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Genetic similarity of social mates predicts the level of extrapair paternity in splendid fairy-wrens

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Why females mate with multiple males, particularly in socially monogamous species, is one of the central unanswered questions in sexual selection and behavioural ecology. Recent theory suggests that socially monogamous females may improve the genetic quality of their offspring by mating with extrapair males with whom they are more genetically dissimilar (relative to their social mates), because decreased genetic similarity between mates may lead to decreased inbreeding depression of offspring and other benefits. We found that levels of extrapair paternity in splendid fairy-wren, *Malurus splendens*, broods were predicted by genetic similarity between social mates. Females whose entire broods were sired by extrapair males were more genetically similar to their social mates than they were to their extrapair mates, but females were no less similar to their extrapair mates than they were to the average male from the population. Within-pair young (WPY) from mixed-paternity broods showed higher levels of inbreeding and lower heterozygosity than did their extrapair nestmates or WPY from broods without extrapair paternity. Several processes could account for these patterns, including female choice of genetically dissimilar mates, differential sperm investment by males or differential survival of embryos as a function of genetic dissimilarity between mates, or postcopulatory processes such as sperm competition, cryptic female choice, or interactions between sperm and ova. Regardless of the mechanism, our results suggest that female splendid fairy-wrens may indirectly benefit from extrapair mating because it leads to lower levels of inbreeding and increased heterozygosity in their offspring.

Although males can increase their fecundity by mating with multiple partners, the same is generally not true for females, and why females mate with multiple males remains one of the central unanswered questions in behavioural ecology and sexual selection (Zeh & Zeh 1996; Petrie & Kempenaers 1998; Jennions & Petrie 2000; Tregenza & Wedell 2000; Griffith et al. 2002; Griffith & Montgomerie 2003). This is particularly true for species in which females form social pair bonds with males but also copulate with males outside of the social pair (‘extrapair males’). For example, the vast majority of birds are socially monogamous, and yet in approximately 75% of such species, females copulate with extrapair males as well as with their social partners (Griffith et al. 2002). This lack of concordance between genetic and social mating systems has led to considerable research focusing on birds as a model system for understanding the function of extrapair copulations and multiple mating by females in general.

Many studies have tested ‘good genes’ and Fisherian hypotheses for extrapair mating, which predict that females copulate with extrapair males bearing phenotypic traits indicative of good health or attractiveness. Although many of these studies have found support for good genes models, many others have failed to demonstrate a clear relationship between male phenotypic traits and extrapair mating success (reviewed in Griffith et al. 2002), suggesting that extrapair mating may sometimes occur for reasons other than those proposed by traditional sexual selection models. An alternative to traditional explanations for extrapair mating is the proposal that females can improve the viability of their offspring by mating with

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extrapair males with whom they are more genetically compatible in comparison with their social mates (Zeh & Zeh 1996; Tregenza & Wedell 2000; Blomqvist et al. 2002; Mays & Hill 2004; Neff & Pitcher 2005). Genetic compatibility between mates may provide several benefits, including increased heterozygosity of offspring, which can lead to a reduction in inbreeding depression or overdominance benefits resulting from an increase in the variety of gene products (Brown 1997, 1999; Penn & Potts 1999; Tregenza & Wedell 2000; Neff & Pitcher 2005). Heterozygosity (as measured by microsatellites) has been shown to have positive effects on individual performance in wild populations of vertebrates (e.g. Coltman et al. 1999; Amos et al. 2001; Hansson et al. 2001; Keller & Waller 2002; Acevedo-Whitehouse et al. 2003; Foerster et al. 2003), and may be particularly important in mate choice by females if offspring immunocompetence is influenced by allelic diversity or complementarity in the major histocompatibility complex (MHC) (Penn & Potts 1999) or other loci (Johnsen et al. 2000; Reid et al. 2003). Recently, investigators have begun to consider whether good genes and compatibility processes may operate simultaneously (Colegrave et al. 2002; Roberts & Gosling 2003; Mays & Hill 2004; Neff & Pitcher 2005).

Genetic similarity between mates is an important and easily measured component of genetic compatibility (e.g. Blomqvist et al. 2002; Pai & Yan 2002; Marshall et al. 2003) because dissimilarity between parental haplotypes increases the chances of heterozygosity at offspring loci. Genetic similarity could influence reproductive patterns through a variety of adaptive and nonadaptive mechanisms. For example, females may choose mates based on genetic dissimilarity or a correlate of dissimilarity (e.g. Foerster et al. 2003; Marshall et al. 2003), or males may invest sperm differentially according to the genetic dissimilarity between themselves and potential mates. Alternatively, postcopulatory processes such as sperm competition, cryptic female choice, or interactions between sperm and ova may result in a higher probability of fertilization of eggs by genetically dissimilar sperm (e.g. Tregenza & Wedell 2002; Pai & Yan 2002; Marshall et al. 2003) or differential survival of embryos as a function of the genetic dissimilarity of their parents (Tregenza & Wedell 2002). These different mechanisms can be difficult to tease apart, and few studies have successfully identified such mechanisms (but see Marshall et al. 2003).

Regardless of the mechanism, reproductive patterns in relation to genetic similarity can indicate the indirect adaptive benefits of multiple mating to females. If selection has favoured mechanisms that enhance the probability that offspring result from genetically dissimilar ova and sperm, several predicted patterns should hold (Griffith et al. 2002). First, the proportion of young sired by extrapair males should increase with increasing genetic similarity between females and their social mates. Second, a female's extrapair mates should be less genetically similar to her than is her social mate. Finally, extrapair mating should affect relative levels of inbreeding and/or heterozygosity between young sired by a female's social mate ('within-pair young', or WPY) and those sired by her extrapair mates ('extrapair young', or EPY). Specifically, WPY from mixed-paternity broods should show higher levels of inbreeding and lower heterozygosity than do their EPY nestmates or WPY from broods without extrapair paternity.

We used microsatellite genetic markers to examine patterns of parentage in cooperatively breeding splendid fairy-wrens, *Malurus splendens*, to test the hypothesis that genetic similarity between social mates influences the level of extrapair paternity in broods. Fairy-wrens are characterized by some of the highest known extrapair fertilization rates among birds (Brooker et al. 1990; Dunn & Cockburn 1999) and up to 65% of splendid fairy-wren offspring result from extrapair mating (Brooker et al. 1990). Moreover, in fairy-wrens, both dispersal distances and opportunities for social mate choice are limited (see Discussion), suggesting that genetic similarity between social mates may be particularly important (Foerster et al. 2003).

METHODS

Field Methods

We monitored 35 to 69 South Australian splendid fairy-wren groups per year during the breeding seasons of 1992 through 1998 (for details, see Webster et al. 2004). Because of drought, only two groups produced offspring during 1994, so data from that year were omitted here. Groups on our study site consisted of a breeding female and male, and from zero to four other nonbreeding adults ('helpers'), most of which were males. Virtually all adults in the study population each year were uniquely colour-banded. Blood samples (5–50 μl) were collected via brachial venipuncture from adults captured in mist nets and from nestlings between 4 and 8 days posthatching, and stored at −70°C or in a lysis buffer until analysis. Unhatched eggs and dead nestlings were collected and either frozen at −70°C or macerated and stored in lysis buffer until analysis.

Microsatellite Markers

We used six hypervariable microsatellite markers to determine paternity of offspring, estimate genetic similarity between females and their reproductive partners (Queller & Goodnight 1989), and measure level of inbreeding ('internal relatedness' or IR; Amos et al. 2001) and standardized heterozygosity (SH; Coltman et al. 1999) of individuals (see below). Three of the six microsatellite loci (*Msp4*, *Msp6* and *Msp10*) were developed specifically for *Malurus splendens* (Webster et al. 2004) and three (*Mcy3*, *Mcy7* and *Mcy8*) were available from the work by Double et al. (1997) on superb fairy-wrens, *Malurus cyaneus*. In our study population, the number of alleles per locus for these six microsatellites ranged from 9 to 24, and observed heterozygosities ranged from 0.635 to 0.945 (Webster et al. 2004). We used the program Cervus 1.0 (Marshall et al. 1998), which utilizes a maximum-likelihood approach to assign paternity (for full details on paternity analyses, see Webster et al. 2004). All individuals included in our heterozygosity and genetic similarity analyses were typed at all six loci.

Genetic Similarity, Inbreeding and Heterozygosity

We estimated genetic similarity as pairwise relatedness between breeding females and their mates with the program SPAGeDi 1.0 (Hardy & Vekemans 2002) using a 'two-genes' relationship coefficient, *r*, based on Queller & Goodnight's (1989) formula. This measure estimates genetic similarity between two individuals based on allele sharing, but weights the influence of alleles by their frequency in the population; thus it provides a maximum-likelihood estimate of relatedness. We excluded offspring when compiling individuals in the data set for analysis of genetic similarity between adults to reduce the problem of overrepresentation of alleles in successful familial lineages. Mean ± SE value of *r* between 32 mother–offspring pairs was 0.4966 ± 0.0240, and did not differ from the expected value of 0.5 (one-sample *t* test: $t_{31} = -0.141$, $P = 0.889$). Relationship coefficients were computed for each pair of adult individuals in the population separately for each year because the coefficients are dependent on the genotypes present in the population, and those change from year to year.

IR and SH were calculated for each individual in the population separately for each year because these measures also are dependent on the genotypes present in the population. IR is a modification of Queller & Goodnight's *r*, but measures similarity of parental half-genotypes within an individual, instead of between individuals; thus it is a measure of inbreeding (Amos et al. 2001). SH is a measure of individual heterozygosity in which the score at each locus is weighted by the population-wide average heterozygosity at that locus; values are then averaged across all loci (modified from Coltman et al. 1999). For calculations of these measures in adults, we excluded offspring when calculating population allele frequencies and mean heterozygosity per locus to reduce the problem of overrepresentation of alleles due to successful familial lineages. We were unable to circumvent this problem when calculating IR and mean SH for offspring, and population heterozygosity and allele frequencies used in offspring calculations were based on all individuals present in the population for that year.

Level of Extrapair Paternity and Genetic Similarity, Inbreeding and Heterozygosity

We compared genetic similarity between females and their social or extrapair mates among pairs that produced only WPY, those that produced mixed-paternity broods, and those that produced only EPY. When positive relationships were detected, we tested whether the patterns were driven by inbreeding or heterozygosity of either the females or the males for each of these categories of extrapair paternity (Cordero et al. 2004). Analyses involving females that produced only WPY or only EPY were restricted to broods comprising at least two sampled offspring to increase confidence in the designated level of extrapair paternity (modal clutch size in our population was three eggs). Because including broods of two could potentially lead to incorrect designations of brood type, we re-ran these analyses using only broods in which at least three nestlings were sampled. The results were qualitatively the same as the two-nestling analyses, and are not reported here (analyses are available from the authors).

We included only one randomly chosen brood per social pair in analyses of the relationship between level of extrapair paternity and genetic similarity between social mates. Only one randomly chosen brood per triad (combination of female, social male and extrapair male) was included in comparisons of social males and the extrapair males that cuckolded them. We used one-tailed statistical tests when comparing inbreeding and heterozygosity between WPY and EPY, because the genetic similarity hypothesis makes clear directional predictions about those patterns. All other analyses were based on two-tailed tests.

Genetic Similarity Between Females and Average Males

Because each female shares a different relationship coefficient with each male, the average similarity between a female and all the males in the population in a given year is unique for that female in that year. We compared the similarity between a female and her partner (social or extrapair male, depending on the analysis) to the average similarity of that same female and all males in the population in that year. For each female we also calculated the difference between the genetic similarity to her partner (social or extrapair) and to the average male from the population as ((similarity between female and partner) − (average similarity between female and each male)). Only one randomly chosen brood per female–male dyad was included in these analyses.

Male Secondary Sexual Characteristics

Splendid fairy-wrens are sexually dichromatic, and males in breeding plumage vary substantially in the amount of blue on the abdomen. Thus, it is possible that females choose extrapair males based on secondary sexual characteristics. We tested for associations between measures of reproductive success and amount of blue on the abdomen, mass, wing length, tarsus length, tail length, condition, cloacal protuberance volume and age. We scored amount of blue on the abdomen as the percentage of the area between the black breast line and the cloaca that was composed of blue feathers. We calculated body condition as the residuals of log(mass) regressed on 3 × log(tarsus) (Pryke et al. 2001). Cloacal protuberance (CP) volume, which is positively related to number of stored sperm in males (Tuttle et al. 1996), was calculated as $\pi \times (D/2 \times W/2) \times L$, where $D =$ CP depth, $W =$ width, and $L =$ length (Tuttle et al. 1996). Adult birds were categorized as 1 year old (i.e. hatched during the previous breeding season) or 2 or more years old.

We used stepwise logistic regression to identify male characteristics that could predict social status (i.e. breeder versus auxiliary, reflecting territory ownership and primary access to the breeding female within the territory; Webster et al. 2004), and whether or not a male sired WPY, EPY, or any offspring at all within a breeding season. We did not attempt to capture and measure every male in the population during each year of the study, yet some males were caught in more than 1 year. Not all characters were measured each time a male was captured. To avoid pseudoreplication, we included only measurements from a single breeding season for each male (values were averaged when a male was caught more than once within a breeding season). If a male was represented by multiple records, we included the record that contained the greatest number of measured characters, with intentional biases towards including those records in which amount of blue on the abdomen was measured and towards including the most recent record available for each male.

The logistic regression procedure ignores entire records for which data are missing for one or more variables. Because we lacked data for one or more characters for many males, inclusion of all the male traits in the variable pools resulted in small sample sizes for the analyses. To address this problem, we ran two sets of models for each analysis. The variable pools of the initial stepwise logistic regression models included all the morphological variables mentioned above, plus age and the interaction between age and amount of blue on the abdomen. We then ran subsequent models that included only those variables that seemed potentially important according to the initial models; we report the results of this second set of models. This procedure substantially increased the sample sizes for the analyses because it allowed the inclusion of records that were missing one or more measurements other than those that seemed important in the initial models. Variables deemed important in initial models were those that were selected by the initial stepwise procedure, or those that were not selected, but had score statistics with P values less than or equal to 0.15 at some stage in the model-building procedure. If the interaction variable seemed important in an initial model, then all components of that variable were made available in the subsequent model. In addition to the logistic regression analyses, we also tested for correlations between each of the morphological measures and SH and IR.

In separate analyses, we tested for differences in male characteristics between social males and the extrapair males that cuckolded them using paired t tests.

Heterozygosity and Level of Inbreeding Between Unhatched Embryos and Surviving Adults

We tested whether heterozygosity and level of inbreeding affected hatching success by comparing these measures between embryos that did not hatch and adult fairy-wrens. We did not include nestlings that died prior to fledging or juveniles that may have died prior to reaching breeding age in this analysis to avoid confounding effects of events that may occur after hatching but before recruitment into the adult population. This analysis included all embryos and all adults (i.e. birds in their second year or older) for which we were able to amplify all six microsatellite loci. Since adults have slightly different values of SH and IR in different years (because these values are dependent on allele frequencies in the year in which they are calculated), we calculated the average of each of these values across all years that an individual was alive in our study.

In all analyses we used parametric statistical tests when the data met the appropriate assumptions; otherwise we used nonparametric tests.

RESULTS

Genetic Similarity and Level of Extrapair Paternity

Genetic similarity between females and their social mates varied according to whether broods contained only within-pair young, mixed paternity, or only extrapair young (one-way ANOVA: $F_{2,111} = 4.801$, $P = 0.010$; Fig. 1). Post hoc tests revealed that similarity between females and their social mates was higher in broods in which the social male was completely cuckolded than in broods without extrapair young ($P = 0.003$) or mixed-paternity broods ($P = 0.022$). This pattern did not result from variation in level of inbreeding or heterozygosity of either females or males among brood type categories (females: Kruskal–Wallis test: IR: $P = 0.246$; SH: $P = 0.362$; males: one-way ANOVA: IR: $P = 0.459$; SH: $P = 0.507$), indicating that the pattern did indeed reflect genetic similarity between social mates.

Social versus Extrapair Males

We found no overall difference in the genetic similarity between females and their social mates versus females and their extrapair mates (paired t test: $t_{106} = 1.314$, $P = 0.192$). However, females that produced only EPY were significantly less genetically similar to their extrapair mates than they were to their social mates (paired t test: $t_{47} = 2.376$, $P = 0.022$; Fig. 2a). In these cases, extrapair males also were less inbred and more heterozygous than

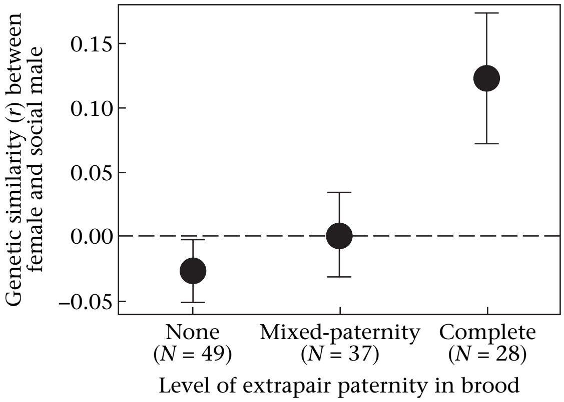

Figure 1. Relationship between genetic similarity ($\bar{X} \pm$ SE) of females to their social mates and level of extrapair paternity.

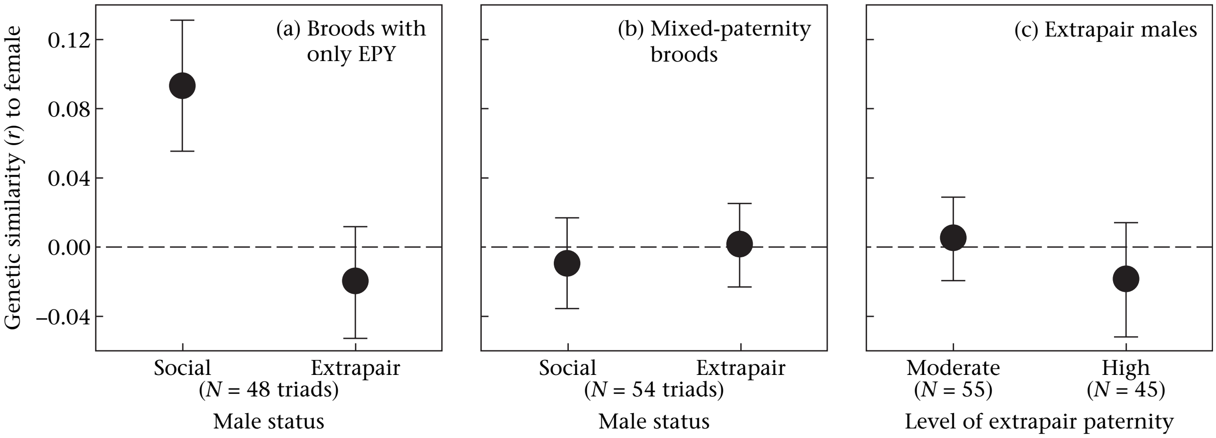

Figure 2. Mean ± SE genetic similarity between females and (a) their social versus extrapair mates when broods contained only extrapair young (EPY), (b) their social versus extrapair mates when broods contained young of mixed paternity, and (c) extrapair mates when broods had moderate versus high levels of extrapair paternity.

the social males they cuckolded (paired *t* test: IR: $t_{47} = 2.060$, $P = 0.045$; SH: $t_{47} = -2.043$, $P = 0.047$). Extrapair and social males did not differ in genetic similarity to the female ($t_{53} = -0.313$, $P = 0.756$; Fig. 2b) or in levels of inbreeding and heterozygosity (IR: $P = 0.999$; SH: $P = 0.903$) when the analysis was restricted to mixed-paternity broods.

Extrapair paternity was associated with genetic similarity between social mates, but genetic similarity between females and the extrapair sires of their offspring did not vary with level of extrapair paternity. Similarity to the female did not differ between extrapair males from mixed-paternity broods and those from broods containing only EPY (Student's *t* test: $t_{98} = 0.583$, $P = 0.561$; Fig. 2c). Moreover, a female's similarity to her extrapair mate did not differ from her average similarity to other males in the population, regardless of the level of extrapair paternity in her brood (paired *t* tests: mixed paternity: $P = 0.494$; only EPY: $P = 0.974$). In contrast, females that produced EPY tended to be more similar to their social mates than they were to the average male (paired *t* test: $t_{67} = 1.98$, $P = 0.052$), especially when the social male was completely cuckolded ($t_{28} = 2.81$, $P = 0.009$), whereas females that produced only WPY were no more genetically similar to their social mates than they were to the average male ($t_{48} = -0.27$, $P = 0.792$). Thus, the difference between female similarity to her social mate and the average male varied with level of extrapair paternity (one-way ANOVA: $F_{2,111} = 4.999$, $P = 0.008$; Fig. 3a). Post hoc tests revealed that the difference was greater in broods with complete cuckoldry than in broods without cuckoldry ($P = 0.003$) or mixed-paternity broods ($P = 0.010$). However, the difference between female similarity to her extrapair mate and the average male did not vary with the level of paternity (Student's *t* test: $t_{98} = 0.391$, $P = 0.696$; Fig. 3b).

Male Morphology

Stepwise logistic regression analyses indicated that both age and the interaction of age and amount of blue on the abdomen significantly predicted male breeding status (Table 1). Older males, and younger males that had bluer abdomens, were more likely to hold breeder status (as opposed to auxiliary status) than were younger males that were not very blue. Amount of blue on the abdomen also was a weak predictor of whether a male sired EPY within a breeding season (Table 1). Thus, amount of blue on the abdomen is to some degree associated with mating success and may serve as a sexual signal (but see Discussion). Only cloacal protuberance volume predicted whether a male sired any offspring at all during a breeding season, but the relationship was weak (Table 1). None of the variables we measured predicted whether a male sired WPY. None of the morphological variables we measured was significantly correlated with either SH or IR (percentage of blue on abdomen: SH: $r_S = 0.036$, $P = 0.704$, $N = 117$; IR: $r_S = 0.022$, $P = 0.811$, $N = 117$; mass: SH: $r_S = 0.067$, $P = 0.383$, $N = 173$; IR: $r_S = -0.072$, $P = 0.348$, $N = 173$; wing length: SH: $r_S = 0.013$, $P = 0.875$, $N = 154$; IR: $r_S = -0.024$, $P = 0.764$, $N = 154$; tarsus length: SH: $r_S = -0.057$, $P = 0.480$, $N = 154$; IR: $r_S = 0.046$, $P = 0.572$, $N = 154$; tail length: SH: $r_S = -0.006$, $P = 0.945$, $N = 145$; IR: $r_S = 0.006$, $P = 0.939$, $N = 145$; body condition: SH: $r_S = 0.051$, $P = 0.540$, $N = 144$; IR: $r_S = -0.041$, $P = 0.622$, $N = 144$; cloacal protuberance volume: SH: $r_S = -0.060$, $P = 0.451$, $N = 159$; IR: $r_S = 0.046$, $P = 0.561$, $N = 159$).

Extrapair males did not differ in morphology from the social males they cuckolded regardless of level of extrapair paternity (paired *t* tests; all pairs: percentage of blue on abdomen: $P = 0.867$; mass: $P = 0.342$; wing length: $P = 0.808$; tarsus length: $P = 0.174$; tail length: $P = 0.357$; body condition: $P = 0.846$; cloacal protuberance volume: $P = 0.339$; only broods with complete cuckoldry: percentage of blue on abdomen: $P = 0.825$; mass: $P = 0.569$; wing length: $P = 0.998$; tarsus length: $P = 0.688$; tail length: $P = 0.342$; body condition: $P = 0.645$; cloacal protuberance volume: $P = 0.969$), suggesting that probability of siring a female's extrapair offspring may not be related to differences in secondary sexual characteristics between extrapair males and the

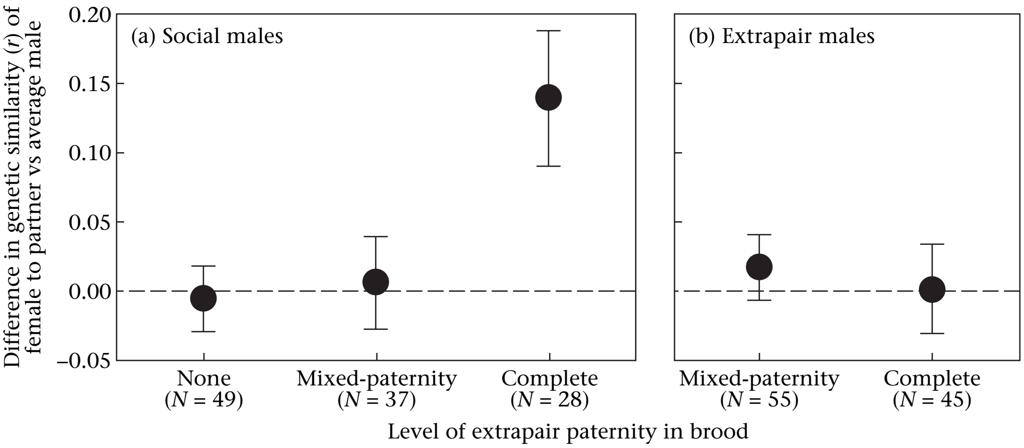

Figure 3. Mean ± SE difference in genetic similarity between females and (a) their social mate versus the average male in the population and (b) their extrapair mate versus the average male in the population for each level of extrapair paternity.

social males they cuckold. Extrapair males tended to be younger than the males they cuckolded (Wilcoxon matched-pairs signed-ranks test: $Z = -2.14$, $N = 108$, $P = 0.033$), especially when the analysis was restricted to broods with complete cuckoldry ($Z = -2.45$, $N = 49$, $P = 0.014$). However, neither IR nor SH varied with male age category (1 year old versus 2 or more years old; IR: $t_{151} = -0.85$, $P = 0.397$; SH: Mann–Whitney *U* test: $U = 2036$, $N_1 = 41$, $N_2 = 112$, $P = 0.284$), so the effect of age on male extrapair reproductive success does not confound the genetic patterns we observed. Thus, although unmeasured phenotypic traits may be involved (e.g. timing of the onset of prenuptial moult, display rate, song quality or rate, quality of structural blue plumage rather than amount of blue), success of extrapair sires over the social males they cuckolded cannot be attributed to the phenotypic traits that we measured.

Consequences for Offspring

Extrapair fertilizations affected levels of inbreeding and heterozygosity of offspring. Offspring from purely within-pair broods ($N = 157$ offspring) were significantly less inbred (Mann–Whitney *U* test: $U = 5025$, one-tailed $P = 0.036$) and more heterozygous ($U = 4735.5$, one-tailed $P = 0.008$) than the WPY from mixed-paternity broods ($N = 75$ offspring; Fig. 4a, b). Within mixed-paternity broods, EPY tended to be less inbred and more heterozygous than their within-pair maternal half-siblings, although the tendencies were marginally nonsignificant (paired *t* tests on values averaged across each type of offspring within each brood: IR: $t_{50} = 1.382$, one-tailed $P = 0.087$; mean SH: $t_{50} = -1.482$, one-tailed $P = 0.073$; Fig. 4c, d).

Heterozygosity, Level of Inbreeding and Egg Hatchability

Individuals that did not hatch ($N = 33$) did not differ from those that were known to survive to adulthood ($N = 379$) in level of inbreeding (IR: unhatched eggs: $\overline{X} = 0.0468$; adults: $\overline{X} = 0.0303$; Mann–Whitney *U* test: $U = 5937$, $P = 0.630$) or heterozygosity (SH: unhatched eggs: $\overline{X} = 0.9711$; adults: $\overline{X} = 0.9973$; Mann–Whitney *U* test: $U = 5666$, $P = 0.371$).

DISCUSSION

The level of extrapair paternity in splendid fairy-wrens increased when social mates were genetically similar, and extrapair mating positively influenced inbreeding and heterozygosity of offspring. These patterns might result from females actively responding to the genotype of their social partners when making decisions about whether to engage in extrapair mating, or from females mating promiscuously yet indiscriminately, with high genetic similarity between mates decreasing fertilization success (e.g. due to sperm competition or interactions between sperm and ova) and/or embryo survival. Although distinguishing among these possibilities is difficult, our data are compelling in that they suggest genetic similarity between social mates affects the likelihood that a female will produce a brood consisting solely of extrapair offspring (or, equivalently, that a social male will sire offspring in his brood). Other recent studies of extrapair mating in birds have drawn similar conclusions (e.g. Kempenaers et al. 1999; Blomqvist et al. 2002; Foerster et al. 2003; Freeman-Gallant et al. 2003; Marshall et al. 2003; Masters et al. 2003), and genetic similarity may affect patterns of paternity in other taxa as well (for reviews, see Zeh & Zeh 1996; Tregenza & Wedell 2000; Mays & Hill 2004; Neff & Pitcher 2005).

These results support recent theoretical work on the benefits of reproductive promiscuity in females that has emphasized genetic compatibility as a potentially important mechanism driving female mating patterns (e.g. Zeh & Zeh 1996; Brown 1997, 1999; Penn & Potts 1999; Tregenza & Wedell 2000; Colegrave et al. 2002; Reinhold 2002). By mating with males having compatible (dissimilar) genotypes, females may increase the heterozygosity or allelic diversity of their offspring, which may reduce the

Table 1. Stepwise logistic regression analysis of the relationship between male characteristics and male reproductive success in splendid fairy-wrens

		Parameter statistics							Model statistics				
												% Correct classification (% correct in each class)	
Response variable	*N*	Variable*	*B*	SE	Wald	df	Exp(*B*)	*P*	R^2†	χ^2	*P*	Step 0‡	Final model
Social status§	76	Age	4.650	1.127	17.02	1	104.59	0.000	0.45	28.72	0.000	71.1 (100, 0)	84.2 (90.7, 68.2)
		Age × % Blue	−0.063	0.027	5.30	1	0.94	0.021					
		Constant	−1.992	0.435	20.96	1	0.14	0.000					
Sired offspring**	137	CP volume	0.007	0.003	4.14	1	1.01	0.042	0.04	4.39	0.036	59.9 (100, 0)	59.1 (89, 14.5)
		Constant	−1.659	0.650	6.52	1	0.19	0.011					
Sired WPY**	53	Constant	−0.582	0.286	4.127	1	0.56	0.042	—	—	—	64.2 (100, 0)	—
Sired EPY**	81	% Blue	0.022	0.012	3.60	1	1.02	0.058	0.07	3.88	0.049	77.8 (100, 0)	77.8 (100, 0)
		Constant	−2.469	0.735	11.27	1	0.09	0.001					

The models for social status, sired offspring and sired extrapair young (EPY) were based on a subset of morphological and age variables indicated to be potentially important in initial models that included the following variables: percentage of blue on abdomen, mass, tail length, wing length, tarsus length, body condition, volume of cloacal protuberance, age, and the interaction between age and percentage of blue on abdomen. None of the variables in the initial model for sired within-pair young (WPY) was potentially important; therefore a subsequent model was not run. See text for further details of model construction.

*Variables in the pools: social status: age, percentage of blue on abdomen, age × percentage of blue on abdomen, cloacal protuberance (CP) volume; sired offspring: cloacal protuberance volume, wing length; sired WPY: all morphological and age variables (see above); sired EPY: age, percentage of blue on abdomen, age × percentage of blue on abdomen.

†Nagelkerke R^2.

‡Initial model run prior to the addition of variables (i.e. model with only a constant).

§Breeder versus auxiliary.

**No versus Yes.

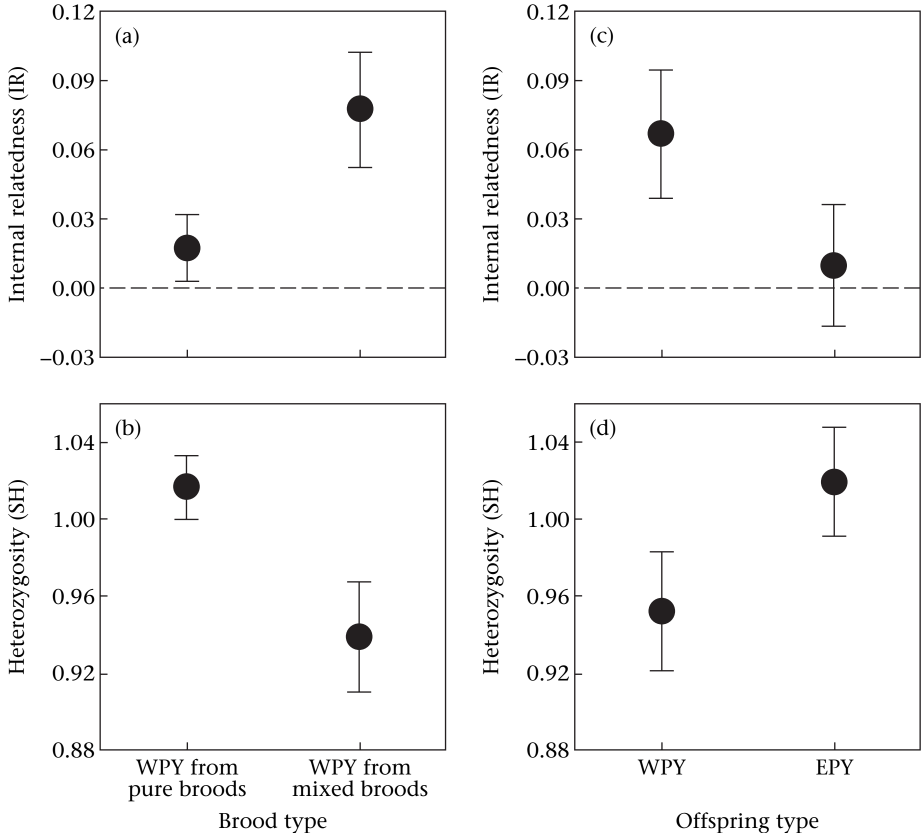

Figure 4. Mean ± SE level of (a) inbreeding and (b) heterozygosity of within-pair young from broods without cuckoldry ($N = 157$ offspring) and from broods with mixed paternity ($N = 75$ offspring). Mean ± SE level of (c) inbreeding and (d) heterozygosity of within-pair and extrapair nestmates. WPY: within-pair young; EPY: extrapair young.

deleterious effects of inbreeding depression (Keller & Waller 2002) and/or enhance offspring immune function (Johnsen et al. 2000; Penn et al. 2002; Reid et al. 2003). Such a strategy could be particularly important in fairy-wrens. Social mate choice is constrained in these species because males from nearby territories quickly fill breeding vacancies (Pruett-Jones & Lewis 1990) and natal dispersal is limited (Brooker & Rowley 1995; Cockburn et al. 2003). Both processes may lead to females frequently pairing socially with suboptimal (genetically similar) males (Brooker & Rowley 1995; Cockburn et al. 2003). Under these conditions, female avoidance of mates that are highly genetically similar may have substantial indirect fitness consequences, and selection may strongly favour discriminatory capabilities (either pre- or postmating) in such systems (Foerster et al. 2003).

The differences in level of inbreeding and heterozygosity that we observed between WPY and their EPY maternal half-sib nestmates were not as striking as might have been expected given the strong association of extrapair mating and genetic similarity between social mates. Although we observed the highest level of similarity between mates in groups that produced only EPY, we could compare heterozygosity of EPY and WPY half-sibs only in broods of mixed parentage. Given the lower degree of similarity between social mates producing mixed-paternity broods, we would not expect extreme differences in heterozygosity between EPY and WPY from such broods. Moreover, the small number of microsatellite loci we used to compare half-sibs in mixed-paternity broods may have limited our ability to detect patterns at more stringent significance levels, even if the effect of parental similarity on offspring heterozygosity is important (Smith et al. 2005; for commentaries regarding the ability of small numbers of microsatellite loci to reflect inbreeding coefficients as derived from pedigree analysis, see: Balloux et al. 2004; Pemberton 2004; Slate et al. 2004). Our comparison of WPY from broods with EPY to WPY from broods without EPY probably better reflects the consequences of genetic similarity between mates for offspring heterozygosity, and these results suggest that extrapair mating by females paired to dissimilar social mates is unnecessary if its function is to improve heterozygosity of offspring. We did not find an effect of offspring heterozygosity or inbreeding on egg hatchability, but our sample size was somewhat limited and other studies have found such a relationship (Bensch et al. 1994; Kempenaers et al. 1999; Kruuk et al. 2002; Cordero et al. 2004; Hansson 2004). A better approach might be to test whether surviving offspring were more heterozygous and less inbred than their full-sib nestmates that did not survive (see Hansson et al. 2001), but our sample size was small and power was too low to conduct this analysis. Nevertheless, decreased inbreeding and increased heterozygosity have been shown to have positive fitness benefits in a variety of vertebrates (e.g. Coltman et al. 1999; Amos et al. 2001; Hansson et al. 2001; Keller & Waller 2002; Acevedo-Whitehouse et al. 2003; Foerster et al. 2003; Reid et al. 2003). Thus, extrapair fertilizations by genetically dissimilar males probably have positive indirect fitness benefits for females.

Recently, Amos et al. (2001) suggested that females might be expected to choose mates that are maximally dissimilar from them, rather than to simply avoid matings with very close relatives. Results from our study do not support this hypothesis, as females were no more dissimilar to the extrapair males that sired their offspring than they were to the average male from the population. Moreover, for each female there were many males on the study site with similarity coefficients much lower than that of her extrapair mate, often in adjacent territories (analysis not shown). These results indicate that female discrimination among potential extrapair mates and/or postcopulatory interactions between extrapair partners are not strongly affected by genetic similarity in splendid fairy-wrens.

Several hypotheses could explain these results. First, females may actively seek extrapair matings when socially paired with genetically similar males, but may not benefit from mating with highly dissimilar extrapair males. For example, if the indirect fitness benefits stemming from genetic dissimilarity between partners peak at some intermediate level of similarity, or if an optimal level of outbreeding exists, then selection may not favour females that seek extremely dissimilar partners (Rätti et al. 1995; Wegner et al. 2003). Under this hypothesis females could use extrapair matings to avoid close inbreeding with genetically similar social mates, but would not be expected to seek highly dissimilar extrapair mates (e.g. Tregenza & Wedell 2000, 2002; cf. Chapman et al. 2003). Similarly, only very high levels of genetic similarity between mates may affect male sperm investment or postcopulatory mechanisms. Alternatively, females might benefit from extrapair matings with highly dissimilar males, but are constrained from doing so by their own discriminatory abilities and/or the high costs of searching out such mates. We do not know what cues females use to assess the similarity of their social mates (or whether they are even able to assess similarity), but discrimination among individuals according to genetic similarity has been demonstrated in other avian species (Petrie et al. 1999; Baglione et al. 2003), and olfaction based on MHC has been suggested as a possible mechanism (Zelano & Edwards 2002).

Importantly, although genetic similarity between social mates clearly influences the likelihood of complete cuckoldry in our population, it does not explain the occurrence of mixed-paternity broods. A possible explanation is that female response to social mate similarity may be nonlinear; that is, the degree of extrapair paternity may increase rapidly only when genetic similarity between mates is high (i.e. when a female is paired with a close relative). Alternatively, the small number (6) of microsatellite loci used in our study may have limited our ability to detect subtle, but real effects of genetic similarity on mating patterns (Balloux et al. 2004; Pemberton 2004; Slate et al. 2004; Smith et al. 2005). Indeed, the degree of genetic similarity between social mates that produced mixed-paternity broods was intermediate between that of pairs that produced either pure within-pair or pure extrapair broods, although post hoc tests were unable to distinguish values associated with mixed-paternity broods from those associated with broods lacking cuckoldry. Nevertheless, our ability to detect highly significant relationships in broods with complete cuckoldry using a small number of loci suggests the effects of genetic similarity on mating patterns in our study population are strong (Smith et al. 2005), although it also is possible that the microsatellite loci we used were linked to other polymorphic loci that affect fitness (i.e. 'local effects'; Hansson & Westerberg 2002; Pemberton 2004). A third alternative is that females may cue on a variety of male characters when actively or passively 'assessing' extrapair mates. Extrapair paternity in mixed-paternity broods thus may reflect female choice or passive processes based on criteria other than genetic dissimilarity (e.g. display or song rate, timing of moult, etc.) and may be better explained by good genes or Fisherian models (see below).

Male age and secondary sexual characteristics appeared to influence male reproductive success in our population. However, those characters did not distinguish extrapair males from the social males they cuckolded, suggesting that the traits we measured are not important to females that are actively or passively comparing potential extrapair males against their social mates. Moreover, the morphological characters we measured were not correlated with heterozygosity or level of inbreeding in males, suggesting that females are unlikely to use those characters to identify particularly heterozygous males. Social males and the extrapair males that cuckolded them were best distinguished by their degree of similarity to the female independent of their morphological attributes. Together, these patterns raise the question of whether female splendid fairy-wrens use one set of male traits (i.e. traits that signal male quality) to assess whether males are acceptable as mates, but use a different set of criteria (genetic similarity) when actively or passively comparing potential mates deemed acceptable based on the first set of traits (Mays & Hill 2004). Recent theoretical studies (Colegrave et al. 2002) and empirical studies of birds (Foerster et al. 2003; Marshall et al. 2003) and mammals (Roberts & Gosling 2003) have shown that both traditional good genes mechanisms (i.e. those in which female preferences converge on a common set of male characteristics) and genetic compatibility mechanisms (those in which the preference of each female is dependent on her own genotype and its similarity to potential mates) may operate simultaneously within a system (reviewed in: Mays & Hill 2004; Neff & Pitcher 2005). If this is the case in our fairy-wren population, then female response to variation in signal traits among the 'acceptable' males when the female and her social mate are genetically compatible could account for mixed-paternity broods.

Several studies have identified female preference for particular traits that signal male quality in extrapair mates (e.g. Kempenaers et al. 1992; Thusius et al. 2001; Forstmeier et al. 2002), and some have shown that females may choose extrapair mates based on traits that are correlated with male heterozygosity (Foerster et al. 2003; Marshall et al. 2003). In these latter systems, females may indirectly benefit from such mate choice because choosing more heterozygous mates should lead to more heterozygous offspring (Mitton et al. 1993). However, such traits do not directly signal genetic dissimilarity between females and potential mates, because the degree of similarity is dependent on the genotypes of both the female and the chosen male. Although female choice or postcopulatory processes simultaneously based on absolute (good genes) and relative (genetic compatibility) criteria is an interesting and compelling proposition, inferences from our data must be drawn with care. Because of the constraints on social mate choice in cooperatively breeding fairy-wrens (see above), the associations between male characteristics and reproductive success we describe may simply result from correlations between the probability of obtaining a breeding position, age and age-dependent morphological characteristics in males, rather than from female choice or passive postcopulatory mechanisms.

As originally proposed by Brooker et al. (1990), extrapair matings for the purpose of avoiding genetically similar males may be particularly likely in fairy-wrens and other species in which natal dispersal and social mate choice are limited (Pruett-Jones & Lewis 1990; Brooker & Rowley 1995; Cockburn et al. 2003; Foerster et al. 2003). Regardless of the underlying mechanism that leads to increased fertilizations by genetically dissimilar social mates or enhanced survival of their offspring, our data indicate that extrapair mating leads to increased heterozygosity of offspring, which potentially can yield substantial indirect fitness benefits for females.

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References

Acevedo-Whitehouse, K., Gulland, F., Greig, D. & Amos, W. 2003. Disease susceptibility in California sea lions. *Nature*, **422**, 35.

Amos, W., Worthington Wilmer, J., Fullard, K., Burg, T. M., Croxall, J. P., Bloch, D. & Coulson, T. 2001. The influence of parental relatedness on reproductive success. *Proceedings of the Royal Society of London, Series B*, **268**, 2021–2027.

Baglione, V., Canestrari, D., Marcos, J. M. & Ekman, J. 2003. Kin selection in cooperative alliances of carrion crows. *Science*, **300**, 1947–1949.

Balloux, F., Amos, W. & Coulson, T. 2004. Does heterozygosity estimate inbreeding in real populations? *Molecular Ecology*, **13**, 3021–3031.

Bensch, S., Hasselquist, D. & von Schantz, T. 1994. Genetic similarity between parents predicts hatching failure: nonincestuous inbreeding in the great reed warbler? *Evolution*, **48**, 317–326.

Blomqvist, D., Andersson, M., Küpper, C., Cuthill, I. C., Kis, J., Lanctot, R. B., Sandercock, B. K., Székely, T., Wallander, J. & Kempenaers, B. 2002. Genetic similarity between mates and extra-pair parentage in three species of shorebirds. *Nature*, **419**, 613–615.

Brooker, M. & Rowley, I. 1995. The significance of territory size and quality in the mating strategy of the splendid fairy-wren. *Journal of Animal Ecology*, **64**, 614–627.

Brooker, M. G., Rowley, I., Adams, M. & Baverstock, P. R. 1990. Promiscuity: an inbreeding avoidance mechanism in a socially monogamous species? *Behavioral Ecology and Sociobiology*, **26**, 191–199.

Brown, J. L. 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology*, **8**, 60–65.

Brown, J. L. 1999. The new heterozygosity theory of mate choice and the MHC. *Genetica*, **104**, 215–221.

Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. 2003. Sexual conflict. *Trends in Ecology and Evolution*, **18**, 41–47.

Cockburn, A., Osmond, H. L., Mulder, R. A., Green, D. J. & Double, M. C. 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. *Journal of Animal Ecology*, **72**, 189–202.

Colegrave, N., Kotiaho, J. S. & Tomkins, J. L. 2002. Mate choice or polyandry: reconciling genetic compatibility and good genes sexual selection. *Evolutionary Ecology Research*, **4**, 911–917.

Coltman, D. W., Pilkington, J. G., Smith, J. A. & Pemberton, J. M. 1999. Parasite-mediated selection against inbred Soay sheep in a free-living island population. *Evolution*, **53**, 1259–1267.

Cordero, P. J., Aparicio, J. M. & Veiga, J. P. 2004. Parental genetic characteristics and hatching success in the spotless starling, *Sturnus unicolor*. *Animal Behaviour*, **67**, 637–642.

Double, M. C., Dawson, D., Burke, T. & Cockburn, A. 1997. Finding the fathers in the least faithful bird: a microsatellite-based genotyping system for the superb fairy-wren *Malurus cyaneus*. *Molecular Ecology*, **6**, 691–693.

Dunn, P. O. & Cockburn, A. 1999. Extrapair mate choice and honest signalling in cooperatively breeding superb fairy-wrens. *Evolution*, **53**, 938–946.

Foerster, K., Delhey, K., Johnsen, A., Lifjeld, J. T. & Kempenaers, B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature*, **425**, 714–717.

Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. 2002. A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal Society of London, Series B*, **269**, 1479–1485.

Freeman-Gallant, C. R., Meguerdichian, M., Wheelwright, N. T. & Sollecito, S. V. 2003. Social pairing and female mating fidelity predicted by restriction fragment length polymorphism similarity at the major histocompatibility complex in a songbird. *Molecular Ecology*, **12**, 3077–3083.

Griffith, S. C. & Montgomerie, R. 2003. Why do birds engage in extra-pair copulation? *Nature*, **422**, 833.

Griffith, S. C., Owens, I. P. F. & Thuman, K. A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195–2212.

Hansson, B. 2004. Marker-based relatedness predicts egg-hatching failure in great reed warblers. *Conservation Genetics*, **5**, 339–348.

Hansson, B. & Westerberg, L. 2002. On the correlation between heterozygosity and fitness in natural populations. *Molecular Ecology*, **11**, 2467–2474.

Hansson, B., Bensch, S., Hasselquist, D. & Åkesson, M. 2001. Microsatellite diversity predicts recruitment of sibling great reed warblers. *Proceedings of the Royal Society of London, Series B*, **268**, 1287–1291.

Hardy, O. J. & Vekemans, X. 2002. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes*, **2**, 618–620.

Jennions, M. D. & Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews*, **75**, 21–64.

Johnsen, A., Andersen, V., Sundling, C. & Lifjeld, J. T. 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature*, **406**, 296–298.

Keller, L. F. & Waller, D. M. 2002. Inbreeding effects in wild populations. *Trends in Ecology and Evolution*, **17**, 230–241.

Kempenaers, B., Verheyen, G., van den Broeck, M., Burke, T., van Broeckhoven, C. & Dhondt, A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature*, **357**, 494–496.

Kempenaers, B., Congdon, B., Boag, P. & Robertson, R. J. 1999. Extrapair paternity and egg hatchability in tree swallows: evidence for the genetic compatibility hypothesis. *Behavioral Ecology*, **10**, 304–311.

Kruuk, L. E. B., Sheldon, B. C. & Merilä, J. 2002. Severe inbreeding depression in collared flycatchers (*Ficedula albicollis*). *Proceedings of the Royal Society of London, Series B*, **269**, 1581–1589.

Marshall, R. C., Buchanan, K. L. & Catchpole, C. K. 2003. Sexual selection and individual genetic diversity in a songbird. *Proceedings of the Royal Society of London, Series B, Supplement*, **2**, 248–250.

Marshall, T. C., Slate, J., Kruuk, L. E. B. & Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7**, 639–655.

Masters, B. S., Hicks, B. G., Johnson, L. S. & Erb, L. A. 2003. Genotype and extra-pair paternity in the house wren: a rare-male effect? *Proceedings of the Royal Society of London, Series B*, **270**, 1393–1397.

Mays, H. L. & Hill, G. E. 2004. Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology and Evolution*, **19**, 554–559.

Mitton, J. B., Schuster, W. S. F., Cothran, E. G. & DeFries, J. C. 1993. Correlation between the individual heterozygosity of parents and their offspring. *Heredity*, **71**, 59–63.

Neff, B. D. & Pitcher, T. E. 2005. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Molecular Ecology*, **14**, 19–38.

Pai, A. & Yan, G. 2002. Female mate choice in relation to heterozygosity in *Tribolium castaneum*. *Journal of Evolutionary Biology*, **15**, 1076–1082.

Pemberton, J. 2004. Measuring inbreeding depression in the wild: the old ways are the best. *Trends in Ecology and Evolution*, **19**, 613–615.

Penn, D. J. & Potts, W. K. 1999. The evolution of mating preferences and major histocompatibility complex genes. *American Naturalist*, **153**, 145–164.

Penn, D. J., Damjanovich, K. & Potts, W. K. 2002. MHC heterozygosity confers a selective advantage against multiple-strain infections. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 11260–11264.

Petrie, M. & Kempenaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology and Evolution*, **13**, 52–58.

Petrie, M., Krupa, A. & Burke, T. 1999. Peacocks lek with relatives even in the absence of social and environmental cues. *Nature*, **401**, 155–157.

Pruett-Jones, S. G. & Lewis, M. J. 1990. Habitat limitation and sex ratio promote delayed dispersal in superb fairy-wrens. *Nature*, **348**, 541–542.

Pryke, S. R., Andersson, S. & Lawes, M. J. 2001. Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution*, **55**, 1462–1563.

Queller, D. C. & Goodnight, K. F. 1989. Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.

Rätti, O., Hovi, M., Lundberg, A., Tegelström, H. & Alatalo, R. V. 1995. Extra-pair paternity and male characteristics in the pied flycatcher. *Behavioral Ecology and Sociobiology*, **37**, 419–425.

Reid, J. M., Arcese, P. & Keller, L. F. 2003. Inbreeding depresses immune response in song sparrows (*Melospiza melodia*): direct and inter-generational effects. *Proceedings of the Royal Society of London, Series B*, **270**, 2151–2157.

Reinhold, K. 2002. Modelling the evolution of female choice strategies under inbreeding conditions. *Genetica*, **116**, 189–195.

Roberts, S. C. & Gosling, L. M. 2003. Genetic similarity and quality interact in mate choice decisions by female mice. *Nature Genetics*, **35**, 103–106.

Slate, J., David, P., Dodds, K. G., Veenvliet, B. A., Glass, B. C., Broad, T. E. & McEwan, J. C. 2004. Understanding the relationship between the inbreeding coefficient and multilocus heterozygosity: theoretical expectations and empirical data. *Heredity*, **93**, 255–265.

Smith, S. B., Webster, M. S. & Holmes, R. T. 2005. The heterozygosity theory of extra-pair mate choice in birds: a test and cautionary note. *Journal of Avian Biology*, **36**, 146–154.

Thusius, K. J., Peterson, K. A., Dunn, P. O. & Whittingham, L. A. 2001. Male mask size is correlated with mating success in the common yellowthroat. *Animal Behaviour*, **62**, 435–446.

Tregenza, T. & Wedell, N. 2000. Genetic compatibility, mate choice and patterns of parentage: invited review. *Molecular Ecology*, **9**, 1013–1027.

Tregenza, T. & Wedell, N. 2002. Polyandrous females avoid costs of inbreeding. *Nature*, **415**, 71–73.

Tuttle, E. M., Pruett-Jones, S. & Webster, M. S. 1996. Cloacal protuberances and extreme sperm production in Australian fairy-wrens. *Proceedings of the Royal Society of London, Series B*, **263**, 1359–1364.

Webster, M. S., Tarvin, K. A., Tuttle, E. M. & Pruett-Jones, S. 2004. Reproductive promiscuity in the splendid fairy-wren: effects of group size and auxiliary reproduction. *Behavioral Ecology*, **15**, 907–915.

Wegner, K. M., Kalbe, M., Kurtz, J., Reusch, T. B. H. & Milinski, M. 2003. Parasite selection for immunogenetic optimality. *Science*, **301**, 1343.

Zeh, J. A. & Zeh, D. W. 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London, Series B*, **263**, 1711–1717.

Zelano, B. & Edwards, S. V. 2002. An Mhc component to kin recognition and mate choice in birds: predictions, progress, and prospects. *American Naturalist, Supplement*, **160**, 225–237.