



Extrapair copulations reduce inbreeding for female red-backed fairy-wrens, *Malurus melanocephalus*

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In many socially monogamous species, females copulate with and produce offspring sired by males other than their social mates, yet it remains controversial whether or how females benefit from these 'extrapair' copulations. Recently, it has been suggested that females might benefit if they are able to copulate with extrapair males that are genetically dissimilar to themselves, thereby potentially increasing the heterozygosity and/or reducing the level of inbreeding of the resulting offspring. However, empirical tests of this hypothesis have been criticized because a low number of molecular markers can lead to biased estimates of relatedness among individuals, and because all studies to date have been correlational and therefore unable to rule out potentially confounding factors. The red-backed fairy-wren is a bird with very limited dispersal, and hence the risks of inbreeding are high. We used a panel of microsatellite markers to examine paternity and relatedness between mates in this species, and also conducted an experiment that manipulated relatedness between a female and her social mate. Results from both approaches showed that females paired to genetically similar males were more likely to produce young sired by extrapair males, and that those offspring were less inbred (more heterozygous) than within-pair offspring. Thus, female fairy-wrens are able to avoid the potential costs of close inbreeding through extrapair copulations.

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It is now clear that females of many socially monogamous species copulate with males other than their social mates (Griffith et al. 2002). It is generally thought that females benefit from production of young sired by these extrapair males, yet despite nearly two decades of work, the adaptive benefits of extrapair paternity to females remain unclear and controversial (Griffith et al. 2002; Westneat & Stewart 2003; Arnqvist & Kirkpatrick 2005; Schmoll 2011). Although females might gain direct benefits by mating with extrapair males (e.g. Gray 1997; Kempenaers et al. 1999; Li & Brown 2002), in most systems it is thought that females benefit indirectly through increased offspring quality (reviewed in: Jennions & Petrie 2000; Zeh & Zeh 2001; Griffith et al. 2002). This might occur if females choose extrapair mates that possess a particular gene or set of genes that impart some benefit to the offspring (Hamilton 1990; Westneat et al. 1990). However, studies of this 'good genes' hypothesis have produced mixed results (e.g. Schmoll et al. 2003; Gustafsson & Qvarnström 2006).

More recently, the focus has turned to the idea that the interaction between the male and female's genes can affect offspring fitness, and thus females might benefit from choosing extrapair mates with whom they are genetically compatible (Tregenza & Wedell 2000; Mays & Hill 2004; Kempenaers 2007). Although 'genetic compatibility' might involve a few specific genes (e.g. the major histocompatibility complex (MHC); see Hughes & Yeager 1998; Penn & Potts 1999; Milinski 2006; Thoß et al. 2011) or extranuclear elements (Zeh & Zeh 1996), more general genome-wide compatibility is likely to have important fitness consequences in many populations. In particular, overall genetic similarity (i.e. genetic relatedness) between parents has been shown to have strong effects on offspring fitness (e.g. Amos et al. 2001; Coltman & Slate 2003; Foerster et al. 2003; Mulard et al. 2009), to affect mate choice in species that do not form long-term pair bonds (e.g. Bull & Cooper 1999; Stow & Sunnucks 2004; Thuman & Griffith 2005), and also to affect social mate choice in species that do form pair bonds (Cockburn et al. 2003; Cohen & Dearborn 2004; Mulard et al. 2009). Genetic similarity might also affect extrapair mate choice, particularly in populations where social mate choice is constrained in some way, as in these cases extrapair mating can provide females with a 'second chance' to choose a genetically compatible mate (Brooker et al. 1990; Freeman-Gallant et al. 2006). Accordingly, genetic compatibility may be a strong force driving the evolution of extrapair mating behaviour in

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some populations (Tregenza & Wedell 2002; Brouwer et al. 2010), particularly those with limited dispersal, such as cooperative breeders and island populations (Frankham 1998), because in these systems the chance of being socially paired with a closely related individual is relatively high (Richardson et al. 2004).

Several studies have examined the effect of genetic relatedness on extrapair paternity in recent years, thanks to the increasing prevalence and ease of genetic tools to determine both relatedness and heterozygosity. However, many such studies use only a few loci to estimate relatedness and heterozygosity (e.g. Smith et al. 2005; Foerster et al. 2006; Edly-Wright et al. 2007), which limits the ability to detect biologically significant differences in relatedness or heterozygosity (Smith et al. 2005), and may also lead to biased results if the same markers are used to assess both parentage and heterozygosity (Wetzel & Westneat 2009). Moreover, all previous studies of the effects of relatedness on extrapair mating in wild populations have been correlative, and therefore, did not experimentally control for possible confounding factors such as male age and attractiveness, pair bond length, or other unknown factors (Griffith et al. 2002). An experimental test would allow the effects of these factors to be removed, but such experimental tests in wild populations are extremely challenging as it is difficult to manipulate the relatedness of pairs (but see Tregenza & Wedell 2002; Pryke et al. 2011).

A related unresolved issue concerns the ways in which genetic similarity might affect extrapair mating. First, if overall heterozygosity is strongly related to individual fitness (reviewed in Hansson & Westerberg 2002), females should choose maximally dissimilar males in order to maximize offspring heterozygosity (Mays & Hill 2004). Under this 'genetic dissimilarity hypothesis', females that are socially paired to closely related males should be most likely to produce extrapair young (relative to other females), and the males that they choose as extrapair mates should be less related to them than expected by chance (Griffith et al. 2002; Tarvin et al. 2005). Alternatively, heterozygosity may not have a strong effect on offspring fitness except in the extreme, that is, when closely related individuals breed to produce highly inbred offspring with low fitness (Keller & Waller 2002; Kruuk et al. 2002; Hansson 2004; Spottiswoode & Møller 2004; Rodríguez-Muñoz & Tregenza 2009). If so, then females paired with closely related social mates might copulate with extrapair males to avoid the costs of inbreeding (Tregenza & Wedell 2000) rather than to maximize offspring heterozygosity. Under the 'inbreeding avoidance hypothesis', females that are paired to closely related males should produce more extrapair young than females that are paired to distantly related males, but the extrapair mates chosen may not be more distantly related to the female than an average male in the population (Tarvin et al. 2005).

In this study we used both correlational and experimental approaches to study the genetic dissimilarity and inbreeding avoidance hypotheses in the red-backed fairy-wren, *Malurus melanocephalus*, a small Australian passerine. Red-backed fairy-wrens are socially monogamous and typically pair for life, but have very high rates of extrapair paternity, with over 50% of offspring being the result of extrapair copulations (Webster et al. 2008). This species is also a cooperative breeder, with some young males ('auxiliaries') remaining on their natal territory to assist their parents in raising subsequent broods. Moreover, like many other cooperative breeders (Hatchwell & Komdeur 2000), natal dispersal is thought to be extremely limited in this species (below).

We used a panel of microsatellite markers to examine whether this limited dispersal leads to a high risk of inbreeding, and whether females use extrapair copulations to reduce this risk. In addition to these correlative analyses, we also conducted an experimental test of the inbreeding avoidance hypothesis by

removing breeding males from groups with and without auxiliaries to create new breeding pairs, each consisting of a female paired with her own son or with an 'unrelated' male from a neighbouring group. This experimental approach allowed us to examine the effects of partner relatedness on extrapair paternity rates while controlling for the effects of social male attractiveness, length of pair bond, male age, and other unknown factors, and we predicted that experimental females socially paired to their own sons would produce more extrapair offspring than would control females paired to unrelated males.

METHODS

Field Methods

We conducted our research on a population of red-backed fairy-wrens at a long-term study site in the forest surrounding the reservoirs of the Herberton Shire on the Atherton Tablelands in Queensland, Australia (145°25'E, 17°22'S). Research was conducted during the breeding seasons (October–February) of 2004–2007 (breeding seasons are designated by the year in which they ended). In each year we captured adults with mist nets to collect a small (ca. 30 µl) blood sample taken from the brachial vein for genetic analysis, and also to individually mark each bird with a numbered aluminium band (Australian Bird and Bat Banding Scheme) and a unique combination of three coloured leg bands. Group compositions and territory boundaries were determined through repeated observations of the birds in the field. We monitored all breeding attempts by groups on the field site. On the sixth day after hatching, nestlings were banded and a small (30 µl) blood sample was taken from the tarsal vein of each nestling for genetic analysis.

Experimental Methods

Removal experiments were conducted in 2006 ($N = 7$) and 2007 ($N = 25$) at a second study site approximately 15 km southwest of our long-term study site. For our experimental treatment, we captured and removed breeding males from groups with a male auxiliary. Auxiliary helpers usually have delayed plumage maturation and are brown rather than the bright red and black of most males. However, they are reproductively capable and occasionally sire young (Webster et al. 2008). The removed breeding males were driven approximately 10 km away and released in suitable habitat where fairy-wrens were present. No males returned within the same breeding season, although one male removed in 2006 did return to the study site in the subsequent year. Within hours of each breeding male's removal, the group's auxiliary assumed the breeding position, socially pairing with his own mother. Our observations confirmed that these former auxiliaries interacted with the breeding females and showed behaviours typical of dominant breeding males (see below; see also Karubian et al. 2011). For experimental control groups, we removed breeding males from groups without auxiliaries. Again, within a few hours a new male, usually an auxiliary male from a neighbouring group, moved in and assumed the breeding position. Occasionally ($N = 4$) females re-paired with an older bright male. These pairings were excluded from further analysis as plumage colour and age also play a role in male reproductive success (Webster et al. 2008). Thus, new breeding males in all manipulated groups used for analysis were 1-year-old former auxiliaries with dull brown plumage; the new breeding males differed between treatments in terms of whether they were closely related to the breeding female (experimental) or not (control).

To control for female breeding status, all removals were conducted when the group female was in the latter stages of nest building ($N = 19$) and/or had begun to lay or incubate eggs ($N = 12$).

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