

Genotype and extra-pair paternity in the house wren: a rare-male effect?

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Females in socially monogamous species may select extra-pair (EP) mates to increase the heterozygosity, and hence fitness, of their offspring. We tested this hypothesis in the house wren (*Troglodytes aedon*), a largely monogamous songbird in which EP young are common. We typed paired males and females, nestlings, and males on neighbouring territories, at five to seven microsatellite loci over 2 years in a Wyoming, USA, population. We identified EP sires at 20 nests with EP young. In pairwise comparisons, we found no significant differences between cuckolded within-pair (WP) males and EP sires in three measures of heterozygosity (mean d^2 , standardized heterozygosity and internal relatedness). However, EP sires had fewer alleles that were common within the population than did the WP males they cuckolded. Nearby males who were EP sires also had fewer common alleles than did nearby males who did not sire EP young. Females in our population may be more prone to accept copulations from males with rare genotypes than from males with common genotypes. Alternatively, selection of rare-male sperm may occur within the female reproductive tract. Because mating with rare males is likely to increase offspring heterozygosity, our data suggest that EP mating may provide genetic benefits to females.

Keywords: extra-pair mating; heterozygosity; house wren; *Troglodytes aedon*; rare-male effect

1. INTRODUCTION

Extra-pair mating (EPM) is common in a wide range of species that form pair-bonds for breeding purposes. The selective advantages of this behaviour are debated, particularly for females. One possibility is that females use EPM to maximize the heterozygosity of their offspring (Müller & Ward 1995; Brown 1997). It is well established that highly homozygous individuals born to closely related parents often have reduced fitness (Crnokrak & Roff 1999). Several recent studies also indicate that the relationship between heterozygosity and fitness, or fitness correlates, can extend to offspring of parents that are not close relatives (Amos *et al.* 2001a; Höglund *et al.* 2002; Keller & Waller 2002; Slate & Pemberton 2002).

In theory, females attempting to maximize heterozygosity in their offspring may employ several strategies, including the following.

- (i) Females may preferentially mate with males who are genetically distant from themselves. This requires a female to assess the genetic differences between herself and potential mates. An example may be the choice of mates based on genes of the major histocompatibility complex (Penn & Potts 1999; Landry *et al.* 2001).
- (ii) Females may preferentially mate with males who appear to have rare genotypes (Farr 1980). Because individuals from the same population are more likely to share alleles (including deleterious recessive alleles), it may be advantageous for females to mate preferentially with males who lack alleles common in the population (Charlesworth *et al.* 1997). Females may employ this strategy when they are

unaware of their own genotype but are still able to assess the relative rarity of the genotypes of males using phenotypic cues.

- (iii) Because the heterozygosity of offspring is correlated with the heterozygosity of their parents (Mitton *et al.* 1993, but see Tregenza & Wedell 2000), females may maximize the heterozygosity of their offspring by preferentially mating with heterozygous males. This requires male heterozygosity to be apparent to females. In some species, phenotypic traits such as developmental stability (evidenced by the degree of fluctuating asymmetry), size and general health and condition are correlated with heterozygosity (Brown 1997; Weatherhead *et al.* 1999).

The hypothesis that females in socially monogamous species use EPM to enhance the heterozygosity of their offspring, therefore, makes the following predictions:

- (i) extra-pair (EP) mates will be genetically more distant from females than within-pair (WP) mates (if females employ strategy (i) from the previous list); and/or
- (ii) EP mates will be less likely to possess alleles common in the population than WP mates (strategy (ii)); and/or
- (iii) EP mates will be more heterozygous than WP mates (strategy (iii)).

We tested these predictions using the house wren (*Troglodytes aedon*), a socially monogamous songbird that shows considerable EPM activity. DNA from females, cuckolded males and potential and actual EP sires was analysed at multiple microsatellite loci. These data were then used to generate heterozygosity and relatedness measures to examine the EP mate choices made by females within their existing social context.

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2. MATERIAL AND METHODS

(a) *Study species*

House wrens are small drab sexually monomorphic cavity-nesting passerines (Johnson 1998). In spring, females visit male territories and choose mates at least partly based on nest-site quality (Johnson & Searcy 1993). The extent to which females consider other territory attributes or male characteristics is unknown. Females lay four to eight eggs. EPM seems to occur primarily when extra-territorial males intrude into the territories of their immediate neighbours (Johnson & Kermott 1989). There is no evidence that females routinely pursue EP copulations off-territory or advertise their fertility. EP young occur in *ca.* 40% of nests in our population and *ca.* 17% of all young are sired by EP mates ($n = 55$ nests over 2 years; B. G. Hicks, L. S. Johnson and B. S. Masters, unpublished data).

(b) *Study site and general field procedures*

We conducted this study in 1998 and 1999 in Wyoming, USA. One goal of our study was to examine how the timing of a pair's breeding cycle relative to the cycles of pairs on immediately adjacent territories affected the likelihood of a pair having EP young in their nest. Results of that study, and a detailed description of the field and laboratory methods appear elsewhere (Johnson *et al.* 2002). Briefly, we visited all territories every 1–3 days to assess the breeding progress of established pairs. For each nest, we obtained DNA from the attending male and female, all nestlings surviving 7–8 days after hatching, and all males on immediately adjacent territories. DNA was extracted from a 10–30 μ l sample of blood taken from the brachial blood vessels.

To assess timing-of-breeding effects on EPM activity, we categorized a pair as 'early' if their breeding cycle was ahead of, exactly synchronous with or only slightly behind the cycles of all immediate neighbours. We categorized a pair as 'late' if the female of one or more adjacent pairs began incubation before the focal female was at least halfway through laying. Late males included those who, on their own, settled and began breeding later than one or more adjacent neighbours ('naturally late' males), and those who settled early but who we manipulated into breeding late by removing their first mates ('forced late' males) (see Johnson *et al.* (2002) for details of the categorizations and manipulations and their rationale).

(c) *Microsatellite and paternity analysis*

We analysed all DNA samples with five primer pairs as described in Johnson *et al.* (2002). In addition, to increase confidence in the paternity assignment, we typed some individuals using two additional primer pairs, TA-A5-2 and TA-C3(B)-2, described by Cabe & Marshall (2001).

The probability of a random (non-sire) male in the population possessing the alleles to be included as a possible sire for a particular nestling, i.e. the probability of false paternal inclusion, was estimated by

$$\prod (1 - x_i)^2,$$

where x_i is the allelic frequency of the paternally contributed allele for each locus analysed. We based allelic frequencies on all males typed in each year, which included at least 75% of males in the study area. We estimated the probability of any one of a group of males (e.g. immediate neighbours, etc.) being falsely included as a sire of a nestling as

$$1 - (1 - \text{probability of false paternal inclusion})^n,$$

where n is the number of males in the group.

All males typed within our population were considered as possible EP sires. We excluded males as possible sires of nestlings if they failed to match at one or more of the five to seven loci typed. We considered an EP male to be a sire of a nestling if the WP male was excluded from paternity, and if the probability of the EP male being falsely included as a sire of that nestling was less than 0.05.

(d) *Genetic assessment of male genotype*

We compared the genotypes of cuckolded WP males and identified EP sires with regard to:

- (i) degree of relatedness to the WP female;
- (ii) possession of alleles common within the population;
- (iii) standardized heterozygosity (Coltman *et al.* 1999); and
- (iv) mean d^2 (Coulson *et al.* 1998).

We also compared males in 'internal relatedness', another measure of heterozygosity, which is related to standardized heterozygosity (Amos *et al.* 2001a). Results for this measure, however, were essentially identical to those for standardized heterozygosity and are omitted for brevity.

We quantified genetic relatedness between individual males and the relevant WP female using the relatedness measure of Queller & Goodnight (1989). Values were calculated using EXCEL. A value of 1 indicates genetic identity, with lower values indicating decreased relatedness. To assess the extent to which males carried alleles common within the population, we used the method of Queller & Goodnight (1989) to compare male genotypes with a hypothetical genotype comprising the most common allele(s) found in this population at each locus. Males homozygous for the most common alleles have a value of 1, while males with fewer common alleles have lower values, with the values weighted according to the frequencies of the common alleles. For three loci, HRU6, POCC1 and PCA μ 3, the most common allele had a frequency (depending on year and locus) of 0.68–0.78, and was used in the hypothetical genotype. The frequencies of 'rare' alleles (i.e. those not used in the hypothetical genotype) at these three loci varied from 0.01 to 0.14. For each of the other two loci, HRU3 and FHU2, three alleles were of substantially higher frequencies than all others, and were treated as a single allele in the hypothetical genotype. The frequencies of these most common alleles combined varied from 0.65 to 0.75. The frequencies of 'rare' alleles at these two loci varied from 0.01 to 0.08.

For those nests with more than one territorial neighbour, we compared the EP sire genotype with the genotypes of all males on immediately adjacent territories whose nests were within 200 m of the focal pair's nest and who were excluded as EP sires. Because males on adjacent territories are the most likely EP sires (Johnson *et al.* 2002), we reasoned that this procedure allowed a comparison between actual EP sires and potential, but unselected, mates.

For any nest for which there was more than one EP sire, or more than one excluded neighbour, we used mean values for all males in the analyses. Statistical comparisons were made using paired *t*-tests. Tests are one tailed because we specifically asked whether EP males were less related to females and genetically rarer or more heterozygous than WP males or excluded neighbours.

Table 1. Comparison of the genotypes of the WP males and the EP sires of 20 female house wrens. (Shown are mean values (\pm s.e.) for all WP males and EP sires and the mean difference in values between individual WP males and their EP sire counterparts. Differences were compared using paired *t*-tests.)

genotypic parameter	WP males	EP sires	mean difference	<i>t</i>	<i>p</i> (one-tailed)
relatedness to female	0.06 \pm 0.06	-0.06 \pm 0.08	0.121 \pm 0.082	1.47	0.08
rarity in population	0.16 \pm 0.09	-0.14 \pm 0.07	0.30 \pm 0.13	2.38	0.014
heterozygosity	1.0 \pm 0.1	1.1 \pm 0.07	-0.084 \pm 0.121	-0.69	> 0.20
<i>d</i> ²	5.06 \pm 1.0	6.49 \pm 0.85	-1.43 \pm 1.57	-0.91	> 0.15

Table 2. Comparison of the genotypes of the EP sire of a particular female and the males that had the potential to sire EP offspring with that same female but were excluded from paternity (*n* = 17; see § 2c,d for criteria). (Shown are mean values (\pm s.e.) for all EP sires and excluded males. Also shown is the mean difference between individual EP sires and their excluded counterparts. Differences were compared using paired *t*-tests.)

genotypic parameter	EP sires	excluded males	mean difference	<i>t</i>	<i>p</i> (one-tailed)
relatedness to female	-0.10 \pm 0.08	0.10 \pm 0.07	0.19 \pm 0.09	-1.66	0.058
rarity in population	-0.15 \pm 0.08	0.04 \pm 0.06	-0.19 \pm 0.09	-2.24	0.02
heterozygosity	1.16 \pm 0.07	1.11 \pm 0.08	0.05 \pm 0.12	0.43	> 0.30
<i>d</i> ²	6.37 \pm 0.92	6.79 \pm 1.11	-0.43 \pm 1.57	-0.28	> 0.95

3. RESULTS

We identified EP sires with high confidence at 20 nests (mean probability of falsely being included as a sire = 0.01, range of less than 0.001–0.03). Six, eight and six nests belonged to early, naturally late and forced late pairs, respectively. EP sires were males on immediately adjacent territories in 17 out of 20 cases. In these 17 cases, all other neighbours were excluded as possible sires except in each of two cases where one neighbour was not excluded as a possible sire, but the probability of that neighbour being falsely included as a sire was greater than 0.05 (0.09 and 0.15). We did not include these two neighbouring males in the analyses. In the remaining three cases, all neighbours were excluded as sires of EP young, but males from non-adjacent territories were identified as EP sires.

WP males and EP sires did not differ in two measures of heterozygosity, standardized heterozygosity and mean *d*² (table 1). EP sires tended, however, to be less related to WP females than were WP males. Most notably, EP sires were significantly less likely to possess common alleles than were WP males.

Similar results were found in comparisons of EP sires and neighbours excluded from paternity (table 2). These two sets of males did not differ in either measure of heterozygosity. However, EP sires tended to be less related to WP females than were excluded neighbours, and EP sires were significantly less likely to possess common alleles than were excluded neighbours.

Overall, the alleles of EP sires were significantly less frequent within the population than the alleles of WP males (grand mean \pm s.e. of individual mean frequencies of alleles at each locus of 0.366 \pm 0.014 versus 0.403 \pm 0.017, respectively, *t*₁₉ = 1.80, *p* = 0.044). The alleles of EP sires were also significantly less frequent than the alleles of excluded neighbours (0.359 \pm 0.015 versus 0.398 \pm 0.009, respectively, *t*₁₆ = 2.13, *p* = 0.025).

4. DISCUSSION

One hypothesized benefit of EPM is increased fitness through increased heterozygosity of offspring. As outlined in § 1, females theoretically can increase offspring heterozygosity through EPM if EP mates are:

- (i) genetically more distant from, i.e. less related to, females than are WP mates;
- (ii) less likely to possess alleles that are common within the population than are WP mates; and/or
- (iii) more heterozygous than WP mates.

We found no evidence for the last strategy: EP mates and WP mates did not differ in heterozygosity. EP mates were, however, significantly less likely to possess common alleles than either WP males or neighbouring males excluded from paternity. In addition, EP mates showed a strong tendency to be less related to females than were either WP males or excluded neighbours. Note that if females are selecting males who lack common alleles as EP mates, then EP mates will also tend to have low relatedness to females. The reverse also holds true. As such, we cannot be certain whether females are selecting genetically rare males or males unlike themselves. Based on the significance of the comparisons, we tentatively suggest that males with fewer common alleles are selected as EP mates and, therefore, tend to be less related to females.

It is unclear why males with fewer common alleles tend to be EP sires. It is possible that such males may be more prone to pursue EPMs, although we know of no reason to suspect that this may be true. Alternatively, females may identify rare males through morphological cues such as subtle variations in plumage or song. In dusky warblers (*Phylloscopus fuscatus*), male song performance affects EP paternity success (Forstmeier *et al.* 2002). Finally, selection of rare males—or, more specifically, their sperm—

might actually take place within the female reproductive tract (Zeh & Zeh 1997). Such selection is reported in several types of animals in which females mate with multiple males before producing a brood. In sand lizards (*Lacerta agilis*), males that are genetically similar to females father less of the brood than do more distantly related males (Olsson *et al.* 1996). In field crickets (*Gryllus bimaculatus*), females mated successively to two full siblings hatch fewer eggs than outbred females. However, females mated successively to a full sibling and an unrelated male experience no reduction in hatching success, suggesting an internal bias towards the sperm of unrelated males (Tregenza & Wedell 2002). Similar results are reported in several other species (Wilson *et al.* 1997; Stockley 1999; Amos *et al.* 2001b).

We saw no evidence that females select EP mates based on any of the typical measures of heterozygosity. It is possible that heterozygosity has no effect on EP paternity in our study population. Alternatively, heterozygous males may have an advantage, but we simply did not detect it with the limited number of microsatellite loci and individuals sampled. It is also possible that EP sires are more heterozygous than WP males (or males that fail to father EP young) under natural conditions, but we did not observe this relationship in our study because of our experimental manipulations. We forced a number of early-settling males to breed late relative to their neighbours. In our population, late-breeding males, whether they are naturally late settlers or early settlers forced to breed late, are more likely to be cuckolded than early-settling males, while cuckolders are typically early-settling males. If higher heterozygosity is correlated with earlier return (which might be the case, given the strong selection on males to return early; Johnson *et al.* 2002), then, under natural conditions, EP sires may indeed be likely to have higher heterozygosity than cuckolded males. Because six out of the 20 cuckolded males in this study were early-settling males forced to breed late, we might have had an unnaturally large number of males with high heterozygosity in our sample of cuckolded WP males. We will need additional data from unmanipulated pairs to determine whether measures of heterozygosity are correlated with EP mate selection under natural conditions. However, if early-settling males are indeed more heterozygous than late-settling males, the fact that early-settling males forced to breed late are cuckolded to the same degree as naturally late-settling males (Johnson *et al.* 2002) suggests that male heterozygosity probably does not directly influence male EPM success.

It is important to note that our observations demonstrating a relationship between genetic rarity and EPM success are unlikely to be an artefact of our experimental manipulations. By forcing some early-returning males to breed late, our experimental manipulations had the effect of mixing the pools of early- and late-breeding males, and any naturally occurring correlation between timing of breeding and genetic rarity would have been decreased. Our observations are therefore likely to be conservative relative to any bias introduced by these manipulations.

The relationship between the genotypes of social pairs and the occurrence of EP paternity has been examined in only a handful of socially monogamous species, sometimes with conflicting results. Blomqvist *et al.* (2002) found that,

in three species of shorebirds, EP young were more common when social pairs were more genetically similar, while Rätti *et al.* (1995) observed the opposite result in pied flycatchers (*Ficedula hypoleuca*). Bensch *et al.* (1994) found that EP sires tended to be less similar to females than were social mates in great reed warblers (*Acrocephalus arundinaceus*), while Kempenaers *et al.* (1997) found no such difference in blue tits (*Parus caeruleus*). Otter *et al.* (2001) found that low male heterozygosity, as determined by d^2 , was associated with an increased chance of being cuckolded in great tits (*Parus major*). None of the above studies asked whether EP males were genetically rarer than WP males, as we did here. Our study also differed from previous studies in that we compared the genotypes of actual EP sires and potential, but 'failed', EP sires.

In conclusion, our results suggest that genetically rare males have disproportionate success in securing EP fertilizations in our population of house wrens. Because the selection of rare males as EP mates is one strategy that has been predicted to increase the heterozygosity, and thus fitness, of offspring, EPM may provide genetic benefits in this species. Whether the selection we observed results from precopulatory discrimination on the part of females, or from postcopulatory events within the female reproductive tract remains unknown.

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