

Research



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Animal behaviour

Working with what you've got:
unattractive males show greater mate-guarding effort in a duetting songbird

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When mates are limited, individuals should allocate resources to mating tactics that maximize fitness. In species with extra-pair paternity (EPP), males can invest in mate guarding, or, alternatively, in seeking EPP. Males should optimize fitness by adjusting investment according to their attractiveness to females, such that attractive males seek EPP, and unattractive males guard mates. This theory has received little empirical testing, leaving our understanding of the evolution of mating tactics incomplete; it is unclear how a male's relative attractiveness influences his tactics. We conducted observations and experiments on red-backed fairy-wrens (*Malurus melanocephalus*) to address this question. We found that older, more attractive (red-black) males sought EPP, whereas unattractive (brown) males invested in alternative tactics—physical and acoustic mate guarding. Younger red-black males used intermediate tactics. This suggests that males adopt mating tactics appropriate to their attributes. Males obtained similar reproductive success, suggesting these alternative tactics may maximize each male's paternity gain. Though it is likely that female choice also determines paternity, rather than just male tactics, we establish that the many interconnected components of a male's sexual phenotype influence the evolution of his decision-making rules, deepening our understanding of how mating tactics evolve under sexual selection.

1. Introduction

In the context of sexual selection, decision-making rules determine the type and amount of effort allocated to reproductive tasks [1,2]. In socially monogamous species, male mating effort can take the form of investment in reproduction with the social mate (within-pair paternity), or investment in seeking matings with extra-pair females (EPP). The net benefit to a male of seeking EPP will depend on fitness gains relative to losses from not engaging in alternative behaviours—mate guarding, territory defence and parental care—leading to a trade-off between investments [3,4]. Fitness returns on mating effort probably depend on the context and the characteristics of the male and female involved [5]. Theory predicts that a male's attractiveness, which is monitored by females choosing within- and extra-pair mates, will influence his decision-making [6,7]. Here, we test the hypothesis that males attempt to optimize reproductive success by adjusting investment in mating tactics according to attributes that influence their attractiveness.

We quantified male age and plumage characteristics, and determined how each influences investment in alternative tactics: foraging to seek EPP and physical/acoustic mate guarding. We used behavioural observations and playback experiments in a population of red-backed fairy-wrens (*Malurus melanocephalus*), a socially monogamous Australian songbird with high levels of EPP (54% of young result from extra-pair copulations [8]). Males foray to neighbouring territories to court widely dispersed females [9], making them ideal for

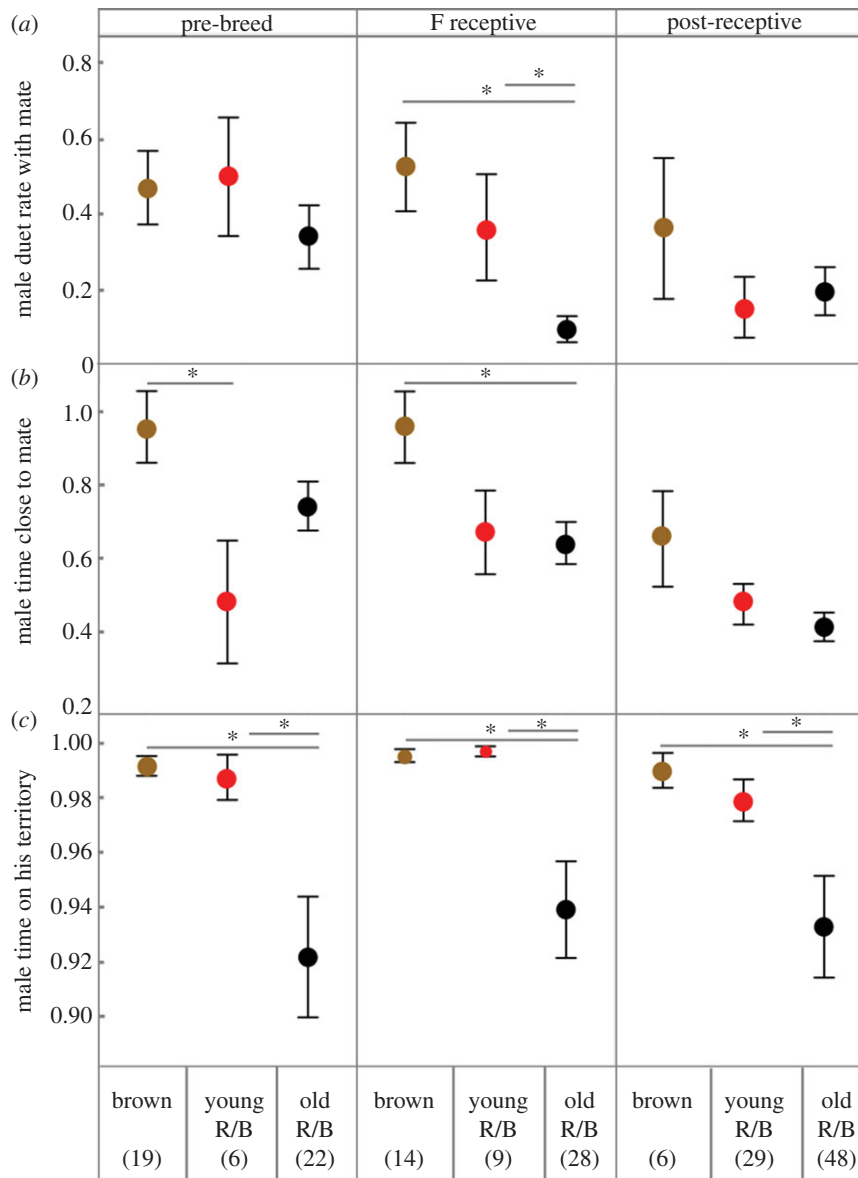


Figure 1. Effect of male age and plumage type on: the male's duet rate with his mate (proportion of female songs the male answered to form a duet) (a), proportion of a male's time he spent less than 10 m from his mate (b), and proportion of the observation the male spent on his territory (c), across three breeding stages. Brown males include both young (less than or equal to 2 years old) and old (more than 2 years old) males in this analysis. Points show mean \pm one standard error. Stars indicate points are significantly different at $p < 0.05$.

testing our hypothesis, since foraging and mate guarding trade-off. Male plumage types vary discretely. Red-black males have colourful plumage; brown males have dull plumage [10]. Females prefer red-black plumage in choice trials [10]. A previous study of the same population shows that older red-black males invest in seeking EPP [10]. This study quantified mating tactics on a fine scale, including tactics used by other male types.

Males more than 2 years old ('old' males) usually have red-black plumage (89% of old males in this study), whereas males aged less than or equal to 2 years ('young' males) can have either brown (50% of 1 year old males, 42% of 2 year olds) or red-black plumage (50% of 1 year old males, 58% of 2 year olds) [8]. Songs between pairs are often given in polyphonic duets [11–14].

We expected that both plumage type and age would affect mating tactics, and predicted that old red-black males would invest in seeking EPP, because their attractiveness predicts extra-pair mating success and protects them

from cuckoldry [7]. By contrast, we predicted brown males would invest in guarding mates physically and acoustically [7,15,16], as their unattractiveness predicts little extra-pair success and high cuckoldry risk [7]. Finally, we predicted that age and plumage would interact, such that young red-black males would have intermediate attractiveness and exhibit intermediate mating tactics.

2. Material and methods

We conducted fieldwork during breeding (October–January) each year from 2009/2010 through 2013/2014 near Herberton, Queensland, Australia (145°25' E, 17°23' S) [17]. We observed 73 groups, for a total of 244 h. We quantified the proportion of female songs a present male answered to form a duet, proportion of a male's time he spent on territory, and the proportion of a male's time he spent less than 10 m from his mate, while he was present, during pre-breeding, female receptive and post-receptive stages. See [13] for detailed methods. We conducted a playback

experiment in 2012 to test differences in breeding male responses to a simulated intrusion by a male alone (male solo song), a female alone (female solo song) and a breeding pair (duet played from two speakers). For the full experimental procedure, see [18]. We calculated a *male approach score* by combining the following in a principal component analysis (electronic supplementary material, table S3): time spent within 5 m of speaker(s), latency to approach within 5 m of speaker(s), closest approach to speaker(s) and number of flights over speaker(s). For details on parentage assignment and calculation of reproductive success, see [19]. Data were analysed using R v. 3.1.2 (R Development Core Team 2015).

3. Results and discussion

During behavioural observations, old red–black males answered fewer of their mate’s songs to form duets, spent less time close to their mates and less time on their territories than did brown males (of which 20% were old males, figure 1, electronic supplementary material, table S1 and figure S4), consistent with our prediction that old red–black males would invest in seeking EPP, and brown males in mate guarding (especially a fertile mate, figure 1). Young red–black males behaved like brown males, or exhibited behaviours intermediate between male types. During playback experiments conducted during the female’s fertile stage, brown males showed stronger physical mate guarding in response to a solo male intrusion than did red–black males (electronic supplementary material, figure S3 and table S2).

The tactics males employed appear to have affected reproductive success. Young and old red–black males had similar EPP, and both had higher EPP than brown males (figure 2*b*; electronic supplementary table S4). Brown males had higher within-pair reproductive success than did old red–black males (figure 2*a*; electronic supplementary material, table S4). Young red–black males sired an intermediate number of within-pair young, but this number did not differ significantly from brown or old red–black males. Summing within- and extra-pair offspring, all three male types had similar total reproductive success (figure 2*c*; electronic supplementary material, table S4). In addition, there was a marginally non-significant trend toward old red–black males being cuckolded more often than brown males (post hoc *z*-test of generalized linear model (GLM): $z = 2.28$, s.e. = 0.51, d.f. = 2, $p = 0.0586$). A direct test of the effect of mate-guarding behaviours revealed that within-pair paternity increased with the amount of time males spent close to mates (GLM, $\chi^2 = 4.76$, d.f. = 1, $p = 0.029$). By contrast, we saw no direct effect of a male’s duet rate with his mate ($\chi^2 = 0.01$, d.f. = 1, $p = 0.91$), or the time he spent on his territory ($\chi^2 = 0.35$, d.f. = 1, $p = 0.55$). These two behaviours may function as imperfect mate guards, which males attempt nonetheless, or may influence reproductive success in ways other than through mate guarding. For example, duetting may stimulate females to mate and/or ovulate and may lead to higher fecundity, which is supported by our observation that brown males tend to sire more total young on average (2.82 young) than red–black males (2.4 young) (two-tailed *t*-test: $t_{44} = 1.8896$, $p = 0.065$).

Our results demonstrate that a male’s attributes influence his mating tactics, dependent on a complex interaction of age and plumage characteristics. Paternity results also suggest that males need not necessarily be attractive to attain high reproductive success, if they employ alternative tactics

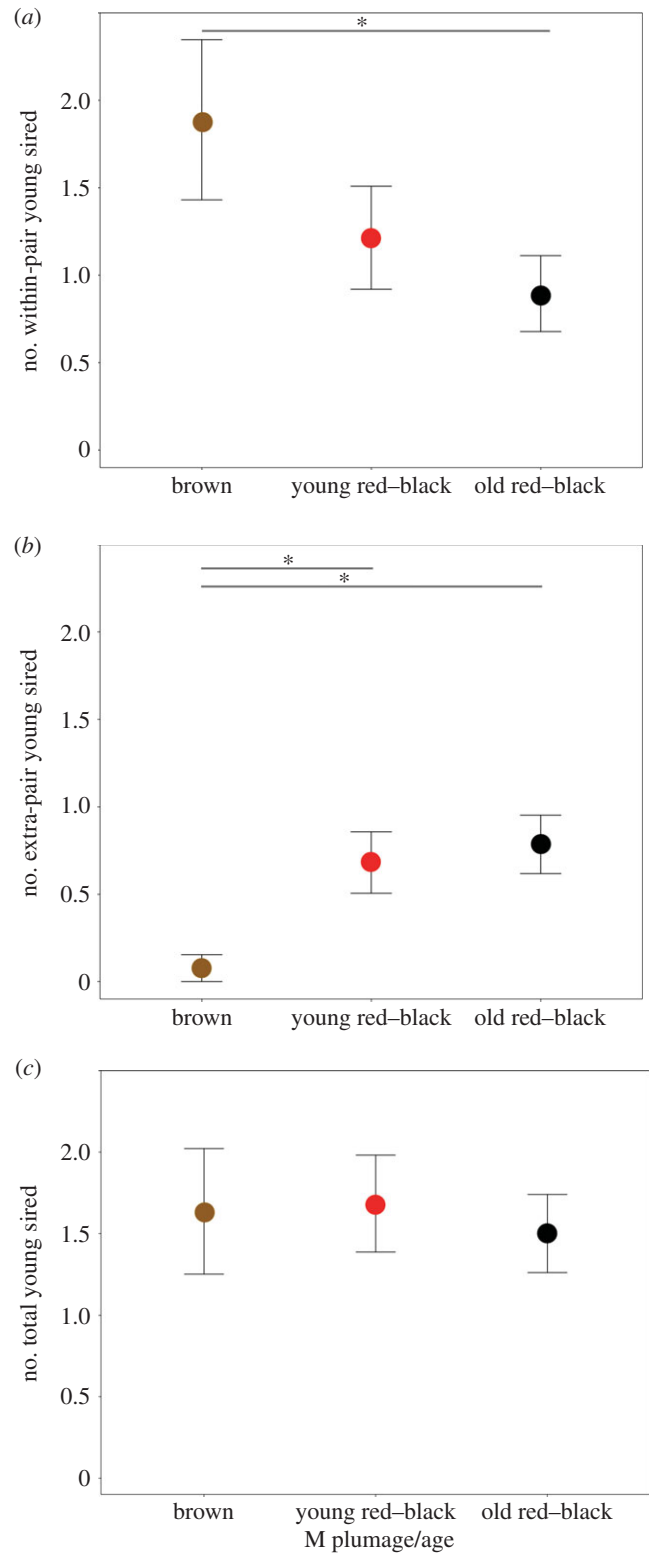


Figure 2. Number of within-pair young (*a*), number of extra-pair young (*b*) and total number of young (*c*) sired by brown, young red–black and old red–black males.

appropriate to their attributes. Paternity may be under male or female control, and the patterns of paternity we see could be equally well explained by either. Brown males, for example, may guard to coerce female choice and prevent mates from copulating with preferred males. If under female control, brown males may guard because females choose to pair and mate with attentive males.

It is important to note that our paternity results contrast with previous studies of this same species. We found equal

total reproductive success between male types. By contrast, another study [13] found that red–black males have higher total reproductive success than brown males. Likewise, another study found that brown and young red–black males were cuckolded more often than were old red–black males [10], whereas we found that old red–black males were cuckolded slightly more often than brown males. As paternity data were collected and analysed similarly in all studies, these results are not likely to be due to methodological differences. Instead, variation between studies may result from differing fitness payoffs for each mating tactic across years. There are a variety of factors that may influence the fitness payoff of a mating tactic, including the frequency of each tactic [20], density of each sex [21,22], operational sex ratio [1,23], current environmental and social factors [24–26], and differing female preferences between years [27]. Understanding how and why the strength of sexual selection fluctuates is emerging as a key challenge in sexual selection theory [28], and mating strategy evolution must be understood in the context of unstable environments.

4. Conclusion

We found support for the hypothesis that males attempt to optimize their reproductive success according to several factors that are assessed by females. This demonstrates the complexity of decision-making rules for mating tactics. A similar degree of complexity may be present in many other systems subject to sexual selection. Moreover, our finding that male types had similar total reproductive success

suggests that use of different tactics can allow even unattractive males to gain high fitness payoffs in some years. We demonstrate that several components of an individual's sexual phenotype influence decision-making rules, which deepens our understanding of the specialized mating tactics produced by sexual selection.

Ethics. Our research adheres to local guidelines and the appropriate animal ethics approval and licences were obtained (Cornell University Animal Care and Use Committee approval 2009-0105, James Cook University Ethics approval number A1340, and Queensland Government Environmental Protection Agency Scientific Purposes Permit number WISP07773610).

Data accessibility. Data from this research have been made available in the Dryad repository [29], titled 'Data from: Working with what you've got: unattractive males show greater mate-guarding effort in a duetting songbird', <http://dx.doi.org/10.5061/dryad.3j4df>.

Authors' contributions. J.D. and M.S.W. both made substantial contributions to the conception and design of the work, interpretation of the data, and drafting/revising the paper critically for important intellectual content. Both authors agree to be accountable for all aspects of the work and to provide final approval of the version to be published.

Competing interests. We have no competing interests.

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