1 Female and male plumage colour is linked to parental quality, pairing and extra-pair 2 mating in a tropical passerine

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10 **ABSTRACT**

11 Sexual selection has been proposed to drive the evolution of elaborate phenotypic traits in
12 males, which often confer success in competition or mating. However, in many species both
13 males and females display such traits, although studies reporting selection acting in both
14 sexes are scarce. In this study, we investigated whether plumage ornamentation is sexually
15 selected in female and male lovely fairy-wrens *Malurus amabilis*, a cooperatively breeding
16 songbird. We found that female and male plumage colour was correlated with parental
17 quality but did not incur survival costs. We also found evidence of positive assortative mating
18 based on plumage colour. Microsatellite analyses of paternity indicated that the lovely fairy-
19 wren has high levels of extra-pair paternity, with 53% of offspring resulting from extra-pair
20 mating. Female and male plumage colour did not predict reproductive success and female
21 proportion of extra-pair offspring in its own nest, but less colourful males obtained higher
22 extra-pair paternity. We argue that plumage colour may be under sex-specific selection,

23 highlighting the importance of looking at both sexes in studies of sexual selection and
24 ornament evolution. The current findings together with previous study, suggest that plumage
25 colour in female and male lovely fairy-wrens appears to be an honest signal relevant in both
26 intra and inter-sexual competition contexts.

27

28 **Keywords:** Assortative mating, Extra-pair paternity, Female ornaments, Mate choice,
29 Parental Care, Sexual selection

30

31 INTRODUCTION

32 In males of many species, sexual selection is thought to have driven elaborated traits that
33 function in competition or to attract females (Darwin, 1871) by advertising male phenotypic
34 or genetic quality (Andersson, 1994). Although such elaborate traits are more commonly seen
35 in males, they are also expressed in females across many taxa (Amundsen, 2000; Price,
36 2019). The expression of elaborate traits in females has been often overlooked and thought to
37 be a by-product of selection on males (reviewed in Amundsen, 2000; Amundsen and Pärn,
38 2006; Tobias et al., 2012). However, more recently, empirical and comparative work suggests
39 that traits are most likely the result of direct selection that can explain female functional
40 signals, either to increase reproductive success (sexual selection; Fitzpatrick and Servedio,
41 2017; Hare and Simmons, 2019), or to increase access to limited resources via competition
42 (social selection; LeBas, 2006; Tobias et al., 2012; West-Eberhard, 1983).

43 Morphological traits, such as plumage colours, may be used to reliably assess potential
44 mates if they are correlated with aspects of individual quality (Hunt et al., 1999; Kraaijeveld
45 et al., 2004; MacDougall and Montgomerie, 2003). Males, like females, may benefit from
46 choosing mates based on direct benefits such as phenotypic or genetic quality, which could

47 affect their reproductive success (Amundsen and Pärn, 2006). Traits may also serve as status
48 signals and evolve through competition over mates or other resources (Tobias et al., 2012).
49 Both social competition and mate choice can lead to positive assortative patterns of pairing
50 and mating because individuals with similar traits are likely to pair or mate more frequently
51 than expected by chance (Burley, 1983).

52 Many socially monogamous bird species engage in extra-pair mating (Brouwer and
53 Griffith, 2019; Griffith et al., 2002). In species that form pair bonds, but sometimes mate with
54 extra-pair individuals, mate choice may involve both choosing a social partner and the
55 genetic parent(s) for offspring (Moller, 1992). In such a case, extra-pair behaviour may be
56 driven by male and/or female mate choice, though most studies have focused only on males
57 traits and how they may affect paternity (Forstmeier et al., 2014; Griffith et al., 2002; Moreno
58 et al., 2015).

59 The expression of elaborate traits in males and females may have similar or different
60 selective drivers, signalling the same or distinct information. Studying traits using similar
61 procedures in both sexes offers an excellent opportunity to understand the mechanisms for
62 the evolution of elaborate traits, by way of identifying the differences between sexes in
63 selective pressures and investment trade-offs in ornamentation (Dale et al., 2015; Jacobs et
64 al., 2015; Kraaijeveld et al., 2004; Price and Eaton, 2014; Simpson et al., 2020; Soma and
65 Garamszegi, 2015). However, the mechanisms that have shaped ornamental traits in females
66 are still debated (Price, 2019; Riebel et al., 2019), including whether sexual selection can act
67 on females traits (Clutton-Brock, 2009; Hare and Simmons, 2019; Tobias et al., 2012).

68 Here, we studied the role of plumage colour of female and male lovely fairy-wren,
69 *Malurus amabilis*, a tropical socially monogamous and cooperatively breeding songbird. The
70 lovely fairy-wren is dichromatic, with both male and female displaying conspicuous, but
71 qualitatively different forms of colouration. In both sexes, plumage colouration is correlated

with aggression in the context of same-sex competition (Leitão et al., 2019a), but its role in mate choice is unknown. In several closely-related fairy-wren species, the timing of moult into nuptial plumage in males is a sexual signal and a predictor of extra-pair mating success (Brouwer et al., 2011; Cockburn et al., 2008; Dunn and Cockburn, 1999; Karubian, 2002). However, in lovely fairy-wrens, males (and females) retain their bright plumage year-round after reaching maturity, and do not undergo a seasonal moult (Leitão et al., 2019b) so other traits, such as plumage colour, are likely to be implicated as sexual signals. The species' mating system was unknown before the present study, but fairy-wrens (*Malurus*) exhibit extremely high but variable rates of extra-pair paternity (EPP), ranging across species from 4.4% to 76% of offspring (Cockburn et al., 2013; Kingma et al., 2009; Mulder et al., 1994; Rowe and Pruett-Jones, 2013).

To understand whether plumage colour of both female and male Lovely fairy-wren is a sexual signal, we investigated the links between plumage colour, individual quality, pairing patterns, reproductive success and EPP. Specifically we assessed whether: (i) plumage colour was related to survival and indicators of individual quality; (ii) individuals paired assortatively based on plumage colour; (iii) females and males with the most elaborate plumage had the highest reproductive success; (iv) females mated with extra-pair males on the basis of plumage colour and brighter males had more EPP.

METHODS

Study system and general field methods

Lovely fairy-wrens are a non-migratory species endemic to the wet tropics of North Queensland, Australia. Field work was conducted in the Cairns area in Far North Queensland

(16.87°S, 145.75°E), where a colour-banded population was established in 2013 and monitored annually until 2017 (for further details see Leitão et al., 2019b).

Lovely fairy-wrens defend territories year-round and breed virtually all year, but with a peak in activity in the Austral Spring, between August and November (Leitão et al., 2019b). Progeny may remain on their natal territory as helpers and assist in subsequent broods. Delayed dispersal is exclusive to males, and females were never seen to help. In our study population, 34.7% of 49 groups included male helpers (Leitão et al., 2019b).

Birds were captured by targeted mist-netting and individually marked with a numbered metal band (Australian Bird and Bat Banding Scheme) and a unique combination of colour bands. At capture, we measured plumage colour (see below) and collected a small blood sample (less than 50 µl) from the brachial vein which was stored in 100% ethanol for later DNA extraction. To assess body size and condition, we weighed individuals (± 0.5 g) and measured tarsus length (± 0.05 mm).

Once individuals were released, we monitored their territories and group members, nesting behaviour and neighbouring territories (density of breeding pairs) weekly. We estimated annual adult survival (presence or absence) by the recovery rate of banded adult breeders (for details see Leitão et al., 2019b).

When possible, blinded methods were used when recording and analysing behavioural data. For some data, it was not possible to record data blindly since it involved focal behavioural observations.

Nesting and parental care

Lovely fairy-wrens exhibit bi-parental care, with the major contribution of the male being in post-hatch offspring care. Females build the nests and incubate, while males remain near

the nest and often engage in courtship feeding. Females lay 2 to 3 eggs and can re-nest several times a year after unsuccessful and successful attempts (Leitão et al., 2019b).

Nests were located using behavioural observations and monitored every 2-3 days. When nestlings were 7 – 9 day-old, we colour-banded and took a small blood sample for paternity analysis. Putative parents were determined by extensive observations of each pair or group, including their attendance at the nest.

Both males and females defend the nest and provision the nestlings and fledglings (Leitão et al., 2019b). Parental care was quantified by recording nestling provisioning as the number of visits by the female, male and helpers from video recordings (GoPro HD Hero2) of active nests. Adults normally resumed feeding within a maximum of 10 min of placing the camera and could be distinguished by their colour bands. We recorded nests for about one hour in the morning (between 0620-1230) when nestlings were 2-5 days (early stage, n=10) and 7-9 days (late stage, n = 9) old. As much as possible, we recorded food provisioning two times per nest (n=6), but some nests do not have repeated measures due to predation of later stage nestlings (n=4), or because the breeding attempt was found at later stages (n=3). For the analysis, we only included nests from pairs that did not have helpers (n = 2 excluded).

Microsatellite analysis, paternity assignment, and genetic similarity

Genomic DNA was extracted from blood samples using a standard salt extraction method (Bruford et al., 1992). In total, 209 individuals were genetically screened by the Australian Genome Research Facility (Melbourne, Australia) for up to 25 loci (Appendix: Table A1). From these, we selected 14 loci for analysis (Table 1) that had high variability, high call rates, did not deviate significantly from Hardy–Weinberg equilibrium, and had low null allele frequencies ($F_{null} < 0.03$, except for Smm1, Mala14, and Mcymu8 where $F_{null} = 0.073$ -

0.118; this was taken into account during paternity assignment). For each locus, we calculated the probability of maternal and paternal exclusion, based on allele frequencies of 117 breeders. In total across all 14 loci, we had 173 alleles ($X = 12.357$) and the combined probability of incorrectly assigning a random male as the sire was less than 1% (Table 1).

To assign parentage of each offspring ($N = 58$ nestlings) we assumed that the female that built, incubated, and fed the nestlings was the genetic mother (in this species, groups have only one adult female). Offspring were only included in the analysis if they mismatch with the putative mother at 2 or fewer loci. We also examined parentage in groups with juveniles (fledglings or subordinates $N = 19$), to determine if they were likely to be offspring of the breeding pair. For both cases, the social male was accepted as the sire if the nestling mismatched the male's genotype at 2 or fewer loci. Additionally, to assign potential extra-pair sires, we used CERVUS 3.0.7. (Kalinowski et al., 2007; Marshall et al., 1998) to select the most likely male sire from the population, by using the log likelihood score (LOD) for each male in the population and comparing to the offspring (pair LOD score). Each paternity assignment was then checked, and we accepted the assignment in 69 out of 77 cases where the selected male had less than two mismatches. In 4 cases no male was assigned, and in 4 other cases we did not accept the assigned male and in 3 of these we did not assign paternity. Evidence suggested that the assigned male was not the most likely sire, for e.g., sibling from the same brood or future brood ($N = 2$), a male from a distant population ($N = 1$; from more than 5 km away, maximum natal and breeder dispersal observed was 1.2 km (Leitão et al., 2019b)), or a male that we knew was dead ($N = 1$).

Rates of EPP for nestlings and juveniles were analysed separately, but results were similar (Table 3). In total, we were able to assign paternity for 70 out of 77 nestlings and juveniles.

We estimated relatedness within social pairs to assess genetic similarity between females and their social and extra-pair mates, by calculating the pairwise r coefficient following the

168 method of Queller and Goodnight (1989) and using the software Coancestry (v.1.0.1.9;
 169 Wang, 2011). Pairs were categorised as incestuous (full sibling pairing and parent-offspring)
 170 when pairwise relatedness was within the range of the mean $\pm 1.5 * SD$ of known first-order
 171 relatives (Brouwer et al., 2017) ($N = 17$, $X \pm SD = 0.46 \pm 0.12$, range: 0.30 - 0.70).
 172

Table 1. Description of microsatellite loci used for parentage analyses, based on 117 dominant, putatively unrelated birds.

Locus	N individuals typed	Nr Alleles	Heterozygosity		Maternal exclusion probability	Paternal exclusion probability	Null allele frequency
			Expected	Observed			
Mcymu7 ¹	116	4	0.573	0.543	0.163	0.282	0.023
Mcymu8 ¹	111	22	0.917	0.721	0.701	0.824	0.118
Tmm6 ²	111	58	0.971	0.946	0.875	0.933	0.011
Smm1 ³	83	7	0.621	0.518	0.225	0.404	0.079
MaLa2 ⁴	115	17	0.874	0.861	0.588	0.742	0.004
MaLa4 ⁴	115	5	0.637	0.652	0.216	0.361	-0.016
MaLa5 ⁴	114	6	0.63	0.658	0.207	0.354	-0.021
MaLa6 ⁴	115	5	0.671	0.67	0.242	0.404	-0.002
MaLa7 ⁴	115	5	0.482	0.513	0.122	0.274	-0.033
MaLa8 ⁴	115	8	0.699	0.73	0.277	0.444	-0.025
MaLa10 ⁴	115	13	0.827	0.809	0.486	0.658	0.007
MaLa13 ⁴	115	8	0.772	0.809	0.39	0.571	-0.030
MaLa14 ⁴	115	9	0.808	0.704	0.452	0.629	0.073
MaLa18 ⁴	114	6	0.763	0.763	0.369	0.549	-0.003
Combined	117	173			0.99	0.99	0.023

Maternal exclusion probability is the probability that at a given locus, a random parent will not match the nestling when no parent is known. Paternal exclusion probability is the probability that a candidate father will be excluded assuming that the mother is known. References for microsatellites are: ¹(Double et al., 1997); ²(Adcock and Mulder, 2002); ³(Maguire et al., 2006); ⁴(Thrasher et al., 2017).

Reproductive and paternity success

We calculated ‘reproductive success’ of each pair as the number of fledglings per year that survived for more than a month. We also calculated male ‘within-pair paternity’ success as the number of offspring a male sired in his own territory; male ‘extra-pair paternity’ success as the total number of extra-pair offspring he sired in the nests of other males, and ‘total paternity’ success as the sum of a male’s within and extra-pair paternity success. These were annual measures for each territory (we did not have more than one surviving brood of the same individual within a year).

Measures of colouration and analysis

Spectral reflectance properties of female and male plumage were measured at capture using a spectrometer (Ocean Optics JAZ) with an inbuilt light source (PX-3 Pulsed Xenon),

connected to a probe and a machined 45° angle end (UV-VIS fiber-optic reflectance). Before measuring each bird, the spectrophotometer was calibrated relative to a white standard (Ocean Optics WS-2) and a dark reference. Methods are described in Leitão *et al.* (2019a). Briefly, we took five readings of different body parts, and summarised reflectance spectra to describe chromatic variation using psychophysical models of avian vision (Vorobyev and Osorio, 1998; Vorobyev *et al.*, 1998). Visual models reduced each spectrum to a set of three (xyz) chromatic coordinates that define its position in avian visual space, where distances are expressed in JNDs (just noticeable differences), using formulas from Cassey *et al.* (2008) as implemented by Delhey *et al.* (2015). Colour vision in birds is mediated by four types of single cones that are sensitive to very short (VS), short (S), medium (M) and long (L) wavelengths. Axis x represents the relative stimulation of the S cone in relation to the VS cone, y axis represents relative stimulation of the M cone in relation to the VS and S cones, and axis the z represents the relative stimulation of the L cone in relation to the VS, S and M cones.

Within each sex, the colours of different (blue) patches are moderately correlated, and cheek and head were the most colourful patches and with higher visual impact in each sex (Leitão *et al.*, 2019a), so we used these two in the analysis. For each sex, we summarised chromatic variation (xyz coordinates) with a Principal Component Analysis (PCA) using a covariance matrix to maintain the JND units of the original data (Delhey *et al.*, 2015). PCA analysis resulted in one factor (PC1_{chroma}) that explained between 73 - 99% of chromatic variance, with low PC1_{chroma} values representing high stimulation of the L relative to the VS+S cones for head and cheek, and high stimulation of M relative to VS + S for only the cheek; so high PC1 values indicated individuals with colours richer in shorter wavelengths (UV/blue, Table A2). We ran PCAs separately for each sex, rather than combining the sexes (cf. appendix and main text analyses in Leitão *et al.*, 2019a), because females and males are

dichromatic, and we sought to test for patterns of assortative mating between sexes without combining them in a PCA.

In a subsample of re-captures, we found that colour was moderately repeatable between years (Appendix Table A3), so we pooled colour data from different years to generate a single measure per individual.

Statistical analysis

All statistics were performed in R (version 3.4.4) and Rstudio (version 1.1.414).

To assess whether plumage colouration indicates individual quality or is related with survival costs, we tested associations between plumage colours and multiple response variables representing (1) body condition, estimated by the scaled mass index following (Peig and Green, 2009), (2) body size, (3) parental care, and (4) survival. For the response variables body size and body condition, we built a linear model with normal error distribution for females and males separately and included cheek and head colour as predictors. For the parental care analysis, we built a general linear mixed model (GLMM) with Poisson distribution and individual number of feeding visits as response variable, and included the explanatory variables cheek and head colour and its interaction with sex of the parent, brood size and nestling age. We also included the time of observation as an offset to control for differences in the duration of the observations, and individual ID and nest ID as random effects to account for repeated measures of the same individual and nest. To test for individual survival, we used a general linear mixed model with survival as a binomial response variable (survived more than 12 months after capture/colour measurement = 1; died before one year = 0), cheek colour, head colour and its interaction with sex as predictors, and with year as a random effect, to account for annual differences in survival probability.

We analysed patterns of assortative pairing and mating, by testing Pearson's correlations between females and their social partner and extra-pair mates in terms of colour (cheek and head plumage), body size (tarsus length) and body condition.

To test for associations between plumage colouration and female and male reproductive success (number of fledglings per year), we used a GLMM with Poisson distribution, to test the predictors plumage colour of both female and male (cheek and head colour) and their interaction, presence of helpers, and territory size (as a measure of territory quality). We included female ID and male ID as random factors to account for repeated measures of the same individuals in different years.

Previous work suggests that there is no single explanation for variation in EPP (Brouwer and Griffith, 2019; Brouwer et al., 2017), so here we considered several possible predictors, while testing whether individual variation in EPP is related to ornament expression. We analysed the proportion of extra-pair offspring in a brood to understand if female plumage colour relates to number of extra-pair fertilizations. We did this by testing the influence of female's plumage colour, her partner's colour, interaction between female and partner's colour, number of neighbouring territories (measure of density and opportunities), presence of helpers, and territory size on proportion of nestlings in brood that were EP offspring. We fitted the model with binomial distribution and included female ID and male ID as random factors.

To determine which factors influenced male paternity success, we used three GLMMs with normal error distribution and log transformed response variables for the total number of offspring that a male sired: 'within-pair paternity', 'extra-pair paternity' and 'total paternity' (within + extra-pair). We assessed the effects on paternity of the male's own plumage colour, partner's colour, and the interaction between the two, number of neighbouring territories, presence of helpers, and territory size. We included male ID and partner's ID as a random

factor. Because of the low number of incestuous pairs and general low relatedness between individuals (see Results), we did not include relatedness in the analysis.

In the models of parental care, reproductive success, female mate choice and male paternity success, we present reduced models, due to the higher number of predictors tested, where non-significant terms ($P > 0.2$) were sequentially removed from the models by stepwise backward procedures, starting with interactions terms. We also present full models for comparison.

We compared extra-pair sires with the within-pair male, using a Wilcoxon paired-test, for plumage colour (head and cheek), body size, body condition, genetic similarity to the female, and reproductive success.

GLMs were conducted using packages lme4 (Bates and Maechler, 2010) and the significance of factors and degrees of freedom were assessed using the lmerTest package (Kuznetsova et al., 2017). Differences in sample sizes between tests are due to incomplete data on reflectance spectra, physical measurements, or parental care for some individuals.

RESULTS

Plumage colour, individual quality, and survival

We found no relationship between plumage colour and body condition or body size in females and males (Appendix Table A4). Colour of the cheek patch was positively correlated with parental care, with more colourful parents feeding their nestlings more (Figure 1, Table 2). No association was found between survival and plumage colour or its interaction with sex (Appendix Table A5).

Figure 1. Higher colour of the cheek is related to increase in parental care (number of visits to the nest) of females and males. Dashed lines depict the linear regression line.

Table 2. Parental care (number of visits to the nest) of females and males. Significant predictors in bold, marginal to significance italicised. $N = 24$

Full Model	β	SE	z	P
Intercept	-7.70	0.50	-15.37	< 0.001
Sex ^a	0.08	0.39	0.21	0.83
Cheek colour	0.27	0.10	2.62	0.008
Head colour	-0.06	0.04	-1.48	0.13
Nestling age	0.10	0.05	1.93	<i>0.053</i>
Brood size	0.03	0.15	0.25	0.79
Sex ^a * Cheek	-0.63	0.48	-1.30	0.19
Sex ^a * Head	0.02	0.09	0.23	0.81
Random Effect	σ^2			
Individual id	0.00 ($N = 14$)			
Nest id	0.00 ($N = 9$)			
Reduced Model	β	SE	z	P
Intercept	-7.56	0.35	-21.26	< 0.001
Sex ^a	0.05	0.39	0.15	0.87
Cheek colour	0.28	0.10	2.73	0.006
Head colour	-0.05	0.03	-1.56	0.11
Nestling age	0.09	0.05	1.90	<i>0.057</i>
Sex ^a * Cheek	-0.59	0.39	-1.51	0.13
Random Effect	σ^2			
Individual id	0.00 ($N = 14$)			
Nest id	0.00 ($N = 9$)			

^a Sex is categorical term and reference is female

Assortative pairing

Females with more colourful cheek patches paired with males who also had bluer cheeks (female cheek and male cheek: $r = 0.32$, $N = 36$, $P = 0.05$, Figure 2). No relation was found between female and male head colour patch (female head and male head: $r = 0.07$, $N = 36$, $P = 0.66$). Additionally, no patterns of assortative pairing were found based on body size (tarsus length $r = 0.02$, $N = 37$, $P = 0.91$), or body condition ($r = -0.15$, $N = 37$, $P = 0.36$).

Figure 2. Assortative (positive) pairing based on plumage colour of the female cheek and male cheek. Dashed line shows regression line.

Frequency of extra-pair paternity and relatedness

Paternity analysis showed that 53% of 58 offspring resulted from extra-pair mating and 58% of 29 broods from 26 groups analysed contained offspring sired by males other than the female's social partner (Table 3). Of 19 juveniles from 11 groups analysed, 32% were extra-pair. Most broods were fathered by a single male (72% of 29 broods: 12 by the social pair male only and 9 by a single extra-pair male). The remaining broods were fathered by up to three different males: 5 broods were fathered by the social male and one extra-pair male; 3 broods were fathered by multiple extra-pair males.

Ten percent of pairs were incestuous pairings (3 of 33 pairs where both male and female were genotyped). Five out of 7 nestlings in the 3 broods from these pairs were EP offspring.

Table 3. Frequency of extra-pair nestlings and juveniles (sired by male other than the female's social partner).

	Nestlings	Juveniles	Total
EPP offspring	53.44 % (31 out of 58)	31.57 % (6/19)	48.05 % (37/77)
Broods with at least one EP offspring	58.62 % (17/29)	33.33 % (4/12)	51.21 % (21/41)
Total offspring sampled	58	19	77
Total broods sampled	29	12	41
Nr of incomplete broods	6	2	8

Reproductive and paternity success

The number of surviving offspring produced by the pair was unrelated to female or male plumage colour or any other variable tested (Table 4). Females had more extra-pair offspring when they had more neighbours (Table 5), and the proportion of nestlings in the brood that were EP offspring did not depend on the female's or her mate's colour or any other variable tested, yet in the reduced model less colourful females tended to have more EPP offspring (Table 5).

Table 4. Annual reproductive success of females and males (number of fledglings produced that survived). Significant predictors in bold, marginal to significance italicised. $N = 26$.

Full Model	β	SE	z	P
Intercept	-1.66	1.40	-1.18	0.23
Female cheek colour	0.25	0.19	1.31	0.19
Female head colour	-0.39	0.44	-0.88	0.37
Male cheek colour	-0.48	0.31	-1.52	0.12
Male head colour	-1.35	0.83	-1.61	0.10
Presence of helpers ^a	0.55	0.52	1.06	0.28
Territory size	0.11	0.12	0.92	0.35
Female cheek * Male cheek	0.19	0.23	0.83	0.40
Female head * Male head	-0.41	0.25	-1.62	0.10
Random Effect	σ^2			
Female ID ($N = 16$)	0.00			
Male ID ($N = 19$)	0.00			
Reduced Model	β	SE	z	P
Intercept	0.70	0.35	1.97	0.04
Female head colour	-0.44	0.36	-1.22	0.22
Male head colour	-1.13	0.69	-1.63	0.10
Female head * Male head	-0.36	0.20	-1.74	0.08
Random Effect	σ^2			
Female ID	0.00			
Male ID	0.00			

^a Helper is categorical term and reference is absence of helpers

Reduced model: Backward stepwise procedures were used to remove non-significant variables ($P > 0.2$).

Table 5. Proportion of nestlings in brood that were EP offspring. Significant predictors in bold, marginal to significance italicised. $N = 28$.

Full Model	β	SE	z	P
Intercept	-7.98	5.17	-1.54	0.12
Female cheek colour	0.26	1.89	0.14	0.88
Female head colour	-1.29	1.60	-0.80	0.42
Male cheek colour	1.69	3.15	0.53	0.59
Male head colour	-0.49	2.59	-0.19	0.84
Neighbours	10.85	11.08	0.97	0.32
Presence of helpers ^a	4.81	5.35	0.90	0.36
Territory size	-3.32	4.71	-0.70	0.48
Female cheek * Male cheek	-0.37	2.38	-0.15	0.87
Female head * Male head	-0.29	0.72	-0.40	0.68
Random Effect	σ^2			
Female ID ($N = 18$)	9.01			
Male ID ($N = 21$)	6.30			
Reduced Model	β	SE	z	P
Intercept	-18.80	7.96	-2.36	0.01
Female head colour	-4.46	2.46	-1.80	0.07
Male cheek colour	5.92	4.61	1.28	0.19
Neighbours	28.38	13.41	2.11	0.03
Random Effect	σ^2			
Female ID	0.00			
Male ID	0.00			

^a Presence of helpers is categorical term and reference is negative (no) presence of helpers.

Reduced model: Backward stepwise procedures were used to remove non-significant variables ($P > 0.2$).

Males had higher rates of within-pair paternity in less dense areas (number of neighbouring territories), and when groups had no helpers (Table 6). Males had higher EPP when they were in more dense areas, when they had less colourful cheeks, and when assorted negatively with their partner (negative relation between male's colour and female's colour, Table 6). Within and extra-pair paternity was negatively correlated, although not significant (Pearson's $r = -0.307$, $N = 28$, $P = 0.11$). Male total paternity success (within and extra-pair paternity) averaged 1.5 ± 1.2 offspring per year (range 0-5, $N = 28$ males) and was marginally negatively related with male cheek colour (Table 6), but not related with any other variable tested (Table 6).

Extra-pair male traits and comparison with social male traits

Females and their extra-pair males did not mate assortatively based on colour (head – colour: $r = -0.16$, $N = 12$, $P = 0.60$; cheek colour: $r = -0.01$, $N = 12$, $P = 0.96$), or body condition ($r = -0.22$, $N = 12$, $P = 0.47$). Females and extra-pair males tended to mate negatively assortatively by body size (tarsus length: $r = -0.52$, $N = 11$, $P = 0.09$).

A paired comparison between extra-pair males and the female's social partner showed that extra-pair males tended to be bigger than social partners (respectively 21.63 ± 0.30 and 21.40 ± 0.61 mm tarsus length, $Z = -1.39$, $N = 16$, $P = 0.08$) and have less colourful heads (respectively -1.53 ± 0.99 and -2.50 ± 1.68 head colour, $Z = -1.47$, $N = 12$, $P = 0.07$), but did not differ in cheek colour ($Z = -1.00$, $N = 12$, $P = 0.15$) or body condition (scaled mass index: $Z = -1.23$, $N = 16$, $P = 0.10$). There was also no difference between extra-pair males and social males in their genetic similarity to the female ($Z = 1.63$, $N = 14$, $P = 0.94$).

Table 6. General linear mixed model showing the predictors of within-, extra-pair and total paternity success of males. Significant predictors in bold, marginal to significance italicised.

	Within-pair paternity (<i>N</i> = 28 male-years)				Extra-pair paternity (<i>N</i> = 30)				Total = Within and extra-pair paternity (<i>N</i> = 28)			
Full Model	β	SE	<i>t</i>	<i>P</i>	β	SE	<i>t</i>	<i>P</i>	β	SE	<i>t</i>	<i>P</i>
Intercept	0.32	0.07	4.54	<0.001	0.10	0.06	1.58	0.13	0.40	0.07	5.10	<0.001
Male cheek colour	-0.04	0.05	-0.71	0.48	-0.06	0.05	-1.13	0.27	-0.07	0.06	-1.15	0.26
Male head colour	0.01	0.04	0.36	0.72	-0.03	0.04	-0.73	0.47	-0.02	0.05	-0.42	0.67
Partner's cheek colour	-0.01	0.03	-0.29	0.77	0.04	0.03	1.27	0.24	0.02	0.04	0.56	0.58
Partner's head colour	0.003	0.02	0.14	0.88	-0.002	0.02	-0.08	0.93	-0.002	0.02	-0.11	0.90
Neighbours	-0.13	0.09	-1.48	0.20	0.14	0.09	1.58	0.15	0.004	0.09	0.04	0.96
Presence of helpers ^a	-0.12	0.10	-1.11	0.28	-0.03	0.10	-0.34	0.73	-0.14	0.12	-1.18	0.25
Territory size	-0.001	0.09	-0.02	0.98	0.06	0.08	0.79	0.44	0.01	0.09	0.14	0.88
Male cheek * Partner's cheek	0.018	0.04	0.43	0.67	-0.06	0.03	-1.76	0.09	-0.04	0.04	-0.93	0.36
Male head * Partner's head	0.0001	0.01	0.009	0.99	-0.003	0.01	-0.22	0.82	-0.005	0.01	-0.32	0.74
Random effect	σ^2				σ^2				σ^2			
Male ID (<i>N</i>)	0 (21)				9.69e-11 (22)				0.0 (21)			
Female ID (<i>N</i>)	0.008 (18)				0.009 (18)				0.0 (18)			
Residual	0.03				0.02				0.05			
Reduced Model												
Intercept	0.32	0.04	7.82	<0.001	0.13	0.03	3.79	0.005	0.37	0.04	7.74	<0.001
Male cheek colour					-0.07	0.03	-2.17	0.04	-0.07	0.04	-1.76	0.08
Partner's cheek colour					0.04	0.02	1.80	0.12				
Neighbours	-0.15	0.06	-2.26	0.03	0.15	0.07	2.25	0.04				
Presence of helpers ^a	-0.16	0.07	-2.31	0.02					-0.11	0.08		0.19
Male cheek * Partner's cheek					-0.07	0.02	-2.54	0.02				
Random effect	σ^2				σ^2				σ^2			
Male ID (<i>N</i>)	0.0 (21)				0.0 (22)				0.0 (21)			
Female ID (<i>N</i>)	0.0 (18)				0.001 (18)				0.0 (18)			
Residual	0.03				0.02				0.04			

^a Presence of helpers is categorical term and reference is positive (yes) presence of helpers

Reduced model: Backward stepwise procedures were used to remove non-significant variables (*P* > 0.2).

366 **DISCUSSION**

367 We investigated whether plumage colouration is a sexually selected signal in female
 368 and male Lovely fairy-wrens. We show that more colourful males and females cared
 369 more for their offspring, and that females and their social males paired assortatively by
 370 plumage colour. We also found high rates of extra-pair paternity, with 53% of nestlings
 371 sired by extra-pair males, and that the number of neighbouring territories, but not
 372 plumage colour, predicted the number of female's EP offspring. Males gained more
 373 paternity in their own nests at low breeding densities and when they had no helpers in
 374 their group. We found that males had higher EPP when they were in more dense areas,
 375 and unexpectedly, when they were less colourful. Taken together, our findings suggest
 376 that plumage colour signals parental quality and is important in mate choice.
 377 Furthermore, males, but not females, may have underlying differences in mating
 378 strategies correlated with plumage colouration.

379

380 **Plumage colour as positive indicator of parental quality that does not incur** 381 **survival costs**

382 Female and male ornament expression may be used for mate choice, if it provides
 383 information about aspects of phenotypic quality or fitness (Jawor et al., 2004; Laczi et
 384 al., 2013). Here, we found that plumage colour predicted parental care, where males and
 385 females with more colourful cheek plumages provisioned more. These results,
 386 consistent with other studies (Dakin et al., 2016; Linville et al., 1998; Siefferman and
 387 Hill, 2003), suggests that plumage colour displayed by both sex is a reliable indicator of
 388 parental quality and that individuals can benefit by choosing a mate based on this trait.

389 We found no further evidence that plumage colour signals size or condition, but it is
390 possible that plumage colouration signals other aspects of quality that were not
391 measured here, such as good genes (Hamilton and Zuk, 1982), immunological capacity
392 (McGraw and Ardia, 2003), or age (Dias et al., 2016). These qualities can co-vary with
393 plumage colour, in such way that individuals are choosing compatible or high-quality
394 sexual partners.

395 Conspicuous colours are often associated with high survival costs, with several
396 studies suggesting that bright colours attract more predation (Götmark and Hohlält,
397 1995; Götmark et al., 1997; Huhta et al., 2003). Still, we found that annual survival was
398 unrelated with plumage colouration. In line with this, an experimental study
399 investigating colour phenotypes in fairy-wrens showed that being brightly coloured did
400 not increase the chances of adult predation (Cain et al., 2019), indicating that increased
401 conspicuousness is not associated with greater predation pressure. The absence of the
402 seasonal plumages characterising other (male) fairywren species in lovely fairy-wrens,
403 paired with living in the tropics and high adult survival (Leitão et al., 2019b), suggests
404 that colourful plumage in the lovely fairy-wren does not incur survival costs.

405

406 **Positive assortative pairing: Mate choice for plumage colour and parental** 407 **qualities?**

408 Consistent with the growing body of evidence that individuals paired assortatively
409 with respect to plumage colouration (de Zwaan et al., 2019; Griggio et al., 2005; Jacobs
410 et al., 2015; MacDougall and Montgomerie, 2003; Rowe and Weatherhead, 2011), we
411 found a similar pattern in the lovely fairy-wrens. Socially monogamous species that

412 contribute similarly to parental care, as seen in this species (Leitão et al., 2019b), are
 413 expected to choose a high quality partner (Fitzpatrick et al., 1995; Safran and McGraw,
 414 2004) and in positive assortative mating, individuals of similar traits are expected to
 415 pair more frequently than expected by chance (Burley, 1983). When only one sex is
 416 selective, patterns of assortative mating are not expected (Burley, 1983). This mating
 417 pattern suggests that plumage colour is expressed in both sexes because it has a
 418 signalling function and is favoured by mutual mate choice (Kraaijeveld et al., 2007),
 419 results that are supported by different empirical work (Heinig et al., 2014; Hunt et al.,
 420 1999; Kraaijeveld et al., 2004; MacDougall and Montgomerie, 2003). Yet, the
 421 possibility that assortative pairing may be due to reasons other than mutual mate choice
 422 cannot be discarded. For example, competition can cause a similar pattern if social
 423 dominance affects pair formation (Creighton, 2001). We have shown that plumage
 424 colouration is involved in male and female competitive interactions (Leitão et al.,
 425 2019a), and thus it can reflect the ability of individuals to compete for territories
 426 (Hasegawa et al., 2014; Wolfenbarger, 1999), and territory quality may co-vary with
 427 plumage colour. Behavioural observations and experiments are needed to distinguish
 428 these possibilities.

429

430 **Reproductive success, extra-pair behaviour and correlates with plumage colour**

431 Males with more conspicuous ornaments are assumed to be of better quality because
 432 ornaments may be costly to produce (Hill, 2006). Showy males can be more successful
 433 when competing for sexual resources and may be preferred as mates (Andersson, 1994;
 434 Darwin, 1871), and so it is expected that these individuals achieve higher reproductive
 435 success. However, we found that male and female plumage colouration was not

436 correlated with reproductive success in the home nest. This was despite finding a
437 relationship between parental quality and plumage colour, and positive assortative
438 mating by plumage colour. We cannot rule out that our measure of breeding
439 performance did not capture a possible relation or effect with plumage colour. For
440 example, individuals that are brighter could have better quality offspring, but may
441 attract and increase predation at the nest (Wallace, 1889), and so, general reproductive
442 performance may be masked by predation, the main cause of nest failure in this species
443 (Leitão, Hall, Venables, et al., 2019).

444 If extra-pair males exert a choice, they may favour females that have brighter
445 colours, a preference that can be reflected in higher number of female EP fertilizations.
446 We found that females with more EP offspring in a nest were in areas with high density
447 of males, but no relation was found with female's plumage colour. These results
448 suggest that males might not be selective or discriminate between different female
449 plumage colours.

450 Interestingly, we found that less colourful males had higher EPP success. Under
451 female mate choice and assuming that brighter males are of higher quality, it is expected
452 that females prefer less colourful extra-pair males because the benefits of mating with
453 this type of male outweigh the costs (Qvarnström and Forsgren, 1998), for e.g.
454 maintenance costs and higher vulnerability to predators (handicap signals; Zahavi,
455 1975) or production costs (physiological investment or nutrients) (Doucet, 2002; Keyser
456 and Hill, 2000; McGraw et al., 2002). Another possibility could be that females do not
457 gain much in being selective about extra-pair partners, and EPP is under male control
458 (although in superb fairy-wrens *Malurus cyaneus* EP behaviour is under female control
459 (Double and Cockburn, 2000)). If that is the case, males that are less colourful may be

460 more aggressive, as we have shown in a previous study (Leitão et al., 2019a) and
461 intrinsically willing to engage in extra-pair behaviour more often (Forstmeier, 2007) or
462 obtain copulations by force (Burg and Croxall, 2006).

463 A male's reproductive fitness can be determined by the ability to sire and care for
464 their offspring and/or by increasing mating effort (extra-pair fertilisation) (Balshine et
465 al., 2002). Since more colourful males provide more parental care, and less colourful
466 ones have higher extra-pair mating success (negatively correlated), we argue that males
467 may be adopting different reproductive strategies that are correlated to their plumage
468 colour. In such context, different strategies related with male colouration may lead to
469 similar payoffs and comparable final fitness, i.e. number of fledgling success. Since this
470 study was observational, we cannot rule out any of these possibilities, therefore further
471 detailed experimental studies will be needed to test for these. Regardless of the
472 mechanisms, our results suggest that plumage colour is relevant in mate choice in this
473 species, in both social and extra-pair contexts.

474

475 **Lovely fairy-wren mating system**

476 We found that lovely fairy-wrens had high rates of EPP despite low frequencies of
477 extra-pair courtship displays, high male care, and low number of helpers compared to
478 other *Malurus* (Leitão et al., 2019b). Previous comparative work in the Maluridae
479 family (which did not include the lovely fairy-wren) showed that multiple factors
480 predicted the variation of EPP rates, including inbreeding avoidance, the number of
481 helpers, male care, and male density (Brouwer et al., 2017). We found similar predictors
482 in this study, since males that were in areas with lower density and with no helpers

483 achieved higher within-pair paternity success and males that were in higher density
 484 areas gained more EPP. Additionally, all (three) cases of incestuous pairings resulted in
 485 EPP (though not all nestlings in these broods were EP), suggesting the possibility that
 486 females may partially avoid inbreeding depression by mating extra-pair when partnered
 487 with a close relative.

488

489 **CONCLUSION**

490 We found support for plumage colouration to have a signalling function in mate
 491 choice in a dichromatic species where both sexes are ornamented. More colourful
 492 individuals invested more in parental care, and females and males paired and mated
 493 assortatively by plumage colour, suggesting mutual mate choice. Lovely fairy-wrens
 494 appear to have sex differences in their reproductive strategies and its relationship with
 495 plumage colouration: while no significant relationship was found between female
 496 plumage colour and EP offspring (male mate choice), less colourful males were more
 497 successful in getting extra-pair paternity (female mate choice). Our results are
 498 inconsistent with more conspicuous plumages being a signal of higher reproductive
 499 success. Instead, less colourful plumages in males seem to confer a reproductive
 500 advantage, at least in the context of extra-pair mating success. It is possible that females
 501 may be more selective than males and choose social and extra-pair males based on their
 502 plumage colour, or males adopt different mating strategies (EPP vs parental care) that
 503 are related with plumage colour, which ultimately have similar fitness. More empirical
 504 work is needed to understand how and what drives females and male mate choice for
 505 plumage colour.

506 Taking these results together with previous work (Leitão et al., 2019a), plumage
507 colour in both sex seems to function in intra and inter-sexual competition contexts,
508 although the information conveyed by plumage colouration seems to be context-
509 dependent in relation to the sex of the bearer, which might partially explain
510 dichromatism in this species. This study contributes to the growing body of the research
511 on the function and evolution of female traits but stresses the need for further work
512 comparing both female and male in a single system, so we can better understand sex-
513 differences in traits, possible mechanisms driving these differences, and their functional
514 and evolutionary consequences.

515

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535

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538

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541

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755

SUPPLEMENTARY DATA

Table A1. Description of microsatellite loci screened for posterior panel, based on dominant birds.

Locus	N samples run	Nr Alleles	Size range	% Successful samples	Variability
Mcymu1 ¹	22	2	-	0	-
Mcymu4 ¹	35	4	190-196	94.29	0.12
Mcymu6 ¹	35	8	151-161	0.28	0.28
Mcymu7 ¹	230	6	118-126	98.26	0.03
Mcymu8 ¹	230	26	258-353	94.35	0.12
Msp4 ²	22	3	169-169	0.60	0.60
Msp6 ²	35	5	279-291	0.17	0.14
Msp10 ²	35	2	189-189	0.06	0.06
Tmm6 ³	230	63	316-469	93.48	0.29
Smm1 ⁴	208	9	257-273	79.33	0.05
Smm2 ⁴	35	4	208-218	0.11	0.11
Smm7 ⁴	35	3	262-264	0.09	0.09
Ase9 ⁵	13	4	143-149	0.31	0.31
MaLa2 ⁶	215	20	203-295	98.60	0.09
MaLa3 ⁶	20	3	297-301	0.15	0.15
MaLa4 ⁶	215	7	337-353	98.60	0.03
MaLa5 ⁶	215	8	193-217	97.67	0.04
MaLa6 ⁶	215	7	190-206	98.60	0.03
MaLa7 ⁶	215	7	290-310	98.14	0.03
MaLa8 ⁶	215	10	233-269	98.14	0.05
MaLa10 ⁶	215	11	271-326	98.14	0.08
MaLa13 ⁶	215	11	331-363	98.60	0.05
MaLa14 ⁶	215	11	250-282	98.14	0.05
MaLa16 ⁶	20	4	186-187	0.22	0.22
MaLa18 ⁶	215	8	258-290	98.60	0.04

References for microsatellite are: ¹(Double et al., 1997); ²(Webster et al., 2004); ³(Adcock and Mulder, 2002); ⁴(Maguire et al., 2006); ⁵(Richardson et al., 2000); ⁶(Thrasher et al., 2017).

Table A2. Loadings for principal component analysis ($PC1_{\text{chroma}}$) of xyz colour for cheek and head for each sex separately. Variable x represents the relative stimulation of S cone in relation to VS cone; y represents relative stimulation of M cone in relation to VS and S cones; and z axis represents the relative stimulation of L cone in relation to VS, S and M cones

	Variables	$PC1_{\text{chroma}}$	
		Female	Male
Cheek	x	-0.05	0.12
	y	-0.25	-0.68
	z	-0.96	-0.71
	Variance	91 %	73 %
Head	x	-0.13	-0.04
	y	-0.01	-0.09
	z	-0.99	-0.99
	Variance	99 %	95 %

Table A3. Repeatability of colour measurement between years using the rptR package (Nakagawa and Schielzeth, 2010). Significant values in bold.

	<i>R</i>	SE	<i>CI</i>	<i>P</i>	<i>LRT</i>
Head Colour N = 9	0.54	0.23	[0-0.86]	0.05	-62.40
Cheek colour N = 11	0.36	0.22	[0-0.76]	0.13	-59.50

Table A4. General linear model for body condition and body size. Significant predictors in bold. $N = 34$

	Female				Male			
	β	SE	t	P	β	SE	t	P
Body condition								
Intercept	8.59	0.20	42.50	<0.001	8.85	0.08	104.81	<0.001
Cheek colour	-0.02	0.10	-0.25	0.80	-0.04	0.06	-0.67	0.50
Head colour	0.03	0.05	0.66	0.51	0.01	0.03	0.27	0.78
Body size								
Intercept	20.44	0.18	112.12	<0.001	21.35	0.13	161.14	<0.001
Cheek colour	0.12	0.09	1.33	0.19	-0.13	0.10	-1.24	0.223
Head colour	-0.07	0.04	-1.64	0.11	0.03	0.05	0.65	0.51

Table A5. General linear mixed model for survival (survived more than 12 months after capture/colour measurement = 1; died before one year = 0). $N = 74$

	β	SE	z	P
Survival				
Intercept	1.38	1.34	1.03	0.30
Sex	0.20	0.95	0.21	0.83
Cheek colour	0.35	0.37	0.95	0.34
Head colour	-0.01	0.23	-0.05	0.95
Sex * Cheek colour	-0.48	0.62	-0.77	0.43
Sex * Head colour	0.05	0.32	0.18	0.85
Random effect				
Year	σ^2			
	3.55			