Sequential mating patterns suggest extra-pair mating is not part of a mixed reproductive strategy by female red-winged blackbirds

Patrick J. Weatherhead

Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6 (pweather@biology.queensu.ca)

Studies aimed at determining why female birds often produce offspring sired by males other than their social mates generally compare traits of social and genetic mates. Here I examine paternity patterns in nests of the same female red-winged blackbirds (*Agelaius phoeniceus*) in successive breeding seasons. Returning females preferentially selected their former social mates as their new social mates when those males were present. However, paternity patterns were much less consistent. A female's behaviour (faithful versus unfaithful) in one year did not predict her behaviour the following year. Females unfaithful in successive years did not prefer the same extra-pair males. Females unfaithful in one year that switched social mates the next year did not preferentially choose their former extra-pair mates as their new social mates. By switching genetic mates, females did not generally improve the quality of their mates. These results, together with previous analyses, suggest that female blackbirds in this population have little control over extra-pair mating. Although females may benefit from extra-pair mating because extra-pair males are generally longer lived, paternity patterns in this population are not consistent with extra-pair mating being part of a finely tuned female reproductive strategy.

Keywords: mate choice; extra-pair mating; mate switching; red-winged blackbird

1. INTRODUCTION

Extra-pair fertilization (EPF) is now well-established as an important component of sexual selection in passerine birds (Møller & Ninni 1998), although the reason that EPF rates vary so markedly within and among species remains poorly understood (Petrie & Kempenaers 1998). Given that female passerines are thought to control whether copulation or insemination occurs (Birkhead & Møller 1992), it should follow that when EPF occurs, females benefit. The benefit most widely posited is that females acquire superior paternal genes for their offspring (Petrie & Kempenaers 1998), with most supporting evidence being in the form of consistent phenotypic differences between social and extra-pair mates (Møller & Ninni 1998). An alternative approach, and one little used to date, is to determine whether mating patterns of individual females over successive breeding seasons conform to expectations from different hypotheses. Here I use data from female red-winged blackbirds (*Agelaius phoeniceus*) nesting in successive years to test the hypothesis that they engage in extra-pair mating (EPM) to produce genetically superior offspring. I also test the alternative hypothesis that females use EPM to assess potential future social mates (Smith 1988; Colwell & Oring 1989; Heg *et al.* 1993; Cezilly & Nager 1995).

There is abundant evidence that birds base decisions of where to breed and with whom to mate on past experience, being more likely to move and switch social mates if the previous breeding attempt is unsuccessful (e.g. Weatherhead & Boak 1986; Beletsky & Orrians 1991;

Bensch & Hasselquist 1991). Thus, it is reasonable to expect that decisions affecting EPF should be similarly flexible. If EPM is part of a mixed strategy whereby females select social mates for the quality of their territories or paternal care and extra-pair males for their superior genes, then paternity in sequential broods of the same female should conform to certain patterns. Given the same choices, females mated to the same social mate in successive years should tend to be consistent, remaining either faithful or unfaithful to their social mates. Females that are unfaithful in that situation should mate with the same extra-pair male if he is present both years. When females switch behaviour with respect to their social mate (e.g. faithful in year 1, unfaithful in year 2), the change should result in the female obtaining a higher quality sire for her offspring.

Consistent with the alternative hypothesis that females use EPM to assess potential future social mates (Smith 1988; Colwell & Oring 1989; Heg *et al.* 1993), Cezilly & Nager (1995) found a positive association between divorce and extra-pair paternity across species. From this hypothesis, females that produce extra-pair-sired young in one year should be more likely to switch social mates the following year, and if the previous extra-pair male is present he should become the new social mate.

Several assumptions underlie the above predictions. First, I assume that females are free to choose both social and extra-pair mates. With regard to social mates, the assumption is reasonable, because red-winged blackbirds are socially polygynous and most evidence indicates that resident females do not constrain new females from

settling on territories (Searcy & Yasukawa 1995). With regard to extra-pair mates, there is evidence from other populations of both male (Westneat 1992) and female control (Gray 1996). Should females not control EPM in this population, most of the predictions above no longer hold, although male control of EPM could still produce some consistency in female mating patterns between years. For example, if one male was able to overcome another male's mate guarding in one year, perhaps he could do so again the next year. However, having the same female involved and constraints such as those associated with breeding synchrony (Weatherhead 1997) be the same both years, makes this scenario likely to be infrequent. An additional goal of this analysis was to consider the implications of sequential mating patterns for which sex controls EPM.

My second assumption is that a female has the same options in successive years. By restricting analyses to females for which the same key males (social and extra-pair mates) are present both years, I increase the validity of this assumption. Furthermore, high site fidelity and mean annual survival of 55% (Weatherhead 1995) mean that many of the other males resident in one year will also be present the following year. Because new males are first-time breeders, and have relatively low breeding success both on (Weatherhead 1995) and off (Weatherhead & Boag 1995) their territories, they should be relatively unimportant to returning females. Thus, in my analyses the males most relevant to females should be the same individuals in both years.

2. METHODS

The data presented here are from a study of red-winged blackbirds conducted at the Queen's University Biological Station in eastern Ontario, Canada. The methods used have already been published in detail (Gibbs *et al.* 1990; Weatherhead *et al.* 1994; Weatherhead & Boag 1997), so here I only present a summary of the aspects pertinent to the present analyses. The birds were studied during the breeding season on three marshes, the smallest of which had as few as three resident males and the largest up to 17 resident males. All the marshes were in beaver ponds surrounded by habitat unoccupied by red-winged blackbirds. Data were collected from the largest of the marshes from 1986 through 1991, and from the other two marshes in 1988 and 1989.

All resident males (except two individuals in the first year of the study) were captured, had their blood sampled, were individually colour-banded and had their territories mapped at the start of each breeding season. Each marsh was searched every second day to locate nests. Females were mist-netted, colour-banded and had their blood sampled once they started nesting, and nests were followed until they failed or the young fledged. Nestlings were banded and had their blood sampled when five to six days old.

Paternity analysis for 617 nestlings using both single and multilocus probes indicated that brood parasitism by females did not occur, and that extra-pair males sired 25.6% of nestlings. Sires were identified for 78% of extra-pair young. These males held territories on the same marsh as the males they cuckolded. Cuckolders tended to be older or longer-lived than the males they cuckolded (Weatherhead & Boag 1995). Nest defence is the principal form of paternal care, and males

defended nests less aggressively when they contained illegitimate young (Weatherhead *et al.* 1994). This made EPFs costly to females, suggesting females must realize some genetic benefit if they are to overcome that cost.

3. RESULTS

In 61 instances where I obtained paternity data from nests of the same female in successive years, 27 (44.3%) females behaved consistently. Nine females were faithful and 18 females were unfaithful to their social mates both years (females are defined as unfaithful if any of their offspring were sired by an extra-pair male). Out of the remaining 34 (55.7%) females, 24 switched from faithful to unfaithful, and ten from unfaithful to faithful. Thus, females appear quite flexible, with little evidence that individuals are generally predisposed to behave one way or the other.

Narrowing the focus to females whose social mate and extra-pair mate (where relevant) were present both years, I had paternity data for 47 cases. Several cases involved the same females returning more than once. If any bias arises from treating these cases as independent, it should be towards increasing mating consistency. Because these individuals often behaved differently between successive returns, I include all cases in the analyses. The overall pattern was for female mating behaviour to be quite variable between years (figure 1). For the 34 females with the same social mate in successive years, the likelihood of infidelity in year 2 was unrelated to whether they had been unfaithful in year 1 ($\chi^2 = 0.72$, $p = 0.40$). Only one out of five females that was unfaithful to the same social mate both years produced young sired by the same extra-pair male in both years, despite the previous extra-pair male being present in each case.

EPM was clearly not a mechanism by which females acquired future social mates. Out of the 19 females that produced extra-pair young in year 1, only one (5.3%) chose the extra-pair male as her social mate the following year when he was present (figure 1). However, there was some evidence that females that produced extra-pair young in year 1 were more likely to switch social mates between years. Out of the 19 females that were unfaithful in year 1, 42% switched social mates, compared to only 18% of the 28 females that were faithful in year 1 ($\chi^2 = 2.23$, $p = 0.14$).

It is apparent from figure 1 that fidelity to social mates is higher than to genetic mates. While 72% of females had the same social mate in two successive breeding seasons, only 34% of females had their young sired by the same male(s) both years. There are several potential explanations for so much mate switching. Females might simply prefer particular male attributes rather than particular males, so their mate choices may be more consistent than they appear. Alternatively, females may use their experience in one year to make better mate choices the next year. To test these alternatives I first scored males on three criteria that should reflect how females assess their quality. Harem size (the maximum number of females nesting simultaneously on a male's territory) and fledging success (the number of offspring that fledge from nests on a male's territory) could both be considered indices of male phenotypic quality (i.e. the

Figure 1. Mating patterns of female red-winged blackbirds that returned in two successive years and whose original social mates and extra-pair mates (where relevant) were present both years. A social mate is the male in whose territory a female nests. Extra-pair (EP) males are the sires of nestlings not sired by social mates. Females were considered unfaithful if any of their offspring were sired by EP males.

quality of his territory and/or his paternal ability). The number of young sired, both on and off his territory, could be considered an index of a male's genotypic quality because it measures his true reproductive success. If females are consistent in the attributes they choose in their social and genetic mates in successive years, then male quality in year x should be correlated with quality in year $x + 1$. I found no evidence to support this prediction, either for social mates or genetic mates (table 1).

If females learn from past experience and improve their choice of mates the next year, then the quality of their mates should increase. There was also no support for this prediction. Excluding ties, the harem size of females' social mates increased 19 times and decreased 16 times in year $x + 1$ relative to year x . The fledging success of social mates increased 21 times and decreased 21 times. The number of young sired by females' genetic mates increased 19 times and decreased 24 times. Note that in

the last analysis I included females twice if they had two genetic mates in one of the years.

4. DISCUSSION

Strong site fidelity between years by both male and female red-winged blackbirds (Beletsky & Orians 1991; Weatherhead 1995) provides females ample opportunity either to be consistent in their choice of mates in successive years, or alternatively, to choose a better mate based on information gained the previous year. There was only equivocal evidence that females took advantage of these opportunities when choosing social mates, and no evidence that they did so when choosing extra-pair sires. Approximately 75% of females that returned chose the same social mate when they had the opportunity to do so. Furthermore, female red-winged blackbirds are more likely to change social mates between years if they nested

Table 1. *Consistency of social and genetic mate choice between years relative to male reproductive performance*

(Males were scored for the number of social mates obtained, number of offspring fledged from their territory, and number of offspring sired each year. Females' mates in year x were compared to their mates in year $x+1$ by Spearman's rank correlation. For females with more than one genetic mate, both males were compared separately to subsequent or former mates.)

	r_s	p	n
social mates			
number of social mates	0.08	0.58	44
young fledged	0.03	0.84	44
young sired	0.18	0.22	44
genetic mates			
number of social mates	-0.06	0.68	49
young fledged	-0.04	0.84	49
young sired	0.12	0.40	49

unsuccessfully the previous year (Beletsky & Orians 1991; P. J. Weatherhead, unpublished data). This accounts for social mate fidelity reported here being higher than previously reported when unsuccessful females were included (Weatherhead 1995). Females were only included in this study if their nests survived at least until the nestlings were old enough to have their blood sampled for paternity analysis. Thus, their nest success, and hence mate fidelity, was higher than when estimated for all nesting females. Although females appear to switch social mates for good reason, they did not appear to choose a new social mate that was superior to the mate they left, a result similar to that reported by Beletsky & Orians (1991). While this may reflect the fact that females know their past success but must predict future success, selection should still only favour divorce when some benefit ensues.

The choice of genetic mates should not be so problematic. If females are able to choose their genetic mates, and males reliably signal their genetic quality (a prerequisite for mate choice based on genetic quality), then the genetic quality of available males should be apparent each year. Thus, if females choose genetic mates on the basis of their genetic quality, females should have made the same choices in successive years. However, they clearly did not. Females were not consistent in whether or not they were faithful to their social mate, and if unfaithful, they were not consistent in their choice of extra-pair male. This lack of consistency resulted in female mating patterns between years being much more promiscuous genetically than socially. Furthermore, there was no evidence that by changing genetic mates, females obtained higher-quality genetic mates.

Inconsistency between years would be expected if females used EPM to choose future social mates. However, with only one record of a female's extra-pair mate in one year becoming her social mate the following year, there was no support for this hypothesis. There was weak evidence of a link between EPF and divorce (Cezilly & Nager 1995), because females that were unfaithful were more likely to change social mates the following year. However, this pattern seems more likely

to be a consequence of females with EPFs having lower nesting success (Weatherhead *et al.* 1994). Because lower nesting success promotes divorce, EPF becomes indirectly associated with divorce. It would seem worthwhile determining whether a similar mechanism underlies the association between EPF and divorce in other species (Cezilly & Nager 1995).

The paternity patterns documented here offer little support for the hypothesis that females engage in EPM to enhance the genetic quality of their offspring, in contrast to previous analyses from this study population. Those analyses showed that extra-pair males were usually older or longer lived than the males they cuckolded (Weatherhead & Boag 1995) and that females suffered a fecundity cost for EPF that could only be recovered if their offspring were of higher quality (Weatherhead *et al.* 1994). These results can be reconciled if EPM is controlled by males, as in the population studied by Westneat (1992), and if older males are better at creating or exploiting opportunities for EPM, as proposed by Weatherhead & Boag (1995). By this scenario, there is little expectation that female genetic mating patterns should be consistent between years.

If males control EPM, one still must ask why females participate, given the cost of doing so. First, if longer-lived males are genetically superior, females could still benefit from EPM, regardless of how it arises. Second, females can reduce the costs of EPM if their social mate has a reasonable prospect of siring some of the offspring, because such mixed-paternity broods are more successful than broods sired entirely by extra-pair males (Weatherhead *et al.* 1994). Those costs can be reduced further if females discriminate against non-resident extra-pair males, because broods that they sire are least successful (Weatherhead *et al.* 1994). However, 19% of nests have all the young sired by extra-pair males and non-resident males are sires in 24% of all nests with extra-pair young (Weatherhead *et al.* 1994). Thus, to the extent that EPM can still be considered part of a female reproductive strategy in this population, it is clearly not a strategy that is finely tuned.

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