Behav Ecol Sociobiol (1997) 40: 151 – 158

Patrick J. Weatherhead

Breeding synchrony and extra-pair mating in red-winged blackbirds

Received: 7 June 1996 / Accepted after revision: 25 November 1996

Abstract Using data from a 6-year paternity study of red-winged blackbirds, I tested the hypotheses that increased nesting synchrony should either promote extra-pair mating by increasing the advantage of extra-pair mating to females, or decrease extra-pair mating by constraining males from seeking extra-pair copulations. Contrary to these hypotheses, the occurrence of extra-pair paternity did not vary with nesting synchrony over the breeding season, or vary with the number of synchronous nests within territories or within marshes, or with nesting order on territories. However, for nearly all nests with extra-pair young, there were fewer females synchronous with that nest on the cuckolder's territory than on the territory of the cuckolded male. This "advantage" of a synchrony difference was less pronounced for older males that cuckolded younger males, particularly when the two males were not neighbors. Collectively, these results suggest that breeding synchrony affects extra-pair mating by affecting mate guarding, but that breeding synchrony alone can not be used to predict which females are more likely to engage in extra-pair mating, nor with which extra-pair males they will mate. Understanding why extra-pair mating by older males is less affected by breeding synchrony may explain much about both the proximate and ultimate causes of extra-pair mating in red-winged blackbirds.

Key words Synchrony · Extra-pair mating · Age · Neighbors · Red-winged blackbird

Introduction

The recent proliferation of paternity studies of birds has revealed that extra-pair paternity constitutes a regular component of male reproductive success of many species, and that substantial variation in the extent of extra-pair paternity occurs among species. Identification of the ecological factors that underlie the variation in extra-pair paternity is an important step toward understanding the basis for the prevalence of extra-pair paternity. Stutchbury and Morton (1995) have proposed that breeding synchrony may be an important ecological factor that influences the extent of extra-pair paternity in a given species. My goal in this paper is to explore the extent to which breeding synchrony is associated with patterns of extra-pair paternity in red-winged blackbirds (*Agelaius phoeniceus*).

In proposing that breeding synchrony might contribute to variation in extra-pair paternity, Stutchbury and Morton (1995) assumed that females exercise substantial control over extra-pair mating. Further, they assumed that females use extra-pair mating to obtain mates of high genetic quality. Given these assumptions, Stutchbury and Morton (1995) reasoned that increased breeding synchrony should promote increased extra-pair mating because females can compare more potential extra-pair males simultaneously, thus maximizing the quality of the genetic mate they choose and thus, the benefits of extra-pair mating. In turn, if female availability for extra-pair mating increases as breeding becomes more synchronized, so too does the relative opportunity for extra-pair mating for males. Thus, Stutchbury and Morton (1995) reasoned that males should expend more effort on extra-pair mating as female fertility becomes more synchronized, further increasing the correlation between extra-pair mating and breeding synchrony. In support of this hypothesis, there is evidence that female birds exercise some control over extra-pair mating (e.g., Smith 1988; Wagner 1991; Lifjeld and Robertson 1992; Mulder et al. 1994; Gray 1996), that higher-quality males are more successful at extra-pair mating (e.g., Kempenaers et al. 1992; Weatherhead and Boag 1995; Yezerinac and Weatherhead 1997a), and that the frequency of extra-pair mating is positively correlated with breeding synchrony within a

Patrick J. Weatherhead
Department of Biology, Carleton University,
1125 Colonel By Drive, Ottawa ON K1S 5B6, Canada
Fax: 613-359-5596; e-mail: pweather@biology.queensu.ca

species (Stutchbury et al. 1994) and among species (Stutchbury and Morton 1995).

Despite the positive evidence cited above, there is also reason to be skeptical of the breeding synchrony hypothesis of Stutchbury and Morton (1995). First, from a theoretical perspective, the logic underlying the hypothesis may be faulty. In particular, it is not obvious that by breeding more synchronously, females alter the availability of potential extra-pair males. As long as breeding is broadly synchronous (i.e., all males are physiologically capable of breeding during the same period), all males should be available as extra-pair mates throughout the breeding season, regardless of how synchronously the females are breeding. One way that synchrony could affect the availability of males is through their need to guard their own mate(s) against extra-pair mating (Birkhead and Biggins 1987; Westneat et al. 1990; Birkhead and Møller 1992). However, that would result in breeding synchrony decreasing, not increasing extra-pair mating. Empirically, we know that the frequency of extra-pair fertilizations is not correlated with breeding synchrony in tree swallows (*Tachycineta bicolor*) (Dunn et al. 1994), despite this species satisfying the prerequisite of females controlling extra-pair mating (Lifjeld and Robertson 1992). Also, in species for which there is evidence that higher quality males are more successful as extra-pair mates, there is also evidence that high quality males are themselves regularly cuckolded (e.g., Weatherhead and Boag 1995; Yezerinac et al. 1995), so extra-pair mating appears to involve more than just females being free to choose the best extra-pair male to sire their offspring. Finally, from a study of socially monogamous yellow warblers (*Dendroica petechia*), Yezerinac and Weatherhead (1997b) found that the incidence of extra-pair paternity was not correlated with either population-wide synchrony or synchrony with neighbors. However, an analysis of males cuckolded in only one of their two nests showed that the nest with extra-pair young was most often that which was asynchronous with the cuckolder's own nest, suggesting that guarding his own mate constrained a male from siring extra-pair young. Moreover, higher quality males were least affected by this apparent constraint of synchrony.

Here I use data from a 6-year paternity study of socially polygynous red-winged blackbirds to assess whether breeding synchrony is associated with patterns of extra-pair mating. Approximately 25–35% of red-winged blackbird nestlings are sired by extra-pair males (Gibbs et al. 1990; Westneat 1993a; Weatherhead and Boag 1995; Gray 1996). I have no evidence of whether or not female red-winged blackbirds control extra-pair matings in the study population, although there is some indirect evidence consistent with females preferring genetically superior males as extra-pair mates (Weatherhead et al. 1994; Weatherhead and Boag 1995). In a western population of red-winged blackbirds, Gray (1996) did find that females actively pursued extra-pair matings. In a study of eastern red-winged blackbirds, Westneat (1992) found no evidence that females actively pursued extra-pair matings, although his observations were consistent with females exercising choice among the extra-pair males that courted them.

Although the evidence cited above suggests that female red-winged blackbirds have some control over extra-pair mating and prefer higher quality males as required by the hypothesis of Stutchbury and Morton (1995), there is also evidence that synchrony does not affect extra-pair mating in red-winged blackbirds. Westneat (1993a) and Gray (1996) compared rates of extra-pair paternity among nests with and without synchronously active nests on the same territory and found no difference. Gray (1996) also found no difference in the incidence of extra-pair paternity relative to nesting order on territories. Here I broaden the analysis to determine whether the incidence of extra-pair paternity varied with seasonal patterns of nesting synchrony within the population, and to assess the influence of synchrony within territories, within marshes, and between the territories of the two males involved in each case of cuckoldry.

There is also evidence that supports the assumptions of the hypothesis that female breeding synchrony might reduce extra-pair mating because mate guarding by males could conflict with their extra-pair mating effort. Westneat (1993b, 1994) found that male red-winged blackbirds appeared to guard their females, both by following them and by chasing intruding males. Males removed briefly from their territories during their mates' fertile period lost paternity to extra-pair males, indicating that mate guarding does protect paternity. Even more relevant, males provided with food so they did not have to leave their territories to forage lost less paternity to extra-pair males than did unsupplemented males, confirming not only that mate guarding is important, but that it can conflict with other activities. Although I have no information on mate guarding in my study population, it seems likely that mate guarding is similar to that in Westneat's population because the study areas are located within several hundred kilometers of each other.

The main prediction I test is that the frequency of extra-pair paternity increases with breeding synchrony. I first assess whether extra-pair paternity increases with breeding synchrony within the population (Stutchbury and Morton 1995). If so, then nests initiated during the peak of nesting when synchrony is greatest should be most likely to contain extra-pair young, and nests initiated either early or late in the season should be least likely to contain extra-pair young. Alternatively, if extra-pair mating is largely a product of male extra-pair mating effort, and males are constrained from extra-pair mating when guarding their own females, then rates of extra-pair paternity would decrease with breeding synchrony. In this case, extra-pair paternity should be least likely at the peak of nesting and most likely early and late in the breeding season.

Next I assess whether extra-pair paternity varies with the number of synchronous females nesting within the same territory or within the same marsh. If synchrony increases extra-pair mating through female choice (Stutchbury and Morton 1995), then females that produce extra-pair young should have nested synchronously with more females on the same marsh, but not on the same territory. If mate guarding by males is important, then high synchrony within territories should be associated with more frequent extra-pair paternity (because males with more synchronous females should be less effective at mate guarding and their territories may attract more potential cuckolders), but high synchrony with the rest of the population should be associated with less extra-pair paternity (because more other males will be occupied guarding their own mates).

I also examine the association between synchronous breeding and extra-pair mating, but consider only the territories of the two males involved in each case of extra-pair paternity (i.e., the cuckolder and the cuckold). If mate guarding is important, then nests with extra-pair paternity should be associated with differences in synchrony between the two territories, such that the cuckolded male will have had more synchronous females (and thus have been less effective at mate guarding) while the cuckolder will have had fewer synchronous females (and thus have been less constrained by having to guard his own mates). I assume here that the effectiveness of mate guarding, and the ability to perform other activities (e.g., seek extra-pair copulations, EPCs) while mate guarding decreases with the number of females being guarded simultaneously.

Finally, should I find that cuckolded males had more synchronous mates than the males that cuckolded them, then I would expect that the males that were generally more successful at extra-pair mating will have been least constrained by synchrony (Yezerinac and Weatherhead 1997b). In this population, older and longer-lived males are most successful at extra-pair mating (Weatherhead and Boag 1995). This prediction could accommodate two possible mechanisms if supported. First, either older or longer-lived males had fewer synchronous females to guard than the males they cuckolded, which seems unlikely given that harem size is positively correlated with male age (Weatherhead and Boag 1995). Second, despite having more females to guard, older males may have been better at gaining extra-pair fertilizations (EPFs), either because they are sneakier (e.g., better at timing their EPC attempts) and/or because their mates are more faithful.

Methods

I conducted this study from 1986 through 1991 at three marshes on beaver ponds within 10 km of the Queen's University Biological Station in eastern Ontario. I captured, banded, and collected blood from > 95% of males resident on the three marshes over the 6 years of this study. Data from the largest of the marshes were used in all 6 years. Preliminary paternity analyses from this marsh for 1986 were presented in Gibbs et al. (1990). In the other two marshes I only analysed paternity in 1988 and 1989, although I did monitor nesting activity throughout, so the age and longevity of the males present in 1988 and 1989 could be estimated. Most relevant details of the methods have been published previously (Gibbs et al. 1990; Weatherhead et al. 1994; Weatherhead and Boag 1995, 1997), so here I provide only a brief overview.

Males were color-banded as they returned and began defending territories in April. Territories were mapped through the breeding season, and beginning in early May, the marshes were searched for nests every second day. Most nests were found before egg laying was completed. Active nests were monitored until they failed or the young fledged. Nestlings were banded and had their blood sampled (Hoysak and Weatherhead 1991) when they were 5 or 6 days old. Because this study was part of an ongoing project on the same red-winged blackbird population, I was able to estimate male ages with reasonable accuracy, and assuming that males first established their territories when they were two years old (Shutler and Weatherhead 1994), I could also estimate the longevity of most males very accurately.

Parentage analysis was conducted using standard multi-locus DNA fingerprinting techniques, summarized in detail for this study in Weatherhead et al. (1994). Here I include data from 1986–1991. Weatherhead et al. (1994) excluded data for 1987, the only year no parentage analyses were conducted for nestlings that did not fledge. Because the eventual fate of nestlings is not directly relevant to this study, and because limiting the analyses to successful nests for 1987 is unlikely to bias the data relative to the goals of this study, I have included results from 1987.

Red-winged blackbirds lay one egg per day, with a modal clutch size of four in my study population. I defined the female fertile period as beginning 5 days before the first egg was laid and lasting until the day the penultimate egg was laid. This allows for the possibility of stored sperm from copulations prior to egg laying to fertilize eggs (Birkhead and Møller 1992), and also, given the uncertainties for males of when a female will start and stop laying, probably approximates the fertility window from the perspective of males. This is also the period during which most copulations (within- and extra-pair) occur in red-winged blackbirds (Gray 1996). I then defined a fine and coarse level of synchrony. By the fine scale, females were considered synchronous if their first egg dates occurred within two days of one another, thereby producing a minimum overlap of approximately 1 week in their fertility windows. By the coarse scale, females were considered synchronous if there was any overlap in their fertility windows. Paired comparisons were limited to the coarse scale because the fine scale provided too little variation in synchrony among individuals. Except where specified, I considered each nest in which extra-pair paternity occurred as an independent event. In the four cases where two extra-pair males sired young in the same nest, I considered this as two independent cases of extra-pair mating for analyses involving direct comparisons of the cuckolded male and the males that cuckolded him. Because patterns of extra-pair paternity were similar across marshes and years (Weatherhead et al. 1994; Weatherhead and Boag 1997), for most analyses I only present results for all marshes and years combined.

Results

To assess whether nests with nestlings sired by extra-pair males were more or less synchronous relative to the general population, I first compared the frequency distributions of first egg dates of nests with extra-pair young ($n = 75$) and all nests initiated on the same marshes during the same years ($n = 337$). The frequency distributions were very similar (Kolmogorov-Smirnov test, $X^2 = 1.59$, $P = 0.90$, Fig. 1). Repeating that analysis just for nests included in the paternity analysis (i.e., those with extra-pair young vs. those without) again failed to indicate any association between synchrony and

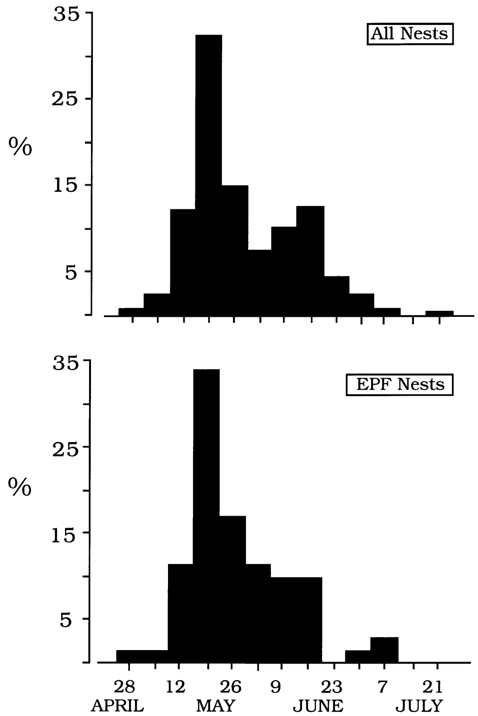

Fig. 1 Frequency distribution (by week) of nest initiation dates for all nests over the 6-year study and for nests with extra-pair fertilizations (EPFs)

extra-pair paternity (Kolmogorov-Smirnov test, $X^2 = 0.56, P > 0.99$). These results do not support either the prediction that synchrony should enhance extra-pair mating or the prediction that females that nest out of synchrony with the general population should be more likely to engage in extra-pair mating. I also determined whether the proportion of a brood sired by extra-pair males varied seasonally in case there was a subtle effect of breeding synchrony not detected by the preceding analysis. There was no evidence that the proportion of extra-pair young in a brood varied with clutch initiation date ($r = 0.04$, $P = 0.77$; note that nonlinear models were equally lacking in significance).

Comparisons of the overlap in the fertility windows of nests also failed to reveal any effect of synchrony on the likelihood of extra-pair paternity. Nests with extra-pair young and nests without extra-pair young did not differ significantly in the number of nests with which they were synchronous, either in the same territory (Mann-Whitney U-test, $z = -0.50$, $P = 0.62$), or in the same marsh (coarse synchrony: $z = -1.30$, $P = 0.19$; fine synchrony: $z = -0.02$, $P = 0.98$). Females with and without extra-pair young also did not differ in the order in which they had initiated nests within territories (Mann-Whitney U-test, $z = -0.68$, $P = 0.48$). Repeating all of these analyses separately by year produced nearly identical results. There were no significant differences between nests with and without extra-pair young in the number of synchronous nests on the same territory (Ps $= 0.23 - 0.87$) or in the same marsh (coarse: Ps $= 0.09 - 0.91$; fine: Ps $= 0.13 - 0.92$). In five of six years there was also no difference in the order in which the females had initiated nests within territories (Ps $= 0.24 - 0.75$), although in 1987 females that produced extra-pair young nested on average ahead of females on the same territory that did not produce extra-pair young (Mann-Whitney U-test, $z = -2.42$, $P = 0.02$). Overall, therefore, these results indicate that synchrony with other females in the same territory or the same marsh, and nest initiation order on territories were unimportant to extra-pair mating.

Among nests with extra-pair young, the proportion of the brood sired by extra-pair males did not vary with the number of synchronous nests, either in the same territory ($r = 0.04$, $P = 0.73$) or on the same marsh (coarse: $r = 0.09$, $P = 0.45$; fine: $r = 0.06$, $P = 0.60$). The order that females nested on the territory also had no effect on the proportion of the brood sired by extra-pair males ($r = 0.00$, $P = 1.00$).

A final way to assess whether there was any general effect of nesting synchrony on extra-pair mating is to score the synchrony in each marsh by territory. For every nest included in the paternity analysis, I determined the number of synchronously nesting females in the same territory, and on every other territory on the same marsh. Then for each nest I determined the number of territories that had fewer synchronous nests than the territory of the nest in question. For nests without extra-pair young ($n = 124$), the mean number of territories with fewer synchronous females was 6.73 ± 4.24 S D (range = 0 – 18), compared to a mean of 7.58 ± 4.75 SD (range = 0 – 18) for nests with extra-pair young ($n = 71$; Mann-Whitney test, $z = -1.19$, $P = 0.23$). Thus, differences in nesting synchrony among territories did not predict which nests had extra-pair young and which ones did not.

In contrast to the results presented above, direct comparisons between cuckolders and cuckolds did reveal that synchrony affected extra-pair mating. For each case of cuckoldry I determined the number of nests on the territories of both the cuckolder and cuckold that were synchronous with the nest with the extra-pair young. The difference between these (i.e., cuckolder–cuckold) I called the "synchrony difference", so a negative value means the cuckolder had fewer synchronous females on his territory and a positive value means he had more. Most often the cuckolder had fewer synchronous females than the male he cuckolded (Wilcoxon test, $z = -4.53$, $P < 0.0001$, Fig. 2). In the preceding analysis the focal nest (ie, the nest with the extra-pair young) was not included in the number of synchronous nests on the cuckolded male's territory. When the focal nests are included, then there was only one instance out of 61 cases (2%) of cuckoldry in which the cuckolder had more females nesting synchronously at the time of the cuckoldry. In 51 out of 61 cases (84%), at the time of the cuckoldry, the male that was cuckolded had more females nesting synchronously than the male that cuckolded him.

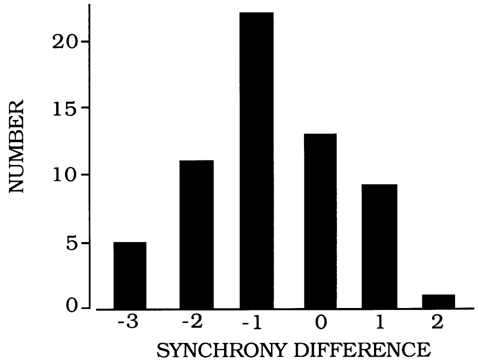

Fig. 2 Frequency distribution of the difference between the number of synchronously nesting females on the territory of the cuckolder and that of the male he cuckolded (excluding the female in question), for all cases of extra-pair paternity

In the preceding analyses I considered only whether or not a nest contained extra-pair young, and not how many extra-pair young there were. Extra-pair males sired from one to four nestlings in those nests. Given that synchrony differences between the two males affected cuckoldry, then it is possible that as that difference increased, the extra-pair male was able to sire more young. However, there was no evidence that the number of extra-pair young sired by a male in a given nest varied with the difference in synchrony between the pair and extra-pair males' territories ($r = 0.08$, $P = 0.53$). Thus, synchrony differences only affected the occurrence of extra-pair paternity, but not its extent when it did occur.

Given that cuckolders usually had fewer synchronous females at the time of the cuckoldry than the males they cuckolded, one might expect that for a given female that produced extra-pair young, the sire of those young would have been the available male with the fewest synchronous females on his territory at that time. To explore this possibility, for each nest with extra-pair young I determined how many of the males on neighboring territories had equal or fewer synchronous females on their territories relative to the male known to have sired the nestlings. I restricted the analysis to neighboring males simply because by their proximity they should have been at least potentially available for extra-pair mating. There were 57 cases of cuckoldry with a known sire and at least one neighbor that was not the sire. Overall, in 39% of these cases there was at least one neighbor with fewer synchronous females, and 61% with at least one male with fewer or equal numbers of females than the cuckolder. Quantified slightly differently, for each of these cases there was an average of 1.1 neighbors with fewer synchronous females and 1.9 neighbors with fewer or equal numbers of females relative to the cuckolder. Given that the average number of neighbors, exclusive of the cuckolder, was 3.0, on average more than half the neighbors of the cuckold had equal or fewer synchronous females than the cuckolder. These results indicate that the synchrony difference alone is a poor predictor of which male will be the cuckolder. The effect of synchrony differences found in the analysis of dyads (above) therefore means that synchrony differences may facilitate extra-pair mating only as long as other factors (e.g., age differences; Weatherhead and Boag 1995) also provide a male some advantage in extra-pair mating.

I predicted that if extra-pair mating was constrained by breeding synchrony, then older and longer-lived males should be least affected by that constraint, given their overall success at extra-pair mating (Weatherhead and Boag 1995). Thus, because cuckoldry appeared to have been facilitated by there being fewer synchronous females on the cuckolder's territory than on the cuckolded male's territory, older males should have been more successful at cuckoldry even when they had fertilizable females on their own territories. To test this prediction, I compared the age or longevity differences with the synchrony difference for each cuckolder-cuckold dyad. Again these are calculated as the age or longevity of the cuckolder minus the age or longevity of the cuckold. The age difference was the difference in minimum estimated ages of the males at the time (ie, year) of the cuckoldry, and the longevity difference was the difference in the estimated longevities of the two males (Weatherhead and Boag 1995, 1997). Overall ($n = 61$), the synchrony difference tended to increase as the age or longevity difference increased (age: $r = 0.34$, $P = 0.07$; longevity: $r = 0.23$, $P = 0.08$). What this means is that younger males generally cuckolded males older than themselves only when the older males had more synchronous females on their territories than the younger males. By contrast, older males cuckolded younger males even when the younger males had fewer synchronous females. This trend suggests that extra-pair mating by relatively older or longer-lived males may have been less constrained by synchrony.

To explore further the interaction between age and synchrony, I considered a second potential constraint. In this study, 52% of the cuckolder-cuckold dyads were neighboring males. Thus, proximity appears to facilitate extra-pair mating. Therefore, breeding synchrony may be more of a constraint on extra-pair mating when the potential cuckolder does not occupy a territory adjacent to that in which the potential extra-pair female is nesting. If so, then any age or longevity advantage in overcoming the synchrony constraint should be more pronounced among non neighbors than among neighbors. In fact, it appears that all the advantage of age was restricted to non neighbors. Among neighbors ($n = 32$), there was no apparent relationship between age and synchrony differences (age: $r = 0.12$, $P = 0.51$; longevity: $r = 0.03$, $P = 0.86$, Fig. 3). However, among non neighbors ($n = 29$), males that were relatively older or longer lived appeared to have been less constrained by breeding synchrony (age: $r = 0.35$, $P = 0.06$; longevity: $r = 0.42$, $P = 0.03$, Fig. 3).

There are several ways that breeding synchrony could have produced the relationship between longevity and synchrony differences among non neighbors. The effect could have been primarily a consequence of the cuck-

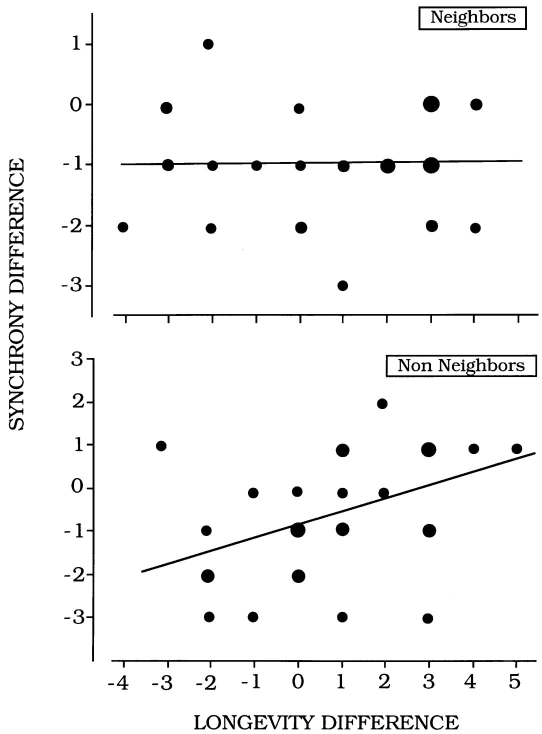

Fig. 3 Relation between the difference in longevity of the cuckolder and the cuckold, and the difference in the number of females nesting synchronously on their territories at the time of the cuckoldry, for neighbors and non-neighbors. *Dot size* indicates the number of entries with equal value (range 1–4). *Straight lines* were determined by linear regression

olded males having a lot of synchronous females on their territories, or the cuckolders having few synchronous females on their territories, or a combination of the two. To assess these possibilities I repeated the analysis in Fig. 3 for non-neighbors, using either just the number of synchronous females on the cuckolded males' territories, or just the number of synchronous females on the cuckolders' territories in place of the difference in synchrony. Both analyses produced similar, non significant results ($r = 0.30$ and 0.34, $P = 0.11$ and 0.08, respectively). Thus, it was the combined effect of high synchrony on the cuckolded males' territories and low synchrony on the cuckolders' territories (i.e., the synchrony difference) that produced the significant relationship between longevity differences and synchrony differences (Fig. 3). Finally, although an age advantage allowed males to overcome the constraint of synchrony when they were not neighbors of the males they cuckolded, age and synchrony differences did not affect the number of young the extra-pair male sired in a given nest (multiple linear regression: $R^2 = 0.04$, $P = 0.58$).

A possible problem with all of the dyad analyses presented above is that the same pair of males is represented more than once when one male was cuckolded by the same male at more than one nest. There was one dyad that involved two nests in the same year, three that involved two nests in different years, and one in which a male was cuckolded by the same individual at three nests in one year and at one in another year. For each of these dyads I averaged values across nests, reducing the sample size to 54, and repeated all the previous analyses. Because all results remained qualitatively the same (i.e., no significant results became non-significant and vice versa), I do not present details of these analyses.

Discussion

I tested two alternative hypotheses that predicted an effect of breeding synchrony on rates of extra-pair paternity. If extra-pair mating is primarily controlled by females, and breeding synchrony enhances the advantage females realise from extra-pair mating (Stutchbury and Morton 1995), then extra-pair paternity should have been more prevalent as synchrony among females increased. Conversely, if males control extra-pair mating, and are constrained from pursuing extra-pair matings while guarding their own mates (Birkhead and Møller 1992), then females that nested asynchronously with other females should have produced more extra-pair young. Neither of these alternatives was supported by the data from the whole study population. Extra-pair mating did not vary with seasonal variation in nesting synchrony, and nests with extra-pair young did not differ from those without extra-pair young in the number of nests with which they were synchronous, either on the same territory, or on the same marsh. Westneat (1993a) and Gray (1996) also found that red-winged blackbird nests with extra-pair young were not more likely to have synchronous nests within the same territory. These results are consistent with data for tree swallows (Dunn et al. 1994) and yellow warblers (Yezerinac and Weatherhead, 1997b), but not for hooded warblers (*Wilsonia citrina*; Stutchbury et al. 1994). Thus, intraspecific studies have failed to show a general effect of breeding synchrony on extra-pair mating in three of four species.

In support of their synchrony hypothesis, Stutchbury and Morton (1995) provided two lines of comparative evidence from songbirds. First, they found that rates of extra-pair paternity increased with breeding synchrony across taxa. Second, they found that tropical songbirds have relatively small testes, and because, among higher latitude species, testes are proportionately larger in species with more extra-pair paternity, tropical species can be inferred to have low rates of extra-pair mating. Because tropical species also tend to breed asynchronously, low rates of extra-pair mating and low breeding synchrony would be consistent with the synchrony hypothesis. These comparative data are obviously at odds with the intraspecific evidence cited above. One possible explanation is that the results of the comparative analyses are spurious, resulting from some additional, uncontrolled variable(s) that are correlated with both synchrony and extra-pair mating. For example, rates of extra-pair paternity have been shown to decrease with breeding density (e.g., Gibbs et al. 1990). A positive correlation between breeding density and breeding synchrony among songbirds could explain the conflicting evidence from the comparative and intraspecific studies. Clearly, the patterns reported by Stutchbury and Morton (1995) warrant further investigation.

Despite failing to find a general association between breeding synchrony and extra-pair mating in red-winged blackbirds, I did find an effect of synchrony just within the pairs of males involved in each case of cuckoldry. At the time of extra-pair mating, the cuckolder usually had fewer fertilizable females on his territory than the cuckolded male had on his territory. This result suggests that males were constrained from extra-pair mating when their own mates were fertilizable, or were better able to overcome the other male's mate guarding as the number of females being guarded increased. The fact that these patterns were not detectable over the entire population indicates that while a synchrony difference between two males may have facilitated extra-pair mating by the male with fewer synchronous females, synchrony differences alone were not sufficient to produce extra-pair matings. Indeed, were synchrony differences sufficient to produce extra-pair mating, then non-territorial floaters should have been very successful at extra-pair mating, because they never have mates to guard, and yet floaters collectively accounted for only a small percentage of all extra-pair fertilizations (Weatherhead and Boag 1995). Thus, breeding synchrony does not explain why some females were faithful to their mates, nor why other females were not. All that can be inferred is that, for those females that were unfaithful, it was usually with a male that was less constrained than her own mate with guarding synchronously nesting females on his territory. However, these results do indicate that mate guarding by males is one element that influences extra-pair mating.

I also found that older males were less constrained by breeding synchrony, particularly when cuckolding males that were not their neighbors. Wetton et al. (1995) also found that older male house sparrows (*Passer domesticus*) were more likely than younger males to sire extra-pair young during their own mate's fertile period, and Yezerinac and Weatherhead (1997b) found that male yellow warblers with more plumage streaking were more successful at extra-pair mating when their own mates were fertile. This result could indicate that older male red-winged blackbirds are at less risk of being cuckolded because their mates are more faithful, and so older males are less constrained by having to guard their own mates. The positive correlation between within-pair and extra-pair reproductive success in this population (Weatherhead and Boag 1997) is consistent with this possibility. Alternatively, if an increasing difference in longevity between two males reflects an increasing difference in genetic quality, then females mated to the lower-quality male may behave in ways that facilitate extra-pair mating with the higher-quality male, thus reducing the constraints of synchrony and distance. A third possibility is that the experience of older males may make them better able to monitor the activities of other males and their mates, and therefore to time their extra-pair mating attempts more effectively. Future research that can explain the basis for extra-pair mating by older male red-winged blackbirds being less constrained by breeding synchrony will go a long way toward explaining the basis for extra-pair mating generally.

Acknowledgements I thank D. Hoysak, P. Boag, R. Montgomerie, L. Gibbs, K. Muma, D. Michaud-Freeman, J. Sechley, C. Roeder, L. Hamilton, L. Tabak and S. Shackleton for technical assistance, Kevin Dufour, Bridget Stutchbury, Dave Westneat and Stephen Yezerinac for comments on the manuscript, Peter Boag for use of the Queen's University Molecular Ecology Lab, the Lister Institute and Alec Jeffreys (University of Leicester) and T. Bargiello (Rockefeller Institute) for the probes used in DNA profiling, Queen's University for the use of the Biological Station facilities and the Natural Sciences and Engineering Research Council of Canada and Carleton University for financial support.

References

Birkhead TR, Biggins JD (1987) Reproductive synchrony and extra-pair copulation in birds. Ethology 74:320–334

Birkhead TR, Møller AP (1992) Sperm competition in birds. Academic Press, London

Dunn PO, Whittingham LA, Lifjeld JT, Robertson RJ, Boag PT (1994) Effects of breeding density, synchrony and experience on extra-pair mating in tree swallows. Behav Ecol 5:123–129

Gibbs HL, Weatherhead PJ, Boag PT, White BN, Tabak LM, Hoysak DJ (1990) Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. Science 250:1394–1397

Gray EM (1996) Female control of offspring paternity in a western population of red-winged blackbirds (*Agelaius phoeniceus*). Behav Ecol Sociobiol 38:267–278

Hoysak DJ, Weatherhead PJ (1991) Sampling blood from birds: a technique and an assessment of its effect. Condor 93:746–752

Kempenaers B, Verheyen GR, Van den Broeck M, Burke T, Van Broeckhoven C, Dhondt AA (1992) Extra-pair paternity results from female preference for high quality males in the blue tit. Nature 357:494–496

Lifjeld JT, Robertson RJ (1992) Female control of extra-pair fertilization in tree swallows. Behav Ecol Sociobiol 31:89–96

Mulder RA, Dunn PO, Cockburn A, Lazenby-Cohen KA, Howell MJ (1994) Helpers liberate female fairy wrens from constraints on extra-pair mate choice. Proc Roy Soc Lond B 255:223–229

Shutler D, Weatherhead PJ (1994) Movement patterns and territory acquisition by floater red-winged blackbirds. Can J Zool 72:712–720

Smith SM (1988) Extra-pair copulations in black-capped chickadees: the role of the female. Behaviour 107:15–23

Stutchbury BJ, Morton ES (1995) The effect of breeding synchrony on extra-pair mating systems in songbirds. Behaviour

Stutchbury BJ, Rhymer JM, Morton ES (1994) Extra-pair paternity in the hooded warbler. Behav Ecol 5:384–392

Wagner RH (1991) Evidence that female razorbills control extra-pair copulations. Behaviour 118:157–169

Weatherhead PJ, Boag PT (1995) Pair and extra-pair mating success relative to male quality in red-winged blackbirds. Behav Ecol Sociobiol 37:81–91

Weatherhead PJ, Boag PT (1997) Genetic estimates of annual and lifetime reproductive success in red-winged blackbirds. Ecology, in press

Weatherhead PJ, Montgomerie R, Gibbs HL, Boag PT (1994) The cost of extra-pair fertilizations to female red-winged blackbirds. Proc Roy Soc Lond B 258:315–320

Westneat DF (1992) Do female red-winged blackbirds engage in a mixed mating strategy? Ethology 92:7–28

Westneat DF (1993a) Polygyny and extra-pair fertilisations in eastern red-winged blackbirds (*Agelaius phoeniceus*). Behav Ecol 4:49–60

Westneat DF (1993b) Temporal patterns of within-pair copulations, male mate-guarding, and extra-pair events in eastern red-winged blackbirds (*Agelaius phoeniceus*). Behaviour 124:267–290

Westneat DF (1994) To guard mates or go forage: conflicting demands affect paternity of male red-winged blackbirds. Am Nat 144:343–354

Westneat DF, Sherman PW, Morton ML (1990) The ecology and evolution of extra-pair copulation in birds. Curr Ornithol 7:331–369

Wetton JH, Burke T, Parkin DT, Cairns E (1995) Single-locus DNA fingerprinting reveals that male reproductive success increases with age through extra-pair paternity in the house sparrow (*Passer domesticus*). Proc Roy Soc Lond B 260:91–98

Yezerinac SM, Weatherhead PJ (1997a) Extra-pair mating, plumage coloration and sexual selection in yellow warblers (*Dendroica petechia*.) Proc Roy Soc Lond B (in press)

Yezerinac SM, Weatherhead PJ (1997b) The effects of synchrony and individual quality on extra-pair mating strategies in the socially monogamous yellow warbler. Anim Behav (in press)

Yezerinac SM, Weatherhead PJ, Boag PT (1995) Extra-pair paternity and the opportunity for sexual selection in a socially monogamous bird (*Dendroica petechia*). Behav Ecol Sociobiol 37:179–188

Communicated by W.A. Searcy