cell types, enzymatic activity, responsiveness to androgens) could affect the

Table 2
Effect tests from a repeated measures general linear mixed model with male type (treatment or control), time (first or second measurement) and an interaction term of male type × time as predictor variables, and male identity as a random effect

	Bill darkness		Cloacal protuberance volume		Extent of nuptial plumage		Body condition		Excreted androgens	
	$F_{1,23}$	P	$F_{1,23}$	P	$F_{1,23}$	P	$F_{1,23}$	P	$F_{1,10}$	P
Male type	2.73	0.11	2.22	0.15	0.001	0.98	0.27	0.61	5.63	**0.039**
Time	43.42	**<0.0001**	14.00	**0.001**	1.34	0.26	0.11	0.74	19.18	**0.001**
Male type×time interaction	10.51	**0.004**	1.47	0.24	1.13	0.29	0.30	0.59	8.46	**0.016**

Bill darkness and level of excreted androgen metabolites increased significantly more among treatment males than among control males between measurements, as indicated by the interaction term. Statistically significant effects are indicated in bold.

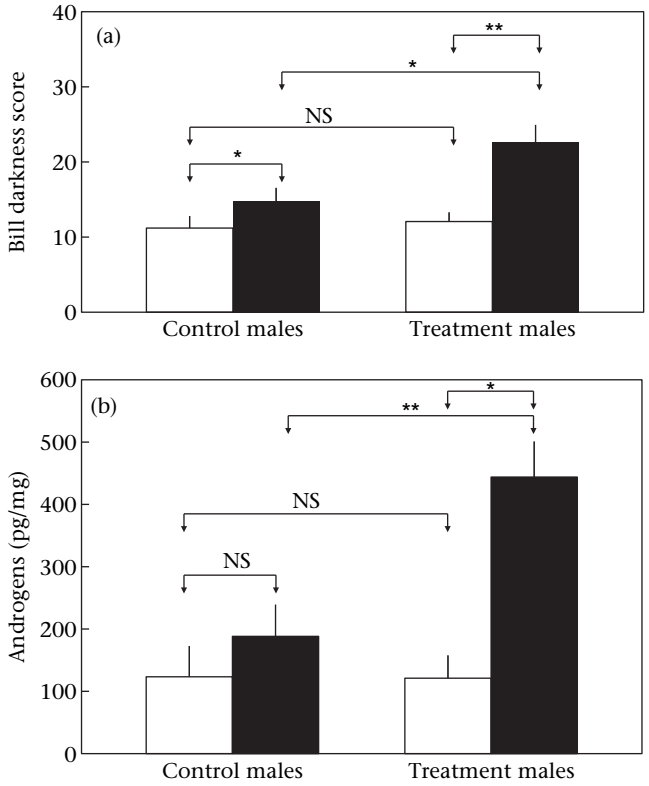

Figure 1. Changes in (a) bill darkness and (b) androgen metabolite concentration within a single breeding season among 1-year-old male red-backed fairy-wrens. □: represent mean trait values the first time that males were measured; ■: represent mean trait values at a second measurement period occurring approximately 1 month later. Treatment males underwent an experimentally induced shift in status from auxiliary helper to breeder between the two measures, whereas control males remained as auxiliaries and did not change status. Results of pairwise tests (motivated by significant interaction terms from a repeated measures mixed model) are reflected by asterisks (*$P < 0.05$; **$P < 0.001$) or by NS ($P > 0.1$).

seasonal flexibility of melanin colour production in bill integument versus tail feather follicles in this species.

These findings suggest that, during the breeding season, red-backed fairy-wrens may use soft tissue as an alternative to plumage to rapidly fine-tune signals of status in relation to changing social environment. In our study, after 1 month the bills of treatment males were significantly darker than those of controls, although strong differences were already apparent by 2 weeks (see also Karubian 2008). Captive male zebra finches also change bill coloration within a similar time period when housed with females (Gautier et al. 2008). This relatively rapid response (detectable to the human eye after 2 weeks) is presumably achieved by mobilizing pigments in the ramphotheca, the vascularized integument of which the bill is composed. Avian bill coloration is influenced by androgens (e.g. Mundinger 1972), suggesting a proximate mechanism for the observed increase in androgen metabolite levels following the experimental change in breeding status. These alterations of androgen-regulated bill colour therefore appear to accurately facilitate signalling of reproductive state associated with corresponding changes in reproductive behaviour and androgen production. In contrast to the 'relatively rapid' and probably androgen-regulated change in bill colour apparent by 2 weeks, treatment males changed their behaviour (e.g. rate of singing, mate guarding) immediately after the removal (J. Karubian, unpublished data). This is reminiscent of studies of social regulation of behaviour and coloration in cichlid fish (e.g. Burmeister et al. 2005) that suggest rapid changes in behaviour independent of gonadal hormones.

These considerations in combination with the fact that soft tissue responds quickly to a wide range of exogenous and endogenous cues beyond social environment (e.g. McGraw & Hill 2000; Rosen & Tarvin 2006; Mougeot et al. 2010) suggest that soft tissue may function as an honest and rapidly updateable signal in a broad range of avian species (e.g. Faivre et al. 2003; Velando et al. 2006; Perez-Rodriguez & Vinuela 2008; Murphy et al. 2009). In this sense, the distinctive response of soft tissue versus plumage coloration we observed informs an ongoing debate concerning the adaptive value of multiple ornaments and context-dependent signalling (Bro-Jørgensen 2010). In the red-backed fairy-wren, bill coloration (and perhaps behaviour) appears to provide information on current status during the breeding season (this study), whereas plumage coloration provides information on condition, circulating levels of androgens and, potentially, status during moult prior to the breeding season (Lindsay et al. 2009). These findings are consistent with the 'multiple messages hypothesis', which proposes that different ornaments provide information about individual quality at different stages of life (Møller & Pomiankowski 1993).

In our experiment, treatment males promptly filled experimentally created breeding vacancies, indicating that auxiliaries are constrained to helping behaviour by a lack of suitable breeding opportunities (see also Pruett-Jones & Lewis 1990), and 'make the best of a bad job' by remaining on the natal territory until a breeding position is available. Accordingly, suppressed expression of ornamental coloration by auxiliary red-backed fairy-wren males may function to reduce aggression from dominant breeders (see Lyon & Montgomerie 1986) and presumably reduce the risk of expulsion from the natal territory (Karubian et al. 2008). This scenario is consistent with the idea that high social costs of cheating may enforce honesty in signals that are physiologically inexpensive to produce, such as melanin-based coloration of bills (Rohwer 1977).

We hypothesize that suppression of visual signals may be beneficial when males are subordinate auxiliaries, but it may become maladaptive when these auxiliaries become breeders because of reduced reproductive success (Webster et al. 2008). Consistent with this idea, treatment males dynamically up-regulated a flexible visual ornament (bill coloration) when provided with the opportunity to breed, apparently via enhanced testosterone production. Overall, plumage did not respond to our treatment, although the hormonal mechanisms for increased plumage brightness appeared to be in place, which highlights the constraints of timing of moult on plumage signalling as well as the potential importance of additional signals as honest and dynamic indicators of current status or physiological state. The phenotypic response we observed was associated with increased levels of excreted androgen metabolites, providing compelling evidence both that testosterone may be a mechanism linking social status with morphological phenotype, and also that testosterone production is probably suppressed in auxiliary males via social mechanisms. This multi-tiered understanding of the causes underlying phenotypic differences among male red-backed fairy-wrens highlights the complex interplay of endogenous and exogenous factors regulating flexible reproductive strategies in birds.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2011.01.012.

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