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ORIGINAL ARTICLE

David J. Green · Helen L. Osmond
Michael C. Double · Andrew Cockburn

Display rate by male fairy-wrens (*Malurus cyaneus*) during the fertile period of females has little influence on extra-pair mate choice

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Abstract Empirical and theoretical studies have only recently begun to examine how females use complex multi-component displays when selecting mates. Superb fairy-wrens are well suited to the study of female choice because females have control over extra-group paternity and cuckold their mates at high rates, while males possess a variety of sexually selected traits. Available evidence suggests that females base their extra-group mate choice on the timing of male moult into breeding plumage or the onset of display. However, males continue to perform elaborate displays throughout the season, and direct most displays to females during their fertile period. We therefore conducted focal observations on fertile females to quantify the frequency of male display and used microsatellite genotyping to compare the role of display rate during the breeding season and the timing of male moult on female mate choice. We show that the addition of data on male display rate does not improve our ability to predict which males obtain extra-group paternity. The timing of male moult into breeding plumage remains the only predictor of male extra-group reproductive success. Nevertheless, we found that males displayed more to females that were unable to select extra-group mates on the basis of the timing of moult or the onset of display. This raises the possibility that there are circumstances when females use display rate to discriminate between potential extra-group sires. Overall this study supports the theoretical prediction that females are more likely to base their mate choice on reliable indicators of male quality such as fixed morphological traits and displays of endurance, in this case an early moult into breeding plumage and the performance of an elaborate display during the winter, than a flexible behavioural trait such as display rate during the breeding season.

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D.J. Green · H.L. Osmond · M.C. Double · A. Cockburn (✉)
Evolutionary Ecology Group, Division of Botany and Zoology,
Australian National University, Canberra, ACT 0200, Australia
e-mail: andrew.cockburn@anu.edu.au
Tel.: +61-2-62493727, Fax: +61-2-62495573

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Introduction

Females often exhibit strong preferences for males with exaggerated male ornaments and complex courtship displays (Andersson 1994). Formal models and empirical studies suggest that female preferences for these traits are likely to provide females with reliable information about the quality of the male, because only superior males in good condition can afford to employ them (Grafen 1990; Andersson 1994; Johnstone 1995a). Early models, and the majority of empirical studies, have chosen to focus on female choice for a single male trait such as tail length or plumage coloration in birds. However, males often possess more than one ornamental or display trait. Only recently have empirical and theoretical studies begun to examine how females could use complex multi-component displays to compare the relative quality of different males (Sullivan 1994; Johnstone 1995b; Buchanan and Catchpole 1997; Kokko et al. 1999).

A female's ability to assess potential mates is likely to vary with both the time available for assessment and the nature of the traits evaluated (Sullivan 1994). Fixed morphological traits may be assessed quickly, whereas behavioural traits, which can vary with social circumstances (e.g. Green et al. 1995), or current environmental conditions (e.g. Gottlander 1987), may need to be sampled repeatedly to obtain an accurate assessment of male quality (Sullivan 1994). Females may therefore be predicted to pay more attention to fixed morphological cues than to flexible behavioural traits (Møller et al. 1998). In contrast to this prediction, a meta-analysis of mating success among lekking species suggested that behavioural traits were of greater importance than morphological traits in explaining female mate choice (Fiske et al. 1998).

Superb fairy-wrens, *Malurus cyaneus*, are well suited to the study of mate assessment and female choice for several reasons. Females have control over extra-group paternity (Dunn and Cockburn 1999; Double and Cockburn 2000) and cuckold their mates at extremely high rates (Mulder et al. 1994). Males possess a variety of potentially sexually selected traits. These include a dramatic blue and black breeding plumage (Rowley 1965), an elaborate courtship display directed to females from outside their social group (Mulder 1997), and a stereotyped song that may signal male quality over large distances (Langmore and Mulder 1992). Available evidence suggests that female fairy-wrens choose extra-group mates principally on the basis of the timing of male moult into breeding plumage, as extra-pair fertilisations are obtained largely by males that moult months before the onset of the breeding season (Mulder and Magrath 1994; Dunn and Cockburn 1999). However, display during the breeding season may also be important, as male display rate during the period of female fertility is highest when they are unencumbered by parental care, and this may allow them to sire a disproportionate number of extra-group young (Green et al. 1995).

In this paper, we investigate the factors affecting male extra-group display rate, examine the relationship between the timing of male moult into breeding plumage and male display, and use microsatellite genotyping to evaluate the relative importance of the timing of moult and the instantaneous level of display for female mate choice.

Methods

Study species and general methods

We have studied a colour-banded population of superb fairy-wrens in and adjacent to the Australian National Botanic Gardens in Canberra, Australia since 1988. Our study area includes approximately 85 territories. Each territory is occupied throughout the year and is maintained by a socially monogamous pair, but on about 60% of territories in any year, the pair are assisted by from one to four helper males. Males are extremely philopatric and are usually recruited into the breeding population on the territory in which they are born. The oldest male is behaviourally dominant over all other males on the territory, and most males achieve dominance by queuing. However, some males disperse to neighbouring territories when the female on that territory loses a mate but lacks helpers that could inherit the vacancy (Mulder 1995). Regardless of their social status, males are capable of breeding at 1 year of age when they develop adult plumage (Mulder and Magrath 1994), fully sized cloacal protuberances (Mulder and Cockburn 1993) and the ability to fertilize females (Dunn and Cockburn 1999). By contrast, females are forced to leave their natal territory to find a breeding vacancy. Juvenile females disperse in two discrete stages (Mulder 1995). Early dispersal occurs at the end of the breeding season, while late dispersal takes place shortly before the following breeding season. Early dispersers often settle with groups that already contain a female, and are forced to disperse for a second time unless they inherit the territory following the death of the resident female, or split the territory by pairing with a helper.

Female fairy-wrens cuckold their mates at extremely high rates (76% of nestlings, 95% of broods; Mulder et al. 1994). Females control extra-group fertilisations, which are obtained only by extra-group males visited by females during pre-dawn extra-territorial forays (Double and Cockburn 2000).

Male fairy-wrens have a brilliant blue and black plumage during the breeding season but usually moult into a brown female-like plumage in winter (Rowley 1965). There is little apparent variation between males in the intensity or extent of the breeding plumage (Mulder and Magrath 1994). However, the timing of the moult into breeding plumage is extremely variable and can take place at any time from March until November. Moult may occur months before the first females become fertile in early September. Individual males moult progressively earlier each year until they reach 5 years of age (Mulder and Magrath 1994; Dunn and Cockburn 1999). During the course of this study, we recorded the plumage status of all males on a five-point scale during censuses at intervals of a week or less (1=no evidence of breeding plumage, 2=25% or less, 3=26–50%, 4=51–75% and 5=100% breeding plumage). The date that moult started and finished was determined from direct observation of the first blue feathers to appear and last brown feathers to be lost, or more rarely for birds first detected in heavy moult, by back-estimation using the average number of days males spend in each moult category (estimated separately for each age class; Mulder and Magrath 1994). We also used weekly censuses and daily visits to territories during the breeding season to determine the composition and social relationships within groups, to locate nests, and to monitor reproduction. We categorised groups into three classes at the start of each breeding season: (1) pairs, (2) groups with one helper, and (3) groups with two or more helpers. Within groups we classified males as being either dominant or a helper.

Extra-group display

Male fairy-wrens perform dramatic courtship displays directed towards extra-group females during frequent intrusions into the territories of neighbouring males (Rowley and Russell 1990; Mulder 1997). Males typically fan their cheek feathers, lower their tail, and flatten their body, before twisting it from one side to the other in front of the female to display their contrasting blue and black breeding plumage. Throughout the study, we collected opportunistic data on intrusions and extra-group displays performed during both the breeding and non-breeding season. We noted the identity of any male seen away from his own territory, the response of the female and her mate to the intruder, and determined whether the intruding male displayed before departing the territory.

Focal observations

To quantify extra-group display we conducted focal watches on females in 24 contiguous territories in the centre of the study area between 19 September 1995 and 9 January 1996. This sample included ten females that were living in a pair, nine from groups with one helper, and five from groups with two or more helpers. We attempted to watch females on five consecutive days prior to the initiation of two separate nesting attempts, one early and one late in the season. We observed each female for 30 min with watches being conducted both in the morning (0900–1200 hours) and afternoon (1400–1700 hours). The time that the first watch of a series was conducted was randomly determined and subsequent watches usually alternated between the morning and afternoon. We did not conduct watches in the rain. During focal watches, we followed the female and noted the identity of any extra-group males that entered the territory, whether they displayed to the female and the response of the female and her mate to the intrusion.

First-year female fairy-wrens vary in the amount of information they have about when males in their local area moult into breeding plumage. Females that disperse early and arrive in the study area in the autumn are able to obtain information on when males complete their moult before breeding for the first time. In this paper, we refer to these females as being “informed”. However, females that disperse late and only arrive in the study area shortly before they attempt to breed for the first time lack access to information on when particular males moult. We refer to these females as “naive”. Though first-year females are thus of particular interest, a severe drought restricted reproduction in 1994. Therefore, few birds of either sex were recruited in 1995 and first-year females were unfortunately under-represented in our sample (2 of 24). We therefore conducted additional focal watches on five informed and three naive first-year females in 1998, using the same protocol as in 1995, to determine if males display more to females that are unable to use the timing of moult as a cue when choosing an extra-pair mate.

Paternity assignment

We used microsatellite genotyping to assign paternity to nestling fairy-wrens produced by females that had been the subject of focal observations in 1995 and 1998. Between five and eight hypervariable microsatellite loci were amplified for each nestling (Double et al. 1997) and run on an ABI377 sequencer (Perkin-Elmer). Internal size standards were run with all PCR products and allele sizes were determined using Genescan 2.1 (Perkin-Elmer).

For each offspring, the paternal alleles were identified by comparison with the maternal genotype. A database of genotypes was searched for males that possessed all the paternal alleles found in the offspring. The database included all males within the study population in 1995, and all males observed to display to focal females in 1998. To reduce the probability of false exclusion through mutation, allele sizes within two base pairs were considered identical. In the rare circumstances that more than one adult male matched the genotype of the chick, paternity was assigned based on parsimony; males in which no mutation was required to assign paternity were preferred to males in which one or more single-step mutations had to be assumed.

Statistical analysis

We used a modelling approach to statistical analysis. Mixed models were used to examine which factors influenced the timing and frequency of display directed at females, and variation in male display rates, as our data included focal females that were observed multiple times, and individual males that were expected to display to a number of different focal females (Bennington and Thayne 1994). Female identity, or female and male identity, were included as random factors in these models. For analysis of extra-group fertilisation success, where birds were represented only once in a data set, we used multiple logistic regression. In all analyses, the assumptions of the models were confirmed using residual plots and normal probability plots to test for unequal variance and deviations from normality among residuals.

Models 1 and 2: variation in intrusion rate and extra-group display prior to egg laying

We first determined whether the time of day (morning or afternoon), season (Julian date), or the number of days remaining until laying of the first egg had an effect on intrusion rates. We conducted focal watches from 14 days before laying (–14) until the day of the first egg (0), but for analyses, this variable was split into eight 2-day categories starting a fortnight prior to clutch initiation. The number of intrusions observed during a focal watch was binomially distributed with no intruding male being observed in 45% of observations (n=310). We therefore examined variation in whether or not an intruding male was observed using the generalised linear mixed model (GLMM) procedure in Genstat v 5.3 (Genstat 1993) where female identity was fitted as a random effect. We initially fitted a full model containing all three explanatory variables and their interaction terms. A final model was selected by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained. To avoid any confounding effects of deletion order, any term that was close to significant (P<0.2) was re-evaluated by adding and dropping it from the final model. We subsequently used the same approach to determine whether the probability that an intruding male actually performed a display to the female in the focal territory was influenced by the time of day (morning or afternoon), season (Julian date) or the number of days remaining until the laying of the first egg.

Models 3 and 4: female traits and display

We next examined the effect of female age, the number of helpers (0, 1 or 2+), the age or moult date of her mate, and the amount of information females had on male moult (naive or informed) on the probability that we observed a display during a focal watch. We fitted separate mixed models to the data collected in 1995 and 1998 because the age structure of females in the two samples differed; females varied in age from 1 to 7 years in 1995, but were all 1 year of age in 1998. In both models, we only used focal watches conducted between 1–8 days prior to the laying of the first egg, as the initial analysis of our data suggested that females were most likely to be the target of a display during this period (see below). We also included the time of day as an additional response variable to control for significant daily variation in display. Once again, female identity was included as a random effect, and final models were selected by progressively eliminating non-significant terms from a full model that included all fixed effects and interaction terms.

Model 5: male traits and display

We examined the effect that male age, male size (tarsus length), the date males completed their moult into breeding plumage (1 April=1), male group size (pair, 1 helper, 2+ helpers), parental duties (presence/absence of nestlings or fledglings), proximity to focal female (1 or 2 territories) and Julian date had on whether a male was observed to display to a focal female. The 32 males included in this analysis were the dominant males from either the 24 contiguous territories sampled in 1995 or close enough to the centre of the study area that the male was within 2 territories of at least 5 of these focal territories. We included both male and female identity as random effects in the mixed model. We also included the time that the focal watch was conducted and the number of helpers in a female’s territory as fixed effects to control for female traits that had a significant effect on whether a display was observed (see below). We again first fitted a full model with all response variables and possible interaction terms and progressively eliminated non-significant interactions and then non-significant main effects to derive a parsimonious model containing only significant terms.

Model 6: male traits and extra-group paternity

The main difference among males in terms of extra-group fertilisation success was whether they gained any paternity, rather than the number of fertilisations. We therefore analysed whether males obtained at least one extra-group fertilisation using logistic regression (see also Dunn and Cockburn 1999). We included both dominant males and helpers from the 24 territories where we had conducted focal watches in this analysis in order to be consistent with a previous analysis of extra-group fertilisation success in fairy-wrens (Dunn and Cockburn 1999). We examined the effect of five male traits on extra-group fertilisation success: age, social status, social group size, number of days during the breeding season when the male was committed to care of nestlings or fledglings, and display rate. Display rate was estimated by dividing the number of times that a male was observed to display during focal watches, conducted between 1 and 8 days prior to egg laying, by the number of focal watches performed within a two-territory radius of his own. We again selected a final model by progressively eliminating non-significant terms from a full model that included all fixed effects and interaction terms.

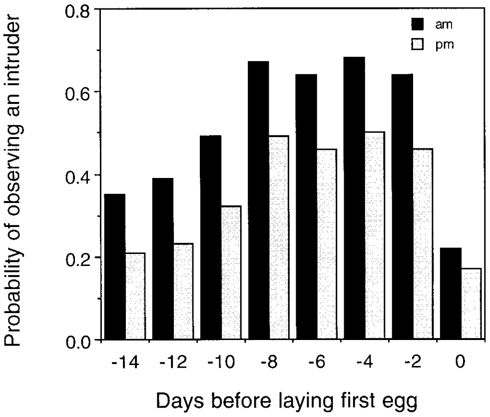

Fig. 1 Relationship between the number of days until an egg was laid and the probability that we observed at least one intrusion by an extra-group male per 30-min observation conducted during either the morning or afternoon. Data are grouped into 2-day periods starting 14 days prior to the laying of the first egg. *Bars* show model predictions. The model is based on data from 32 females and 310 focal watches conducted between 14 days prior to egg laying and the day that the first egg was laid in 1995 and 1998

Results

Focal observations and display

We conducted 310 focal watches between 14 days prior to egg laying and the day that the first egg was laid (1995: *n*=255; 1998: *n*=55). We watched a total of 32 females (1995: *n*=24; 1998: *n*=8), with females being observed for their fertile period preceding one to four clutches (mean±SE=2.1±0.2).

We observed a total of 341 intrusions during the focal observations. All were by males in full breeding plumage. The majority of intrusions (73%) resulted in a display, which could last for as long as 30 s, directed at the female resident on the territory. Intruding males occasionally carried a yellow petal that they used to augment subsequent displays (7% of all intrusions). The intruder was usually able to display without interruption or eviction by the dominant male (78% of cases, *n*=249).

Table 1 Model summaries for mixed models

Final model	Random factors	Term dropped	Wald χ^2	*df*	*P*-value
Model 1: probability of an intruder being observed during a focal observation					
Time until egg laid+time of day	Female	Time until egg laid	14.4	7	**0.04**
		Time of day	8.0	1	**0.005**
		Julian date	0.1	1	0.75
Model 2: probability that a display occurs if an intruder is observed					
–	Female	Time until egg laid	2.8	7	0.90
		Time of day	2.4	1	0.12
		Julian date	2.6	1	0.11
Model 3: probability that a female elicits a display during the fertile period in 1995					
Group size+time of day	Female	Group size	7.0	2	**0.03**
		Time of day	4.1	1	**0.04**
		Female age	1.5	2	0.47
		Male age	0.5	2	0.78
		Male moult date	2.3	1	0.13
		Julian date	0.0	1	1.00
Model 4: probability that a first-year female elicits a display during the fertile period in 1998					
Information+group size+time of day	Female	Information	5.0	1	**0.03**
		Group size	9.5	2	**0.01**
		Time of day	4.0	1	**0.04**
		Male age	0.1	2	0.95
		Male moult date	0.2	1	0.65
		Julian date	0.1	1	0.75
Model 5: probability that a male displays to a fertile female in any territory within a radius of two					
Distance+time of day+focal group size	Male+female	Distance	36.6	1	**<0.001**
		Time of day	7.4	1	**0.01**
		Focal group size	2.8	2	0.25
		Male age	2.6	2	0.27
		Male size	1.2	1	0.27
		Male moult date	2.1	1	0.15
		Male group size	0.6	2	0.74
		Care	0.1	1	0.75
		Julian date	0.1	1	0.75

Timing of intrusions and frequency of displays

The probability that we observed an intrusion during a focal watch peaked 8 days prior to the laying of the first egg and dropped just before the first egg was laid (Fig. 1, Table 1). Intrusions were also more frequent in the morning than the afternoon regardless of the number of days remaining until an egg was laid (Fig. 1, Table 1). The probability of observing an intruder did not change through the season (Table 1).

The probability that an intruding male was observed to display to a focal female before departing the territory did not change significantly as the number of days until the first egg was laid decreased (Table 1). There were also no diurnal or seasonal effects on the probability that an intrusion resulted in a display (Table 1).

Do female traits influence male display?

In both 1995 and 1998, displays were more likely to be observed during a focal watch if the female lived in a large group than in a pair or group with one helper (Fig. 2, Table 1). Displays were also more likely to be observed in the morning than the afternoon in both years (Table 1). In 1998, we were also more likely to observe a display when watching naive females that had no information on when males completed their moult into breeding plumage (Fig. 3, Table 1). In contrast, we found that female age, the age of her mate, the moult date of her mate, and the date that the watch was conducted all had no effect on whether a display was observed in either year (Table 1).

Display and male moult date

The date that males were first seen to display in 1995 was strongly correlated with the date that they completed their moult into breeding plumage in that year (Fig. 4; r=0.92, n=32, P<0.0001). Males were never observed to display before completing their moult but several males were seen displaying in the week immediately after their moult was completed (Fig. 4). We suspect that all males begin to display immediately after completing their moult.

In contrast, we found that early moulting males were no more likely to display to females during focal watches than males that had moulted late (Fig. 5, Table 1). However, we were four times more likely to observe a display by neighbouring males than males living two ter-

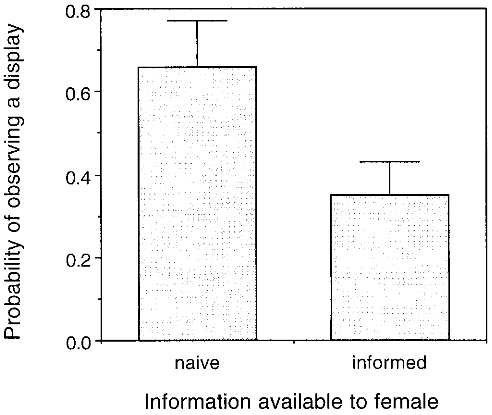

Fig. 3 Relationship between the amount of information available to first-year females concerning the timing of male moult into breeding plumage and the probability that we observed at least one display per 30-min observation period. *Bars* show model predictions (±SE) controlling for the effect of the time focal observations were conducted and the number of helpers in a female's social group. The model is based on data from 7 females and 48 focal observations conducted over the 8 days before the first egg was laid in 1998

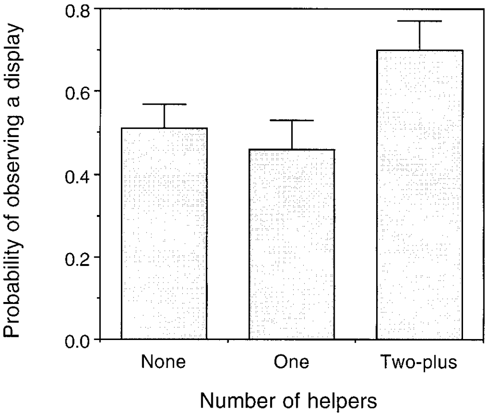

Fig. 2 Relationship between the number of helpers in a female's social group and the probability that we observed at least one display per 30-min observation period. *Bars* show model predictions (±SE) controlling for the effect of the time at which focal observations were conducted. The model is based on data from 24 females and 218 focal observations conducted over the 8 days before the first egg was laid in 1995

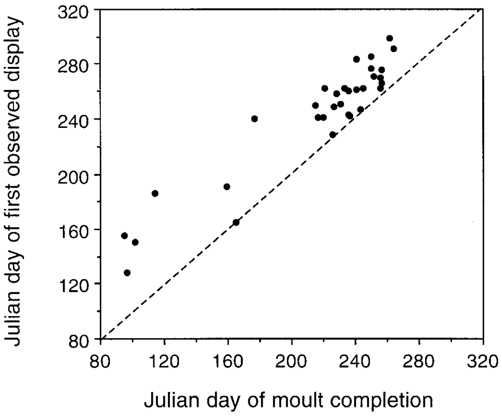

Fig. 4 Relationship between the day males completed their moult into breeding plumage and the day that they were first observed to perform a display to a female outside their social group. Data are presented for the 32 dominant males used to examine variation in male display rates in 1995. The *dashed line* shows the time males complete their moult

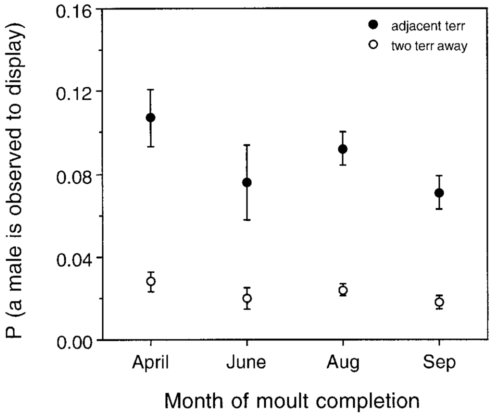

Fig. 5 Relationship between the position of a male relative to the focal female and the month that he completed his moult into breeding plumage and the probability that he was observed to display during a 30-min period during the fertile period of focal females within two territories of their own. *Points* show model predictions (±SE) controlling for the time of day that observations were conducted and the number of helpers in the social group of the focal female. The model is based on data for 32 males and 24 females with 218 focal observations conducted over the 8 days before the first egg was laid in 1995

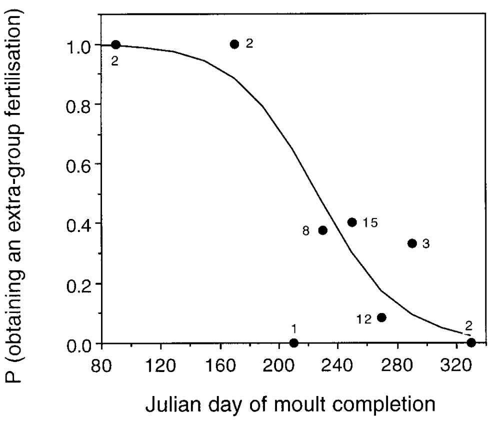

Fig. 6 The effect of moult date on the probability of obtaining an extra-group fertilisation. The *curve* is the logistic regression of extra-group fertilisation success on moult date, and the *points* depict actual probabilities for 20-day periods with their associated sample sizes

Table 2 Relationship between female age and level of information concerning the timing of male moult and how they select extra-pair mates. Females were assumed to use display as a criterion in extra-pair mate choice if they produced nestlings that were sired by males that performed the highest proportion of the displays directed at a female during the breeding season. Alternatively, females were assumed to use the timing of moult as a criterion if sires were either the first male within two territories to moult into breeding plumage (or a male from a greater distance that moulted earlier) or another male that moulted prior to the beginning of July. The latter males made up 13% of the study population. Proportions are expressed with respect to the number of females that cuckolded their mate. Sample sizes are in *parentheses*. Females are excluded when either the extra-group sire was unsampled and therefore from outside the study area, or insufficient displays were observed to predict choice on the basis of display

Female age and status	Criteria used to select extra-pair sire		
	Early moult	First to moult	Display
2+ and informed	0.69 (16)	0.44 (16)	0.31^{a} (16)
1 and informed	0.25 (4)	0.25 (4)	0.25^{b} (4)
1 and naive	–	–	0 (3)

^{a} Two of the five males selected also moulted early
^{b} The male selected was also the first to moult

ritories away (Fig. 5, Table 1). There was no effect of male age, male size, the number of helpers in his group, the presence of nestlings or fledglings requiring care and the date on whether we observed a male to display during focal watches conducted within two territories of his own.

Extra-pair paternity and female choice

In the 2 years of this study, we found that 68% of nestlings (*n*=127) were sired by extra-group males, and that 44 of the 47 broods sampled contained extra-group young. In the majority of broods (77%, *n*=44) only one extra-pair male gained paternity. Females also consistently produced broods with the same extra-pair sire (10 of 12 females where we sampled multiple broods). Almost all females sampled (96%, *n*=27) produced at least one extra-group offspring. The only female that did not raise any extra-group offspring was a first-year bird breeding in a pair with an old mate, conditions that are likely to have restricted her ability to obtain an extra-pair mate (Dunn and Cockburn 1999).

The date on which males completed their moult into breeding plumage was the only male trait that predicted extra-group fertilisation success: early moulting males were far more likely to sire extra-group young (Fig. 6; moult date effect, χ^2=11.0, *df*=1, *P*<0.001). After controlling for the date males completed their moult, there was no effect of display rate (χ^2=1.3, *df*=1), male age (χ^2=0.3, *df*=1), or male social status (χ^2=0.7, *df*=1), on extra-group fertilisation success. There were also no significant interaction terms in the final model (all *P*>0.2).

We also examined the relationship between the timing of male moult, male display and female choice of extra-group sire for 23 focal females that produced broods with extra-group young for which we could assign paternity. This sample of females elicited an average of 14 displays (range 7–51) during watches and regular visits to the territory during the breeding season. First-year females were less likely than females of 2 or more years to select males that either moulted early or performed a high proportion of the displays as extra-pair sires (1 year olds: 6/7 cases; 2+ year olds: 4/16 cases; χ^2=7.3, *df*=1, *P*=0.007). Females that were 2 years of age or older usually selected males that moulted at least 2 months prior to the start of the breeding season as extra-pair sires (11 of 16 females; Table 2). Mate choice in females of 2 or more years was not entirely predictable, however, as the early moulting male selected was not always the earliest male within two territories to complete his moult into breeding plumage (4 of 11 cases). Nevertheless, the males selected as extra-pair sires by older females moulted more than a month earlier, on average, than other males within a two-territory radius that were not selected (difference in the mean moult date of selected males vs mean moult date of rejected males=–47±13 days; paired *t*-test=–3.54, *df*=15, *P*=0.003). Old females also occasionally selected as extra-group sires males that displayed at a relatively high rate (5 of 16 cases; Table 2). However, two of the five males that may have been selected on the basis of display rate also moulted early and males selected as extra-pair sires did not perform a significantly greater proportion of the displays that were directed at females than males that were not selected (difference in the mean proportion of displays performed by selected males vs mean proportion of displays performed by rejected males=0.06±0.04; paired *t*-test=1.69, *df*=15, *P*=0.11). Our data therefore suggests that instantaneous display rate is relatively unimportant in extra-group mate choice.

Discussion

Female fairy-wrens have the highest recorded rate of extra-group fertilisations among birds (Mulder et al. 1994; Dunn and Cockburn 1999). This study confirms that the best predictor of whether male fairy-wrens obtain extra-group paternity is the date of their annual moult into breeding plumage, and shows that females may use the onset of extra-group display as the trait used to discriminate between males. In contrast, although male fairy-wrens continue to display to females throughout the breeding season, these display rates appear to be relatively unimportant in explaining female extra-group mate choice. Nevertheless, males display more to females that lack information on when males completed their moult into breeding plumage than to females that were able to select extra-group mates on the basis of the timing of moult or the onset of display. This raises the possibility that there are circumstances when display rate may be used to discriminate between potential extra-group sires.

Timing of displays

Double and Cockburn (2000) showed that extra-group fertilisations take place before sunrise 4–2 days before the first egg is laid. Here we show that male display to females reaches a plateau about 8 days before egg laying and then falls rapidly once the female is no longer receptive (see also Mulder 1997). However, displays almost never result in copulations on the territory of the female (0.2%; *n*=1,930 displays; Green et al. 1995). Instead, pre-dawn copulations are initiated by the female on a foray to the territory of the male. Male superb fairy-wrens were also more likely to perform extra-group displays in the morning than the afternoon. This diurnal pattern is also unlikely to be associated with an increased chance of obtaining copulations, as the morning focal watches were conducted hours after the pre-dawn period when females leave their territories to seek extra-group copulations. The diurnal pattern may reflect different energetic trade-offs, reflecting the importance of accumulating energy reserves for the night, and the greater costs of flight when conditions are hot and/or windy.

How does male display influence female mate choice?

Paternity data from this study confirmed previous work on this population demonstrating that the timing of the annual moult into breeding plumage is the only strong predictor of whether males obtain extra-group paternities (Dunn and Cockburn 1999). The timing of moult is likely to be an honest indicator of male quality because the early acquisition of breeding plumage and its maintenance throughout the winter months are costly (Mulder and Magrath 1994; Dunn and Cockburn 1999). We found that males start to perform extra-group displays immediately after they have completed their annual moult into breeding plumage, so the onset of display provides females with precise information about a costly trait, the timing of moult.

Display rates, by contrast, provide female fairy-wrens with relatively little information about overall male quality. We found no correlation between the probability that a male was observed to display to a female during a focal observation and his age, body size, or date that he completed his moult into breeding plumage. The frequency of male displays during the breeding season only provided females with information about the proximity of the displaying male, as neighbours displayed to focal females at approximately four times the rate of males that lived two territories away. Females can traverse up to five territories to mate with extra-group males, and despite their dominating display during the fertile period, neighbours contribute less than 50% of extra-pair fertilisations (Double and Cockburn 2000). Display rate may be an unreliable indicator of male quality because it can vary according to the social circumstances of the displaying male and the reproductive condition of his mate (Green et al. 1995).

These results support theoretical predictions that a display of endurance, the timing of the annual moult into breeding plumage, should be used in preference to a flexible behavioural trait, instantaneous display (Sullivan 1990; Kokko et al. 1999). Dunn and Cockburn (1999) contended that such displays are analogous to the fixed morphological traits predicted to be reliable indicators (Sullivan 1994; Møller et al. 1998).

Although we found that male display rate during the breeding season did not predict extra-group fertilisation success, the paternity data suggested that a few females mated with males that displayed to them at a high rate. We can think of three contexts where short-term information from display rate may be particularly valuable to females, despite being less reliable than moult date as a cue to male quality in fairy-wrens. First, in displays of endurance lasting many months, there is a possibility that the chosen male will die before fertilisation takes place. In 1995, 25 of 188 males in our study area completed moult before 1 July, but 9 (36%) died before 15 November, before most young were produced. One female initially mated with the first male in her neighbourhood to complete his moult. However, after his death she switched preference to the local male with the highest display rate.

Second, there is a class of females who can have no long-term information. These naive females also routinely cuckold their partner, but may be forced to use an alternative cue, such as display rate, in extra-pair mate choice. Males directed more displays to naive first-year females than to informed first-year females. These females differed only in the amount of information they had concerning the timing of male moult. This suggests that males may be sensitive to constraints on female mate choice and adjust their display accordingly. However, we found no evidence that naive females select extra-group sires on the basis of instantaneous display rate. Nonetheless, as the paternity data for naive females is currently limited, we require additional data before we can conclude that display rate during the breeding season does not influence the mate choice of these females.

Third, variation in female mate preferences may result from condition-dependent mate choice (Jennions and Petrie 1997; Bakker et al. 1999). Female fairy-wrens may traverse several territories when selecting an extra-pair sire (Double and Cockburn 2000), but some females may be less capable or reluctant to travel substantial distances to find an appropriate mate. Instantaneous display rate may provide these females with detailed information about a restricted sample of males, immediate neighbours. Limiting mate choice to neighbours may also benefit females by improving the accuracy with which they are able to express their preference for a particular male. Multiple extra-group paternity within a brood is far less likely when females only visit neighbours to solicit extra-group copulations (Double and Cockburn 2000). Recent experimental work has found that female condition affects the choice of mates by female sticklebacks *Gasterosteus aculeatus*, and condition-dependent mate choice may repay greater attention in many systems where females express choice (Bakker et al. 1999)

Males may adjust their behaviour in response to such variation. In addition to displaying at a high rate to naive females, male fairy-wrens display at higher rates to females living with two or more helpers. We might have predicted that males would target females with helpers because these females are more likely to cuckold their social mate completely, and hence provide greater rewards to extra-group sires (Mulder et al. 1994). However, females with one helper cuckold their mate only slightly less often than females with two or more (Mulder et al. 1994), yet are no more likely to be the target of display than females in pairs. Males may therefore target females in large groups simply because they have been the most successful in the past, and extra-pair paternity with these females is consequently more likely to result in the production of independent young. There is a positive relationship between productivity and group size in this population of fairy-wrens that is associated with differences in territory or female quality rather than being a direct consequence of male help (Green et al. 1995).

Alternative explanations for extra-group display in fairy-wrens

Although most females appear to base mate choice on information obtained well before they become fertile (Dunn and Cockburn 1999; this study), males continue to display even when their own female is fertile (Green et al. 1995). There appear to be four plausible explanations for the maintenance of display, in addition to any advantage males might gain from displaying to females unfamiliar with moult or unprepared to traverse great distances to locate a sire. First, males may need to display at a fixed level throughout the breeding season in order for females to be aware that they are still alive and available as potential extra-group sires. Second, though females now express no preference for males that display at a high rate, and alternative male sexually selected traits and female preferences have evolved, males may be constrained to display throughout the season because females discriminate against males that fail to maintain display above a threshold level (Wallace 1973; Holland and Rice 1998). Third, females may select males on the basis of attributes of display other than rate per se. Displays vary in duration and males also occasionally augment displays by carrying a yellow petal. Males may therefore visit females repeatedly to maximise the quality of the display observed by the female. Finally, displays may not be used by females to select extra-group sires but may encode geographic information that allows females to locate extra-group males when soliciting copulations on the males’ territory during their fertile period (Double and Cockburn 2000). Repeated display may reinforce and increase the accuracy of the information provided, thereby increasing the likelihood that females can locate the displaying male. The “sea-horse flight” (Rowley and Russell 1990; Mulder 1997), sometimes performed by males when departing a territory at the conclusion of an extra-group display, is a uni-directional flight display that could possibly be used to advertise the location of the territory of the displaying males.

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