

The relative importance of male tail length and nuptial plumage on social dominance and mate choice in the red-backed fairy-wren *Malurus melanocephalus*: evidence for the multiple receiver hypothesis

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Understanding why males of many species exhibit two or more sexual ornaments depends upon identifying both the information conveyed and the intended receiver(s) for each signal. Here we focus on identifying the intended receivers for two sexual signals exhibited by male red-backed fairy-wrens *Malurus melanocephalus*, extent of nuptial plumage and tail length. In doing so we test the multiple receiver hypothesis, which predicts that each trait is directed toward a different type of receiver (e.g., males vs females). Male red-backed fairy-wrens in nuptial plumage exhibit reversed sexual dimorphism for tail length in the breeding season, when their tails are significantly shorter than those of females or males in eclipse plumage. Using both aviary-based experiments and indices of mate choice and social dominance from a natural population, we found that extent of nuptial plumage and age primarily affected female mate choice and that shorter tails were primarily associated with male:male dominance signaling. The field and aviary studies combined are consistent with the multiple receiver hypothesis, in that each trait appears to be directed primarily to a different set of receivers (plumage for females and tail length for males), though each trait may also signal information to the other set of receivers as well. We propose that sexual selection may favor shorter tail lengths in male red-backed fairy-wrens through social competition mechanisms.

Darwin's (1871) proposal that male ornamentation evolves through female mate choice and/or male-male competition has been supported by a host of studies and remains a central pillar of sexual selection theory (Andersson 1994). Recent theory predicts signals used in mate choice should converge upon a single signal type (Iwasa and Pomiankowski 1994, Johnstone 1996), yet multiple male ornaments are widespread in nature (Candolin 2003). A complete understanding of the function and adaptive significance of multiple male ornaments depends upon answering two basic questions: (1) what information about the sender is conveyed by each signal (Møller and Pomiankowski 1993), and (2) who is the intended receiver for each signal (Andersson et al. 2002)?

Two early and influential hypotheses for multiple male ornaments, the 'multiple messages' and the 'redundancy' hypotheses, focused on the information about the sender conveyed by each ornament (Møller and Pomiankowski 1993). The multiple messages hypothesis proposes that each ornament carries different information about the sender, such as condition during development and current physio-

logical condition. Alternatively, the redundancy hypothesis proposes that different ornaments convey complementary or back-up information about a single aspect of male quality to receivers. Since their publication in 1993, these two hypotheses have driven much of the research into multiple male ornaments. Although the redundancy hypothesis has been supported in some cases, available evidence suggests that the multiple messages hypothesis may apply more broadly (reviewed by Candolin 2003).

A third and more recent hypothesis shifts the focus from the information about the sender that multiple ornaments may convey to their signaling function(s) and intended receiver(s). This idea was formally adapted to the existence of multiple male ornaments by Andersson et al. (2002) as the 'multiple receivers' hypothesis, which suggests that males may have evolved multiple ornaments because each ornament is directed toward a different set of receivers. For example, in the red-collared widowbird *Euplectes ardens*, tail length is positively associated with mate choice but not male-male interactions (Pryke et al. 2001a), whereas red collars are associated with male-male interactions but not

mate choice (Pryke et al. 2001b), suggesting that multiple ornaments may have evolved because of the distinct signaling roles they play (Andersson et al. 2002).

Demonstrating whether the multiple receiver hypothesis applies to a specific set of signals requires information on how each ornament independently affects both male-male interactions and female choice (i.e., affects multiple receivers). Isolating the effects of each trait in a multi-trait signal is a difficult task that is further complicated by the fact that interactions between multiple ornaments may be complex (e.g., Hegyi et al. 2007), that the signaling roles of ornaments may vary geographically (Dunn et al. 2008), and that some ornaments may be unreliable or not currently related to sexual signaling (Westneat 2006). Perhaps because of these difficulties, there are few published reports examining the applicability of the multiple receiver hypothesis (but see Andersson et al. 2002, Loyau et al. 2005, Tarof et al. 2005). Here, through experimentally-controlled aviary trials and analyses of female mate choice and social dominance from a natural population, we attempt to partition the relative influences of two sexual signals on male-male social dominance and female mate choice in the red-backed fairy-wren *Malurus melanocephalus*.

The red-backed fairy-wren is a small passerine bird in which males exhibit at least two distinctive sex-limited ornaments: extent of nuptial plumage and tail length (Schodde 1982, Rowley and Russell 1997, 2007). The extent of the body covered in nuptial plumage varies in adult males from “dull” brown, female-like plumage to full “bright” black and red nuptial plumage. Extent of nuptial plumage is associated with increased attractiveness to females in controlled mate preference trials (Karubian 2002) and higher reproductive success in a natural population via increased extra-pair paternity (Webster et al. 2008). Extent of nuptial plumage is also associated with social dominance, in that males in red-black nuptial plumage are socially dominant to males in brown plumage (Karubian et al. 2008).

In addition, although males are larger than females in most morphological traits, during the breeding season males in red-black nuptial plumage develop tails that are significantly shorter than those of females (Schodde 1982, Rowley and Russell 1997, 2007). Phylogenetic analyses indicate that this reversed sexual dimorphism has most likely evolved via directional selection for shorter tails in nuptial males (Swaddle et al. 2000), but the signaling role and fitness consequences of this tail signal remain poorly understood. Males in brown plumage, conversely, develop tails similar to those of females during the breeding season and, therefore, have tails significantly longer than those of red-black males (Swaddle et al. 2000). In addition to extent of nuptial plumage and tail length, other ornaments such as song and spectral characteristics of plumage may also play a signaling role in this species, but are not considered in this paper.

We examined the signaling function of these two male sexual ornaments in the red-backed fairy-wren to address two inter-related questions. First, we examined the signaling function of reduced male tail length. Several authors have proposed an intraspecific signaling role for tails in red-backed and other fairy-wren species (Schodde 1982, Rowley

and Russell 1997, 2007, Swaddle et al. 2000), yet there have been no direct studies of this possibility. Second, we tested the multiple receiver hypothesis by examining the extent to which male nuptial plumage and tail length are signals directed to other males, to females, to both, or to neither. Although available evidence suggests that nuptial plumage is related to both mate choice and social dominance in male red-backed fairy-wrens (above), either of these findings may in fact be due to the inverse relationship between tail length and extent of nuptial plumage (i.e., red-black males have shorter tails than do brown males). Therefore, we used both aviary experiments and indices of female choice and social dominance from a natural population to separate the relative effects of these two signals.

Methods

Study species and field study

The red-backed fairy-wren is a small, cooperatively breeding Australian passerine. In the breeding season, most adult males adopt either bright red-black nuptial plumage or retain dull brown, female-like plumage; males with intermediate plumage are present but rare (Webster et al. 2008). Acquisition of nuptial plumage is flexible in this system (Karubian 2002), with some males molting into nuptial plumage a year or more earlier than other males. There is also variation in when males obtain their own breeding territory, with some males (who are nearly always brown) remaining as auxiliaries (helpers) on their natal territory for their first and subsequent potential breeding seasons (Rowley and Russell 1997). In our study population nearly all second-year males (i.e., in their second breeding season as an adult) develop red-black nuptial plumage and obtain their own breeding territory, and reversals of plumage type are very rare (Webster et al. 2008). The analyses presented in this paper are restricted to ‘red-black’ males with >67% nuptial plumage coverage on their body (see below).

Adults undergo a pre-alternate (pre-nuptial) body molt before or during the breeding season, and then a pre-basic (post-breeding) body molt at the end of the breeding season (J. Karubian unpubl. data). Most males and all females pass the winter in brown plumage and there is no difference in tail length between the sexes during this period (Swaddle et al. 2000). In the pre-breeding season molt, however, all adults grow a new tail and develop new plumage and it is only during the breeding season that sexual dimorphism exists in both the plumage coloration and tail length (Swaddle et al. 2000).

We studied a population of red-backed fairy-wrens breeding in open forests surrounding the Herberton Shire Reservoirs on the Atherton Tablelands in Queensland, Australia (145° 25'E, 17° 22'S). Birds in this population start breeding in the early rainy season (typically early Oct.) and continue breeding until the heavy cyclone rains begin (typically mid-Feb.). We monitored the breeding of this focal population for every breeding season from 1998–2000 and 2003–2006 (breeding seasons are designated by the year that breeding ended; i.e., the 1998 season began Oct. 1997 and extended to Feb. 1998). During each breeding

season we captured most adults and marked them with a unique combination of colored leg bands and an Australian Bird and Bat Banding Scheme (ABBBS) numbered aluminum band. We monitored the breeding activity of each group through daily observations of nesting behavior and by searching appropriate areas for nests. Nests were monitored by brief visits once every three d. When nestlings were approximately six days old we counted, banded, and measured them (body mass, tarsus), and collected a blood sample for genetic analyses. Date of the first nesting effort for each male was calculated relative to the first registered nest of that season, with laying d. of the first egg as our measure of nest initiation. Young were considered to have reached independence at approximately 50 d post-fledging, at which point they forage independently (J. Karubian, unpubl. data).

Each year we captured most or all adults on the study site. At the time of capture, we collected a small (ca. 20–50 μ l) blood sample for genetic analyses and measured several morphological traits, including tail length, tarsus length, volume of the cloacal protuberance (a sperm storage organ, Tuttle et al. 1996, Rowe and Pruett-Jones 2006), and body mass. Tails were measured from the base of the uropygial gland to the tip of the longest central tail feather using calipers (to 0.01 mm precision) and only birds with fully-grown complete tails were included in analyses. Age was determined precisely for birds banded as nestlings or juveniles or whose skulls were incompletely ossified, or calculated as a minimum age for birds that were already adults with fully ossified skulls the first time they were trapped. We also calculated an index of body condition (defined as size-corrected body mass) at time of capture by using the residuals of a linear regression of $\log(\text{body mass})$ on $3 \times \log(\text{tarsus length})$; Andersson et al. 2002).

To measure the extent of nuptial plumage displayed by each male we scored the proportion of the body that was covered in black or red versus dull brown plumage using the system described in Karubian (2002). Briefly, each bird's body was divided visually into 5 parts (head, back, belly, chest, tail) and each area was scored on a scale of 0–10 for the proportion of that area that was in red-black or brown plumage. These scores were then summed and multiplied by two to produce an overall plumage score ranging from 0 (completely covered in brown plumage) to 100 (completely covered in red or black plumage; see also Webster et al. 2008). It is important to note that the measure of plumage used in this study is not a direct measure of the spectral characteristics of the plumage ('color'), but is rather an index of the proportion of the body that is covered in red-black nuptial plumage.

Aviary experiments

Aviary experiments were conducted on-site in the 2000 breeding season using birds captured 3 to 15 km from the primary study site in qualitatively similar habitat. Each bird included in the experiments was measured and marked as described above. Only adult birds in breeding condition were used in the experiments and in no case was the same bird used in two replicates of the same experiment. Most birds were captured as family groups and housed as such in

aviaries. Family groups were kept in visual, but not acoustic, isolation from each other. 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 were provided with mealworms and water *ad libitum*, and were released at their point of capture at the end of the experiments. We employed a relatively small sample size in these trials as we wanted to minimize our effects on the breeding status of natural populations.

In our experimental design for aviary-based dominance and mate preference trials (below), we paired two males with full nuptial plumage and similar body mass, but one male possessed a shorter tail than the other. We adopted this protocol to minimize phenotypic differences between the two males other than tail length. The mean (\pm SE) within-trial tail length difference between long- and short-tailed males was 3.59 (\pm 0.43) mm. On average, long-tailed males possessed tails of 47.34 (\pm 0.64) mm and short-tailed males of 43.75 (\pm 0.58) mm. All males had plumage scores >93 on the scale from 0–100 described above, and the mean within-pair difference in plumage score was very small (0.31 ± 0.41 on the 100 point scale; paired t-test, $t = 0.76$, $n = 8$ pairs, $P = 0.472$). There was also no size difference between pairs of males (paired t-test of body mass, $t = 0.11$, $n = 8$ pairs, $P = 0.915$). We did not know the age of most of these males, and were therefore unable to control for age in the aviary trials.

Social dominance trials

Following 60 minutes of food deprivation, paired males were placed in a small wire cage ($0.3 \times 0.3 \times 0.4$ m) that consisted of two horizontal perches that spanned the width of the cage and two feeders at the front of the cage, one containing mealworms and the other water. Researchers hidden behind a blind recorded all dominance interactions (perch displacements, aggressive chases, and grabbing food out of bills) for each 15-minute trial (see Karubian et al. 2008 for more details). In most cases, observers knew the experimental category of each of the two males used in the experiment, but we had no a priori predictions at the time these experiments were conducted. We also recorded all displays and vocalizations by all birds in each trial, but these behaviors were too rare to permit statistical analyses. We determined which bird won each interaction, where a win was indicated by gaining access to the resource (i.e., the food, water, or perch) and/or the retreat of the other individual following a display. There was a clearly dominant bird in each trial (i.e., one bird always won nearly all interactions, see below), and on the basis of these interactions we assigned the dominant bird a value of "2" and the subordinate bird a value of "1" to analyze dominance scores. We analyzed the results of social dominance trials using two-tailed paired t-tests and non-parametric Friedman tests.

Female preference trials

We constructed a two-stimulus preference chamber (approx. $2 \times 0.6 \times 0.6$ m) out of wire mesh. The chamber consisted of a central compartment where the test bird was placed and two compartments at each side of the central

compartment where each of the stimulus birds were placed. The central compartment had two areas from which a test bird could view either stimulus bird and a neutral section in which the test bird could not see either stimulus bird (see Karubian 2002, Karubian and Alvarado 2003). For each trial, a single female test bird was released into the central section and one stimulus bird was released into each side compartment. We monitored (from behind a blind) the time spent viewing the stimulus birds and any display activity. Time spent foraging, preening, and bill-wiping was ignored. Each female test bird was pre-exposed to the choice chamber for 1 hr at least one day before preference trials commenced. In pre-exposure trials, food was placed at either end of the chamber, which encouraged the females to explore the cage. Females visited all sections of the choice chamber during pre-exposures. All females then experienced 1 hr preference trials in which one red-black male and one female were placed in the stimulus compartments to establish that females were making a sexual preference in these and subsequent preference trials. Immediately before the preference trials, the birds were placed in their compartments and allowed to acclimatize to the chamber for 10 min. We rotated the choice chamber through 180° 30 min into the trial and allowed the birds to acclimatize for a further 10 min. The day after male-female trials, we exposed the same test female to preference trials in which she could choose between two red-black males paired for tail length differences, as described above. We used the same method for recording test female preference as in previous trials. We used new test females, stimulus females, and stimulus red-black males in each trial so that all birds were naïve to each other.

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 one 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 female spent associating with one stimulus bird relative to the total time spent associating with both stimulus birds combined (i.e., stimulus bird 1/(stimulus bird 1 + stimulus bird 2)). After confirming that these data did not differ significantly from a normal distribution (Shapiro-Wilk Goodness-of-Fit test, $W = 0.91$, $P = 0.13$), we conducted two-tailed t-tests comparing the proportion of time associating with a given class of stimulus bird (females in the male-female trials and short tailed males in tail length trials) to a pre-determined mean of 0.5 (as expected under the null model of no preference). We also recorded all displays and vocalizations by all three birds in each trial, but these behaviors were too rare to permit statistical analyses.

Genetic analysis of paternity

We assessed paternity of all nestlings sampled using a panel of ten microsatellites as described in Webster et al. (2008). Briefly, we used standard PCR methods with labeled primers for separation in an ABI 3730 or 377 automated sequencers. Fragment sizes were calculated with GeneScan (1998–2000) or GeneMapper (2003–2005) software (Appl. Biosyst.), and verified by eye. All microsatellites used for

parentage analyses were highly polymorphic and informative for parentage analyses. The average probability of excluding a randomly chosen female as the mother (i.e., the probability that the female would not possess one of the offspring's alleles at the locus in question) was high, with a combined probability of exclusion of 0.996 for non-dams. Similarly, the combined probability of paternal exclusion for these loci (following Jamieson 1994) was 0.9999.

To assign the parentage of each nestling, we assumed that each breeding female was a biological parent of the nestlings in her own nest, and assessed the validity of this assumption by examining allele mismatches between females and nestlings. We used CERVUS 2.0 (Marshall et al. 1998) to select the male from the population who, based on genetic evidence, had the highest likelihood of being the sire and based our final designations of paternity using standard 'total evidence rules' (see Webster et al. 2008 for details). We used paternity results to calculate male reproductive success and its component parts for each male in the dataset. A male's annual within-pair reproductive success was the number of within-pair young that he produced – that is the number of young that he sired in the nest(s) of his social mate. A male's extra-pair reproductive success was defined as the total number of extra-pair young that he sired in the nests of other males within a year. Finally, the male's total reproductive success within a year was the sum of within-pair and extra-pair young that he sired.

Statistical analyses

Analyses are restricted to males with red-black plumage (nuptial plumage score >66%) because it is this subset of males that have reduced tails relative to females and brown males. In cases where we obtained multiple measures from the same individual within the same breeding season we used a single mean value per individual for that year. There was no relationship between tail length and body size ($r^2 = 0.004$, $P = 0.3$, $n = 278$ males), so we used tail length without attempting to correct for body size in our analyses.

Because age, extent of nuptial plumage, and tail length are inter-correlated in male red-backed fairy-wrens (Swaddle et al. 2000, Karubian 2002), we employed a general linear mixed model using residual maximum likelihood (REML, Patterson and Thompson 1971) to conduct F-tests for the effects of age, extent of nuptial plumage, and the interaction of the two on male tail length. Male identity was included as a random effect in this model to account for the fact that we had multiple years of data from some individuals. For these analyses, males of known age were grouped into two classes, one year of age or two years of age and older, and age was treated as a categorical variable. Other age classification schemes did not qualitatively change the outcome of this analysis.

We conducted count and ordinary least squares regression models to test the relative importance of extent of nuptial plumage, age, and tail length on seven response variables associated with mate choice and social dominance (see below). These analyses were conducted on 113 males for which we had relevant data for at least one year and we used cluster robust standard errors clustered on individual to account for the fact that some males had

more than one year's worth of data (Williams 2000). In these models, we used minimum (rather than exact) age as a categorical variable because we had data on exact age and response variables for a prohibitively small number of males. We used count models with negative binomial distributions to examine relationships between our three predictor variables and three direct measures of reproductive success: (1) number of within-pair young sired within a season, (2) number of extra-pair young sired within a season, and (3) the sum of these two measures, the total number of young sired within a season, because each of these response variables are count data that closely fit a negative binomial distribution. We calculated b , the unstandardized slope for each predictor variable on each response variable, as well as $\exp(Z_x)$, the factor change in the expected count of the response variable for one standard deviation (SD) change in the standardized predictor variable, Z_x (Long and Freese 2006). We used ordinary least squares regression models with post-hoc effect tests for each predictor variable on four indirect measures of reproductive success: date of first nesting attempt, average clutch size, total number of social young produced at the nesting stage, and number of social young surviving to independence. The term "social young" as we use it here differs from "number of within-pair young sired" (response variable 1 above) because "within-pair young" refers only those young that the male actually sired, whereas "number of social young" refers to all young produced in the nest of a given male and his social mate regardless of whether the young are sired by him or by an extra-pair male.

We chose these direct and indirect metrics of reproductive success for analysis because we consider it likely that they are associated with different components of sexual selection. Number of extra-pair young appears to be influenced primarily by mate choice in fairy-wrens (Double and Cockburn 2000). Conversely, date of first nesting attempt, clutch size, and numbers of social young produced and surviving to independence are likely to be influenced by male-male interactions because social dominance often affects access to resources which in turn may determine these parameters. We had no clear a priori predictions for the relationship between within-pair young sired and total number of young sired with either component of sexual selection. Analyses were conducted using JMP software (SAS Institute, Cary) and STATA software (STATA Corp., College Station) employing two-tailed tests of significance. Data are reported as means \pm 1 standard error (SE) unless otherwise stated.

Results

Tail length, plumage and age

Mean tail length among red-black breeding males was 46.66 ± 0.15 mm ($n = 281$ males, range 41.48–56.38). Mean plumage score for these males was 95.20 ± 0.42 (range 67–100). Among known-age red-black males ($n = 60$) tail length was strongly and negatively related to the extent of nuptial plumage: as extent of nuptial plumage increased, tail length decreased (Table 1). Tail length was also significantly negatively related to age, in that older

males developed shorter tails, though this relationship was not as strong as that between nuptial plumage and tail length. In this model, the interaction term of nuptial plumage-by-age was also significant. Calculating the effect size (i.e., the slope of the relationship, b) of extent of nuptial plumage on tail length within each age class revealed a much stronger relationship among males two years of age or older ($n = 44$, $b = -0.21$, $P < 0.001$) than among one-year-old males ($n = 16$, $b = -0.07$, $P = 0.09$; overall effect size averaged across all age classes: $b = -0.14$, $P < 0.001$). There was no relationship between our index of body condition (i.e., size-corrected body mass) and either tail length or extent of nuptial plumage across all red-black males or within age classes ($r^2 < 0.1$, $P > 0.2$ in all cases).

Aviary experiments

During the social dominance trials, we recorded an average of 6.0 ± 1.0 aggressive encounters (range 2–11) per 15-min trial, and we scored the winner in each of these encounters. In our paired experimental design, short-tailed males had significantly more wins than did long-tailed males (Fig. 1; paired t -test, $t_7 = 3.15$, $P = 0.02$). There was a clear dominant male in each trial (dominants were separated from subordinates by an average of 4.13 ± 0.52 wins per trial, range 2–6), and in all but one of the trials, short-tailed males were socially dominant over long-tailed males (Friedman $S_1 = 4.5$, $n = 8$ pairs, $P = 0.03$). In the female preference trials, test females showed a clear preference to associate with red-black males over females ($t_7 = 4.39$, $P = 0.003$; Fig. 2a). In contrast, there was no difference in amount of time test females spent with long-tailed vs. short-tailed males ($t_7 = 0.08$, $P = 0.94$; Fig. 2b).

Field data

Plumage, age, and tail length were each related to at least one direct measure of reproductive success (Table 2). Extent of nuptial plumage was significantly related to total number of young sired within a year. Partitioning overall reproductive success into within-pair and extra-pair components reveals that this relationship was driven by a strong positive relationship between extent of nuptial plumage and number of extra-pair offspring; there was no relationship between extent of nuptial plumage and number of within-pair offspring produced. Age was also positively associated with number of total young sired. This relationship was driven by equivalent weak positive relationships between age and the number of within-pair and extra-pair young

Table 1. Effect tests from a general linear mixed model with extent of nuptial plumage, age, and an interaction term of plumage \times age as predictor variables, tail length as the response variable, and male identity as a random effect. Nuptial plumage and age were both significantly and negatively related to tail length; the interaction term of plumage \times age was also significant.

	F (df)	P value
Plumage	19.6 (1, 47.3)	<0.001
Age	4.27 (1, 26.3)	0.048
Plumage \times age interaction	5.44 (1, 44.4)	0.024

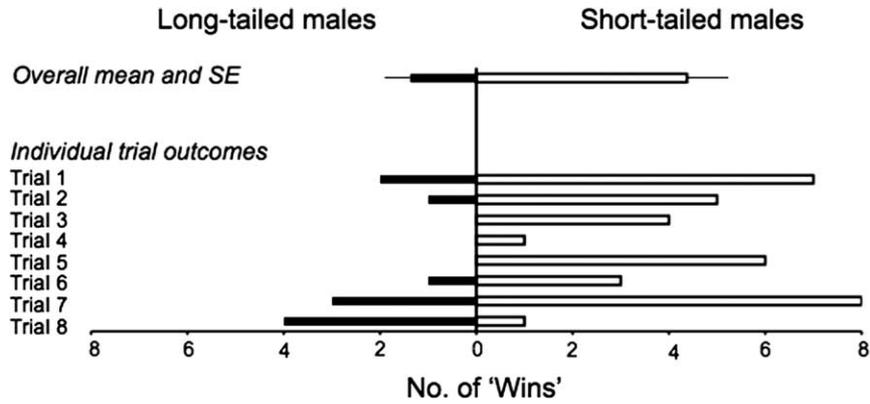


Figure 1. Shorter-tailed red-backed fairy-wren males are socially dominant to longer-tailed males. Shown are the results of aviary-based social dominance trials between pairs of males matched for similar body size and extent of nuptial plumage but exhibiting large differences in tail length. Black bars represent relatively longer-tailed males and white bars represent shorter-tailed males; the top bars represent the average of all 8 trials (\pm SE), and each of the bars below represent the outcome of an individual trial. Shorter-tailed males were clearly dominant to longer-tailed males in 7 of the 8 trials.

sired (Table 2). Therefore, age does not appear to skew components of male fitness between within-pair or extra-pair productivity. Although male tail length was not noticeably related to total number of offspring sired, tail length was associated with the number of extra-pair young sired, but in the direction opposite to that which we predicted: males with longer tails sired more extra-pair young.

A qualitatively different pattern emerged between these predictor variables and four indirect indices of social dominance (Table 3). Male tail length was negatively related to clutch size such that short-tailed males were paired to females who laid larger clutches (effect size $b = -0.11$). There also were also non-significant trends toward shorter-tailed males producing higher numbers of social young ($b = -0.12$) and surviving young ($b = -0.11$) that

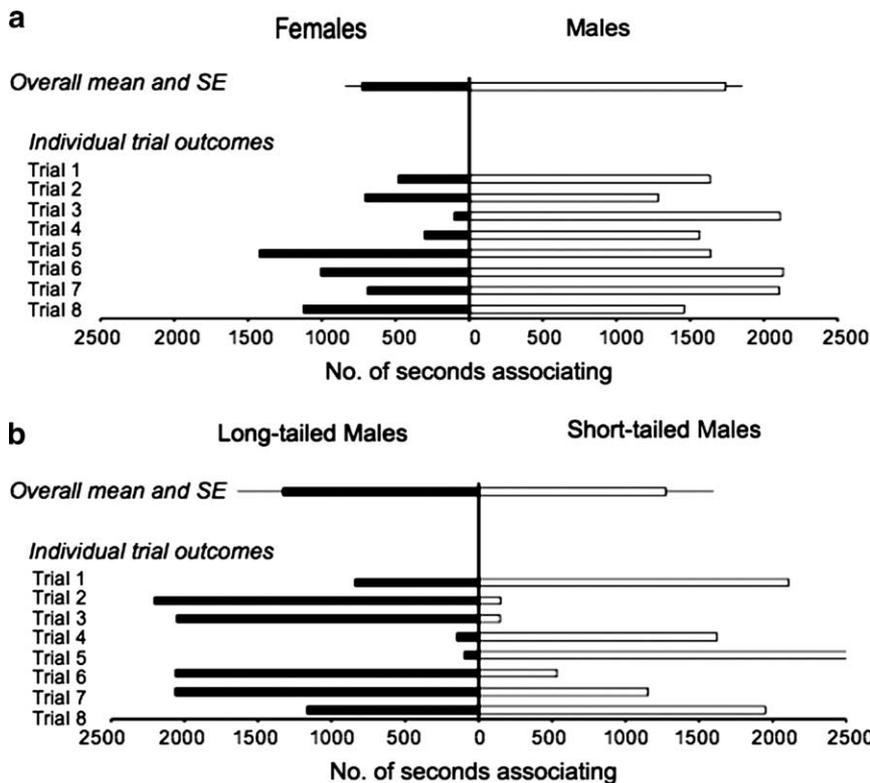


Figure 2. Results of aviary-based female mate choice trials. Panel 'a' shows results of trials in which a female in breeding condition was given a choice between an adult female and an adult male. Panel 'b' shows results of trials in which the same females were given a choice between two adult male red-backed fairy-wrens that were similar in body size and plumage but exhibited large differences in tail length. In each of the two panels, the top bars represent the average of all 8 replicates of a given type of trial (\pm SE), and each of the bars below represent the outcome of an individual trial, with stimulus birds labeled beside their corresponding bars. Females exhibited a strong preference for stimulus males over stimulus females (a), but no discernible preference in relation to tail length (b).

Table 2. Effects of nuptial plumage, age and tail length on three direct measures of reproductive success in male red-backed fairy-wrens. Count model Z scores and corresponding P values are provided, along with the unstandardized slope coefficients (b) for each predictor variable and the factor change in the expected count of the response variable for a 1 SD increase in the predictor variable ($\exp(Z_{x_i})$). Extent of nuptial plumage was positively related to number of extra-pair young and total number of young sired; age was positively related to total number of young and non-significantly related to both extra-pair and with-in pair young, and tail length was positively related to number of extra-pair young. Bold font highlights results at $P < 0.05$.

	Overall Model χ^2 value (df), P	Plumage Z, P (b, $\exp(Z_{\text{plumage}})$)	Age Z, P (b, $\exp(Z_{\text{age}})$)	Tail Z, P (b, $\exp(Z_{\text{tail}})$)
Within-pair young	7.07 (94), 0.07	1.04, 0.30 (0.03, 1.03)	1.80, 0.07 (0.30, 1.35)	-0.44, 0.66 (-0.02, 0.95)
Extra-pair young	20.05 (94), <0.001	3.07, 0.002 (0.14, 1.80)	1.95, 0.052 (0.45, 1.42)	2.42, 0.015 (0.17, 1.48)
Total sired	19.23 (94), <0.001	2.91, 0.004 (0.08, 1.40)	2.69, 0.007 (0.35, 1.32)	1.41, 0.16 (0.06, 1.16)

may or may not have been their genetic offspring. There were no noticeable relationships between extent of red-black plumage or age with any of these indirect measures of social dominance.

Discussion

In this study we examined the relative signaling roles of extent of nuptial plumage and tail length in male red-backed fairy-wrens while controlling for age. Our objective was to independently assess how each of these traits affects elements of mating and reproductive success from a natural population. Extent of nuptial plumage was significantly and positively associated with the number of extra-pair young a male sired within a season, which contributed to males with more nuptial plumage having higher total reproductive success. This finding is consistent with previous work which showed that red-black males sired more young than did brown males (Webster et al. 2008). Because the present study is restricted only to those males with >66% of the body covered in nuptial plumage, it suggests that even among red-black males increased nuptial plumage is associated with increased reproductive success via extra-pair paternity. Because female fairy-wrens are likely to exercise considerable control in choice of reproductive partners (Double and Cockburn 2000), we hypothesize that red-black nuptial plumage may make males more attractive to females as extra-pair mates, and/or indicate males that have an advantage in sperm competition, thereby increasing extra-pair aspects of mating success.

We also found that age was significantly related to overall reproductive success, with significant or near-significant effects on both the number of within-pair and extra-pair young produced (see also Webster et al. 2008). It is also notable that age, unlike plumage, influences both within-pair and extra-pair reproductive success, suggesting that age may contribute to male mating success by additive effects associated with mate choice and mate guarding. However, the effect of plumage on extra-pair young is stronger than that of age (Table 2), corroborating the basic

conclusion of previous studies that plumage likely plays a primary role in mate choice in this species (Karubian 2002, Webster et al 2008).

There were a priori reasons to expect that shorter tail length might also be involved in male-female interactions (i.e., mate choice). Shorter tails are exhibited only by red-black males during the breeding season and phylogenetic analyses suggest that this trait reduction has evolved via directional selection in males but not females, all of which is consistent with a mate attraction role for reduced tail length (Swaddle et al. 2000). For example, reduced tail length could act as a flight performance handicap that allows females to better assess male quality, similar to the situation in the golden-headed cisticola *Cisticola exilis* (Balmford et al. 2000). In the case of the red-backed fairy-wren, this might take place when males engage in the “puffback” display, in which they erect the red feathers on their back and sometimes hold their tail flat behind them while flying and vocalizing (Schodde 1982). Also, red-black males frequently depart their territories to intrude on neighboring groups with fertile females and solicit extra-pair copulations, whereas females and brown males do not (Karubian 2002). Hence, flight costs may enforce honesty on a tail length signal, with only the most energetically efficient individuals being able to carry the cost of a short tail (Zahavi 1975, 1977).

Contrary to these predictions, however, we found that males with longer tails, not shorter tails, acquired more extra-pair matings. The aviary-based female preference experiments failed to uncover any effect of tail length on male attractiveness. This lack of a significant result could be due to relatively small sample sizes employed in the trials (though no trends were discernable in the trials we did conduct), or to the fact that we did not control for male age in these trials, or to shortcomings inherent with aviary-based mate choice trials. However, previous experiments using a similar protocol (Karubian 2002) demonstrate a behavioral preference by females for males in red-black nuptial plumage over those in brown plumage, consistent with field measures of male extra-pair success (Webster et al. 2008). Similarly, in the pre-trial portion of our experiments

Table 3. Effects of extent of nuptial plumage, age and tail length on four indirect indices of social dominance. Results of effects tests with t values and corresponding P value are shown from separate linear regression models for each outcome variable. Shorter tails were associated with increased clutch sizes. Bold font highlights test results at $P < 0.05$.

Variable	Plumage t (df), P	Age t (df), P	Tail t (df), P
Lay date	0.71 (1,68), 0.48	-1.14 (2,64), 0.26	-0.27 (1,44), 0.79
Clutch size	-1.49 (1,39), 0.15	0.69 (2,20), 0.50	-2.65 (1,39), 0.01
No. social young	-0.18 (1,108), 0.86	0.58 (2,66), 0.56	-1.04 (1,104), 0.30
Surviving young	1.37 (1,76), 0.18	-0.27 (2,68), 0.80	-1.73 (1,73), 0.09

females associated preferentially with males over females. Therefore, based on the combined results of the field data and aviary trials, it seems reasonable to conclude that there is no extra-pair mating advantage associated with shorter tails (we return to the possibility that longer tails may confer an extra-pair mating advantage below).

Instead, our aviary and field studies suggest that tails are primarily involved in male-male interactions. In our experimental trials featuring pairs of males matched for similar body size and extent of nuptial plumage, shorter-tailed males were clearly dominant to longer-tailed males. This suggests that shorter tails may confer a competitive advantage in access to resources. We did not know the age of most males used in these experiments, so it is also possible that the dominance exhibited by shorter-tailed males results from age-related superior competitive ability rather than tail length per se. However, we were able to control for age (and plumage) in our analyses of field data from a natural population, and these tests therefore provide insights into the relationship of tail length per se with our indirect indices of social dominance. We found that nests of shorter-tailed males had significantly larger clutch sizes independent of age and plumage, which would be expected if shorter tails were associated with better access to resources. Relationships between tail length and two other indirect indices of social dominance – number of social young and number of young surviving to independence – were not statistically significant but were also in the predicted direction and had a similar effect size. In these same models, neither age nor plumage were significantly related to any of our indirect indices of social dominance, which is consistent with the idea that tail length, or some unmeasured trait correlated with it, signals intra-sexual social dominance in this species.

Based on the data presented here, therefore, it seems likely that increased extent of nuptial plumage (or unmeasured variables associated with it) is associated primarily with mate choice and that shorter tail length (or unmeasured variables associated with it) is associated primarily with social dominance. In nature, both traits are related to each other and to age: males with more red-black plumage tend to have shorter tails and are older individuals. Therefore, in addition to its' primary signaling role, each trait may also have secondary communication functions. For example, previous experiments have shown that red-black males are socially dominant to brown males (Karubian et al. 2008), suggesting that nuptial plumage is also related to social dominance. However, this pattern may exist, in part, because the expression of red-black plumage is related to tail length and age. Therefore, although we have taken statistical care to partition the relative effects of red-black plumage, tail length, and age from each other we advocate factorial experimental approaches to study the function of potential signaling traits in multiply ornamented species. To this end, we have devised ways in which to effectively manipulate tail length and are exploring ways to realistically manipulate plumage color with the aim of altering these traits in a factorial manner in birds of known age to disentangle the relative roles of the multiple traits on breeding and mating parameters.

Our findings that nuptial plumage and tail length, or unmeasured traits correlated with them, signal information to different but potentially overlapping groups of receivers are consistent with the multiple receiver hypothesis (though they do not exclude the multiple messages or redundancy hypotheses, as these hypotheses do not need to be mutually exclusive). As such, this study concurs with other tests of the multiple receiver hypothesis conducted in the red-collared widowbird (Andersson et al. 2002), the peacock *Pavo cristatus* (Loyau et al. 2005), and the common yellowthroat *Geothlypis trichas* (Tarof et al. 2005). Taken as a whole, these studies suggest that the multiple receiver hypothesis may be a relatively widespread explanation for multiple male ornaments. As sexual selection will be manifest in terms of the net selection acting on both traits, it is perhaps not surprising that there is a natural positive relationship between the favored states of these traits (i.e., those with the greatest extent of red-black plumage have the shortest tails).

We suggest that reduced tail length may function as a badge of social status, with shorter tails signaling dominance. When a dominance cue is not particularly costly to produce and is not causally linked to competitive ability, trait values may be determined by the high social cost incurred by cheating (Rohwer 1975, van Dongen and Mulder 2007). We propose that one-year old red-black males may invest heavily in production of nuptial plumage used for mate attraction but may not develop shorter tails because of these potential costs. As they become older and their social dominance presumably increases, males may develop shorter tails that accurately reflect their intrasexual dominance. This hypothesis is consistent with our findings to date, but requires further testing.

Another question requiring further study concerns the non-breeding season, when most males molt into brown plumage with long tails (a small proportion of older males molt into red-black plumage with short tails). Presumably, dominance signaling would also be valuable all year round, and if reduced tail length plays a role in male:male signaling why is it restricted only to the breeding season? In this sedentary species, the increased resources available in the breeding season (i.e., the availability of mates) and the increased competitiveness among males associated with these resources (i.e., breeding site territoriality) may result in the expression of this putative badge of status only during the breeding season. Outside of the breeding season, either the costs of falsely advertising social dominance or the need to advertise dominance through development and maintenance of a sexual ornament may be sufficiently low that the badge is not expressed in the same manner when males are not breeding. The present study was not designed to address such issues, but we hypothesize that social dominance may have greater influence on individual fitness during breeding than during the non-breeding season.

Overall, we conclude that red-black male red-backed fairy-wrens possess at least two sexually-selected traits that convey information to different receivers. Extent of nuptial plumage appears to reveal important information to conspecific females and influences elements of reproductive success, especially extra-pair paternity, that are primarily influenced by female choice mechanisms. In contrast, tail length appears to function primarily in

male-male competition mechanisms, with shorter-tailed males being socially dominant to those with longer tails. Intriguingly, longer tailed males may be somewhat preferred by females as extra-pair partners. Hence, tail length may play contrasting signaling roles for different receivers, setting up the possibility of selection on tail length creating conflict between males and females (Rice and Chippendale 2001): male competition mechanisms may result in selection for shorter tails which may be somewhat opposed by seemingly weaker selection imposed by females for longer tailed extra-pair mates. Overall, it appears that males develop these separate traits (red-back plumage and tail length) for different but potentially overlapping audiences, generally supporting the multiple receiver hypothesis and also further demonstrating the complex multivariate manner in which sexual selection operates under natural conditions.

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