The cost of extra-pair fertilizations to female red-winged blackbirds

PATRICK J. WEATHERHEAD[1], ROBERT MONTGOMERIE[2], H. LISLE GIBBS[3] AND PETER T. BOAG[2]

[1] *Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6*
[2] *Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6*
[3] *Department of Biology, McMaster University, Hamilton, Ontario, Canada L85 4K1*

SUMMARY

It has recently become apparent that females of many species of birds often copulate with, and produce young sired by, males other than their social mates. Understanding the adaptive significance of this behaviour requires knowing whether extra-pair matings entail any cost to females. We investigated nest success relative to paternity in red-winged blackbirds (*Agelaius phoeniceus*) over 5 years and found that nest success declined as the proportion of nestlings that was sired by extra-pair males increased. Nest defence against potential predators is the principal form of paternal care in this population. Males defended nests less vigorously when they contained nestlings sired by other males, suggesting that the lower success of those nests was a consequence of reduced paternal care. Nests with extra-pair young were more successful when the true father was a local resident, suggesting that resident males may defend other males' nests if they have sired some of the young. Our results indicate that females must realize substantial improvement in offspring fitness if they are to compensate for the cost of extra-pair fertilizations.

1. INTRODUCTION

As paternity analysis using DNA profiling is more widely applied in studies of avian mating systems, it is becoming apparent that females of many species regularly copulate with, and produce young sired by, males other than their social mates (Birkhead & Møller 1992). Much less apparent is why females engage in such behaviour (Westneat *et al.* 1990). To answer that question one must know the consequences for females of copulating with males other than their mates. It is clearly contrary to the evolutionary interests of males that are cuckolded to help rear young to which they are unrelated and there is evidence that males may be capable of assessing their probability of paternity (Burke *et al.* 1989). Therefore, a plausible cost to extra-pair mating by female birds could be reduced parental assistance from their mates. For example, Møller (1991) reported that male swallows (*Hirundo rustica*) defended nests less if their mates participated in extra-pair copulations and Lubjuhn *et al.* (1993) showed that nest defence by male great tits (*Parus major*) increased as the number of young they sired in the nest increased. Reduced paternal nest defence could result in lower reproductive success (Weatherhead 1990).

Demonstration of a reproductive cost to females would greatly restrict the possible explanations for extra-pair mating (Westneat *et al.* 1990); not only would any immediate benefit from the behaviour be ruled out, but for the behaviour to be adaptive for females, some long-term benefit sufficient to outweigh the initial cost would be necessary. For the same reason, demonstration of a cost to females for extra-pair matings would provide valuable insight into the issue of how females choose mates generally (Kirkpatrick & Ryan 1991). The study of mate choice in natural populations is often constrained by a lack of knowledge of the alternatives available to females. By contrast, when a female has the opportunity for extra-pair mating, she may also have the alternative of copulating only with her social mate. Thus we can compare the consequences for females that engaged in extra-pair matings and those that did not. Here we present the results of a paternity study of red-winged blackbirds (*Agelaius phoeniceus*) that show a substantial reproductive cost to females that produced young sired by males other than their mates.

2. METHODS

We examined parentage and parental behaviour in an individually marked population of blackbirds on three beaver marshes in eastern Ontario, Canada over a five year period, beginning in 1986. The marshes were located within 1 km of each other with no suitable breeding habitat between them; marshes had 3–17 resident males. In all but the first year of the study, when there were two unbanded males, all resident males were banded and had their blood sampled. Most territorial males are socially polygynous and the only substantial parental care they provide in this population is defending nests against potential predators (Weatherhead 1990).

Most nests were found while being built and were visited every 2–3 d until the young fledged or the nest failed. When nestlings disappeared between visits, we assumed they had fledged if they would have reached fledging age (> 9 d) since the last visit, the nest remained intact and the nest lining contained abundant debris from feather sheaths – signifying maturation of the feathers. A nest was considered successful if at least one nestling fledged. Blood was collected from nestlings when they were 6–7 d old (Hoysak & Weatherhead 1991). All females attending nests from which nestling blood was obtained were banded and their blood sampled.

On most nest visits in 1988–90 we recorded the nest defence behaviour of the resident male following the procedure of Weatherhead (1990). In brief, the observer scored the aggressiveness of the male toward the observer for the first 2 min of the nest visit. Responses varied from males leaving their territory at the start of a trial (score = 0) to repeatedly striking the observer (score = 7). Because responses are most intense and vary most among males between days 4 and 10 of the nestling period (P. J. Weatherhead, unpublished data), we used the mean score for all visits to a nest during this period as the overall nest defence score for that nest. All nest defence data were collected before any paternity analysis was undertaken for those nests.

DNA profiling has shown that approximately 25% of all red-winged blackbird nestlings are sired by males (often neighbours) other than the individual in whose territory the nest is found (Gibbs *et al.* 1990; Westneat 1993). To assess any cost to females from such extra-pair matings we determined the fate of nests relative to the paternity of their nestlings during the 4–5 d between our sampling the nestlings' blood and the nestlings fledging. For the first year of the study (1986), paternity was analysed using both single and multilocus probes as described by Gibbs *et al.* (1990). Because the two techniques were redundant and because the multilocus probes were more powerful for assigning paternity, we used only the multilocus probes (Jeffreys 33.15 and *Per*) for samples from subsequent years. Southern blots of AluI-digested blackbird DNA were hybridized with these probes to produce multilocus DNA 'fingerprints'. Nestlings and their putative parents were always run on the same gel to facilitate comparison of their fingerprints (see Westneat 1993).

Gibbs *et al.* (1990) describe the methods used to score fingerprints from 1986. For samples from the four subsequent years, the molecular size (MS) of fragments (bands) on each fingerprint was determined by using GelReader software (version 2.0.3; National Centre for Supercomputing Applications, Champaign, Illinois). Autoradiographs digitized by using an Apple® OneScanner were analysed by comparing fragments revealed by each probe to known molecular sizes of fragments in a lambda standard (see Galbraith *et al.* 1991) run in each lane of the gel. Fragments were considered homologous between individuals if the molecular size of a fragment in one bird fell within the 99.9% confidence limits of a fragment in another and was of similar intensity – all other fragments were considered novel. Confidence limits were estimated as MS ± 1.07%, determined by analysis of fingerprints of the same individuals within and between gels. Fragments revealed by each probe were analysed separately and the results pooled for further statistical analysis. While this computerized scoring method is more efficient and objective than scoring by hand, it usually results in fewer bands being scored – particularly when bands are light and can yield anomalous results when lanes being compared differ greatly in intensity. In all cases where we were uncertain about the results from computerized scoring, the fingerprints we rescored by hand (see for details Smith *et al.* 1991).

We assessed parenthood of the 466 nestlings sampled in the final four years of this study generally following methods described by Westneat (1993) using band-sharing coefficients (D) and novel fragments for diagnosis. In other studies using this computerized scoring method (see, for example, Hill *et al.* 1994) we have found that D-scores between nestlings and their true genetic parents average 0.50–0.60 and are usually greater than 0.40. In addition, nestlings rarely have more than three novel bands (presumably resulting from mutation) which do not occur in the fingerprints of either genetic parent (see also Westneat 1993).

We therefore began our analysis using the conservative criterion that the 330 nestlings with $D_f \geqslant 0.40$ (i.e. D with respect to their putative mother) and $\leqslant 3$ novel bands were the offspring of that female. Of the remaining 136 nestlings, 57 had $\leqslant 3$ novel bands when their genetic father had been identified and the other 79 were clearly the genetic offspring of the attending female (by the above criteria) when their fingerprints were rescored by hand. Thus we make the conservative assumption that all females were the genetic mothers of the nestlings in the nests they attended. Average D_f for these 466 nestlings, as determined by computerized scoring, was 0.524 (± 0.006 s.e.).

For analysis of paternity, we initially assumed that the 277 nestlings with $D_m \geqslant 0.40$ and $\leqslant 3$ novel bands with respect to the attending male were the offspring of that male. Of the remaining 189 nestlings, 80 were identified as the genetic offspring of the attending male either because they had $\leqslant 3$ novel bands ($n = 30$) or because rescoring by hand ($n = 70$) revealed characteristics that indicated genetic paternity ($D_m \geqslant 0.40$ and $\leqslant 3$ novel bands). The remaining 109 nestlings were excluded by these criteria and were considered to be the result of extra-pair matings by the attending female. Average D_m for the 357 nestlings that were the offspring of both attending parents, as determined by computerized scoring, was 0.518 (± 0.006 s.e.).

To find the genetic fathers of the 109 excluded nestlings, we calculated D_m between each nestling and all other males resident on the marsh. The male with the highest D_m and $\leqslant 3$ novel bands was considered to be the real father. In each case, hand scoring of fingerprints for the five males with the highest computer-generated D scores confirmed that no other male on the marsh was a better match. Of the 109 extra-pair nestlings, 29 could not be assigned to any male resident on the marsh, using these criteria. Band-sharing coefficients between nestlings and their genetic mothers and fathers ($D_m = 0.514$, $n = 437$ nestlings) were not significantly different ($t = 1.26$, $p = 0.21$) but were both significantly higher than that between extra-pair nestlings and their putative fathers (0.314, $n = 109$ nestlings; t-tests, $p < 0.001$ in each case).

When scoring large numbers of multilocus fingerprints there may well be some error in the assignment of parentage. In this study we have been conservative, erring on the side of identifying attending adults as genetic parents. Without other kinds of genetic analysis (e.g. single locus probes) it is difficult to determine the magnitude of such errors but they are estimated to be small (see, for example, Gibbs *et al.* 1990) and should be random with respect to the questions we were interested in addressing. Moreover, all analyses of fingerprints and assignment of parentage were performed by technicians who had not studied the birds in the field, were unaware of which nestlings had fledged and which had died and were naive to the questions being asked, all of which would further insure that any errors would have been random with regard to the objectives of this study.

3. RESULTS

During the study, we analysed 546 nestlings from 174 nests. The putative father sired 409 nestlings, 108 were sired by a resident male other than the putative father and 29 were unassigned – assumed to have been sired by non-resident males. (Neither of the two unassigned nestlings from the first year of the study was from a territory adjacent to the two unbanded males). Non-resident 'floaters' are common in this population and are regularly observed trespassing on the territories of resident males (Shutler & Weatherhead 1994).

Analyses of parentage data suggest a substantial cost to females who engaged in extra-pair mating. Nests in which all nestlings were sired by the putative father were most likely to fledge young, broods sired entirely by males other than the putative father were least likely to fledge young and mixed broods had intermediate success (see figure 1). To control for possible differences among years and marshes we performed logistic regression (using JMP software from SAS Institute): nest success was recorded as the dependent variable (0 = failure, 1 = success) and years, marshes and the proportion of nestlings that were sired by the attending male (i.e. paternity) were recorded as independent variables. This analysis revealed a highly significant effect of paternity on success ($G = 9.30$, $p = 0.002$, d.f. = 1), with the effects of marsh ($G = 2.70$, $p = 0.27$, d.f. = 2) and year ($G = 1.60$, $p = 0.80$, d.f. = 4) both non-significant. Because males usually had more than one nest and often had nests in more than one year, this analysis may have been influenced by some lack of independence among nests. Therefore, to further evaluate this relation, we performed a bootstrap analysis by running 100 logistic regressions as described above, using, each time, one randomly selected nest from each male. The results support our conclusion that nest success was significantly related to paternity (mean $G = 4.34$, $p = 0.037$, d.f. = 1) but not to either marsh (mean $G = 3.14$, $p = 0.21$, d.f. = 2) or year (mean $G = 2.63$, $p = 0.62$, d.f. = 4).

The association between nestling paternity and nest success could have arisen if males that were unsuccessful at preventing extra-pair copulations by their mates were also unsuccessful at deterring nest predators. To assess this possibility, each nest was scored as successful (1) or unsuccessful (0) and an average success for the nests with and for those without extra-pair nestlings was calculated for each male over the entire study period. A comparison of the average success of nests with (grand mean = 0.79) and without (grand mean = 0.57) extra-pair nestlings for the 25 males that had both classes of nests, confirmed that nests containing extra-pair nestlings were less successful (Wilcoxon test, $T+ = 135$, $p = 0.03$, $n = 25$). To avoid the effects of possible changes in male behaviour from year to year, we restricted this analysis to data from only one year (the year with the most nests) for each male and reached the same conclusion (Wilcoxon test, $T+ = 73$, $p = 0.05$, $n = 22$).

Conceivably, the relation between nestling paternity and nest success could also have arisen because nest dispersion (for example, proximity to the edge of the marsh or to the nearest neighbour) rendered some nests more vulnerable to predation and their attendant females more likely to mate with extra-pair males. However, data from the largest and longest-studied of our sites refute this possibility. Although nests that failed tended to be closer to the marsh edge than were successful nests (Mann–Whitney test, $p = 0.09$, $n = 32$, 103), nests without extra-pair nestlings were as close to the marsh edge as those with one or more extra-pair nestlings (Mann–Whitney test, $p = 0.46$, $n = 83$, 52). Also, successful and unsuccessful nests did not differ significantly in their distance to the nearest neighbouring territory (Mann–Whitney test, $p = 0.79$), nor did nests without extra-pair nestlings and those with one or more extra-pair nestlings (Mann–Whitney test, $p = 0.19$).

We can also rule out some other potentially confounding factors. Nests with extra-pair young and those without extra-pair young did not differ in their date of initiation (Mann–Whitney test, $p = 0.70$) or in the order that the attendant females settled on their respective territories (Mann–Whitney test, $p = 0.55$). In addition, a detailed analysis of extra-pair paternity relative to female age and nesting synchrony (P. J. Weatherhead, unpublished results) revealed no effect of female age on extra-pair mating and no differences in nesting synchrony within or among territories between nests with and without extra-pair young ($p > 0.50$ in all cases). Thus even if nest success varied with any of these factors, this effect could not account for the relation we observed between extra-pair paternity and nest success. Westneat (1992) also found no effect of initiation date, settlement order or female age on the occurrence of extra-pair fertilizations in red-winged blackbirds.

Predation was the known, or suspected, cause of nest failure in all cases where nests failed after we had collected blood samples from nestlings. In this population, male defence of nests against predators increases nest success (Weatherhead 1990). To assess whether the variation in nest success associated with extra-pair paternity may have been due to males varying their nest defence with their likelihood of paternity; we compared the aggressiveness of 20 males observed in

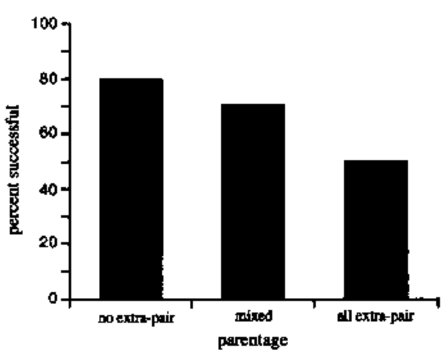

Figure 1. Nest success relative to whether broods were all sired by the putative father ($n = 107$), all sired by extra-pair males ($n = 20$) or contained both types of nestlings (mixed) ($n = 47$); nest success is significantly dependent on paternity ($G = 10.29$, d.f. = 2, $p = 0.006$).

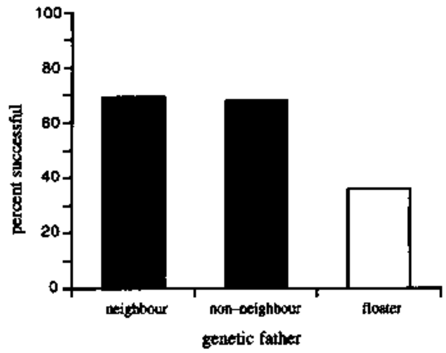

Figure 2. Success of nests with ⩾ 1 nestling sired by an extra-pair male when the genetic father was either a neighbour (held an adjacent territory) ($n = 29$) or a non-neighbour resident on the same marsh (solid bars) ($n = 22$) versus when the true father was unknown (and therefore probably a non-territorial floater) (open bar) ($n = 16$).

the same year defending both a nest that proved to contain only nestlings that they had sired and a nest with one or more extra-pair nestlings. In a paired comparison, males tended to be more aggressive defending nests without extra-pair nestlings (Wilcoxon test, $p = 0.09$, $n = 20$ males). By scoring each male as simply more (+) or less (−) aggressive for each nest, we found that males were more aggressive defending the nests without extra-pair young significantly more often than expected by chance (sign test, $p = 0.05$). For nests containing no extra-pair nestlings, males were more aggressive in 13 cases, less aggressive in four cases, and showed no difference in three cases.

Given that males appeared to defend nests in their own territories less vigorously when their paternity was reduced, it is conceivable that they might help defend nests in other males' territories if they have sired some of the young. If so, then the success of a nest with extra-pair young should be higher when the true father is resident on the same marsh. There were 16 nests for which the paternity of the extra-pair nestlings could not be assigned to a male resident on the marsh. Only 42.8% of these nests were successful. We initially classified genetic fathers that were resident on the marsh as neighbours or non-neighbours. Since the success of nests with extra-pair young sired by these two classes of genetic father were virtually identical, we pooled them as 'residents' for further analysis. The success of nests (68.6%) with extra-pair nestlings sired by a resident male was significantly higher than for those where the genetic father was non-resident ($G = 4.90$, $p = 0.027$, see figure 2). This result suggests that resident males may defend young they sire in other males' territories.

4. DISCUSSION

Our results indicate that extra-pair mating by female red-winged blackbirds lowers their probability of nest success, at least in part because males defend their nests less vigorously when they have not sired some or all of the nestlings. The fact that we detected reduced success of nests containing extra-pair young in the 4–5 d between sampling and fledging suggests that extra-pair paternity may be more frequent, and the cost to females higher, than our data indicate. Indeed, 68% of all nests that failed did so before the nestlings were old enough for us to sample their blood for DNA profiling. The relation between paternity and nest success from nestlings we did sample implies that extra-pair paternity in those failed nests would have been higher than in nests that survived to sampling or to fledging.

Two general factors are predicted to determine how males should respond to reduced parentage in a brood (Westneat & Sherman 1993) and the behaviour of male red-winged blackbirds in this study appears to be in accordance with both those predictions. First, males must have some basis by which they can assess that their parentage is reduced. Although it is unlikely that males can recognise their own young (Burke *et al.* 1989), other cues (for example, female behaviour) could allow reliable assessment of parentage. Second, if the cues indicate that a male's parentage may be reduced, the male should withhold parental care if doing so increases his opportunity for additional mating or for caring for other broods in which his parentage is likely to be higher. The socially polygynous mating system of red-winged blackbirds should often provide males with opportunities both for obtaining additional matings and for redirecting parental care to other broods. Other males' mates clearly provide additional potential mating opportunities and our data suggest that males may sometimes even direct parental care to young they have sired outside their territory.

In contrast to our main result, Westneat (1992) found no difference in success between nests with and without extra-pair young in red-winged blackbirds. However, he only had 11 cases of predation in the 62 nests he sampled, so the substantially smaller sample sizes may account for the difference between his study and ours. Westneat did find that broods sired by more males fledged more young, which suggests a benefit rather than a cost to extra-pair mating by females. Having eliminated courtship feeding or nestling feeding by males as explanations of this result, Westneat suggested that extra-pair males might have enhanced fledging success by defending nests in which they had sired young. We found indirect evidence of paternal care by extra-pair males, so the difference between Westneat's study and ours could be that nest defence by extra-pair males in Westneat's study more than compensates for the reduced defence by the pair male, whereas in our study it does not.

Our evidence for males defending young they had sired on other males' territories was indirect. Nests with extra-pair nestlings were more successful when the true father was a resident male rather than a floater but we did not observe males trespassing to defend other males' nests. In another study of the same population specifically looking for evidence of 'cooperative' nest defence by males, Weatherhead (1995) never observed neighbours defending each other's nests. Although the paternity of the nestlings involved in that study was unknown, and only a small number of nests was observed, it seems unlikely that none of the nestlings would have been sired by other resident males. However, the fact that nests with extra-pair young sired by resident males were less successful than nests without extra-pair young suggests that any nest defence provided by extra-pair males may be infrequent or of low intensity and, therefore, difficult to detect. Clearly this result warrants further investigation.

Our results suggest that the consequence for females of extra-pair fertilizations was lowered reproductive success, resulting from a reduction in male parental care. This reduction in reproductive success means either that females were forced to accept extra-pair copulations (EPCs), or that females were pursuing a mixed reproductive strategy (Trivers 1972) wherein they increased their overall fitness through EPCs, despite the immediate fecundity cost. Although the lack of a male intromittent organ makes forced copulations unlikely for passerine birds (Birkhead & Møller 1992), females might nonetheless be coerced to accept EPCs to avoid even greater costs from continued harassment (Westneat 1992). However, females are courted by and observed to copulate with extra-pair males much less often than expected given the paternity realised by extra-pair males (Monnett *et al.* 1984; Westneat 1992). These observations suggest that female red-winged blackbirds are not extensively harassed by extra-pair males and that most EPCs occur out of sight of human observers (and presumably the females' mates), as expected if females cooperate in extra-pair matings.

If there is an advantage to extra-pair mating, it can only be realized through the superior survival and reproductive success of the resulting progeny. Because female birds appear to select higher quality males for EPCs (Møller 1988; Smith & Montgomerie 1991; Kempenaers *et al.* 1992; Graves *et al.* 1993; P. J. Weatherhead & P. T. Boag, unpublished results), any resulting offspring will be of higher quality if male attractiveness and viability are correlated and heritable (see for example, Norris 1993). In a species such as the red-winged blackbird with both polygynous and extra-pair matings, the variance in male reproductive success is very high, particularly over males' lifetimes (Orians & Beletsky 1989; P. J. Weatherhead & P. T. Boag, unpublished results). Thus if females recover the fecundity cost of extra-pair matings, they would do so primarily through the success of their sons (Weatherhead & Robertson 1979; Weatherhead 1994). The very low rate of return to their natal area by male red-winged blackbirds (Shutler & Weatherhead 1994) will make testing this hypothesis extremely difficult.

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