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Pair and extra-pair mating success relative to male quality in red-winged blackbirds

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Abstract We tested whether the reproductive success of male red-winged blackbirds (*Agelaius phoeniceus*) varied with male secondary sexual traits or with haematozoa prevalence, and whether these patterns were consistent with females preferring genetically superior males. We also determined whether the traits that correlated with male success on their own territories were also correlated with male success at siring young on other males' territories. Our analysis included data from a 6-year study involving 617 nestlings for which paternity was determined by DNA profiling. Larger males sired more young on their territories, principally because they obtained larger harems. The success of larger males at acquiring more mates did not appear to be a consequence of larger males holding larger or better-quality territories. Older and longer-lived males sired more young by extra-pair fertilizations. Larger males sired the most offspring overall (on territory + off territory). Variation in epaulet size and color, responses to male and female models, nest defence and parasitism was not correlated with male success either on or off their territories or overall. Male success in a given year was significantly correlated with success the previous year, as expected if females were selecting genetically superior males. The male that was by far the most successful individual in this study was highly consistent from year to year. Because male body size is positively correlated with survival in this population (although not within the sample of males included in this study), female preference for larger males may have reflected a general preference for males with superior survival ability. We propose that the direct advantage realized by older males in extra-pair matings might indicate that experience is important, such that experienced males are better at creating or exploiting the opportunities for extra-pair mating. This hypothesis is consistent with a pairwise analysis of cuckoldry that showed that cuckolders were most often older than the males they cuckolded.

Key words Mating · Extra-pair mating · Reproductive success · Sexual selection · Red-winged blackbird

Introduction

Males of many bird species have elaborate ornamentation and behaviour that they appear to use to attract females. Although the association of these secondary sexual traits with competition for mates has long been recognized (Darwin 1871), the debate about which traits females prefer, and why, remains unresolved (Kirkpatrick and Ryan 1991). The lack of resolution stems in part from the difficulty in studying mate choice in natural populations (because of e.g. small samples; Zuk et al. 1990), and, at least in some cases, the acceptance of false assumptions (e.g. females copulate only with their mates) that may have caused investigators to overlook important components of sexual selection. Here we present the results of a 6-year study of male reproductive success relative to male secondary sexual traits in red-winged blackbirds (*Agelaius phoeniceus*), using DNA-based methods to assign paternity.

Red-winged blackbirds are socially polygynous, highly sexually dimorphic, and widespread in North America, attributes that collectively have made them one of the avian species most studied in sexual selection research. Despite all the attention, however, how female red-winged blackbirds choose their mates remains unclear. At least two important factors may have contributed to our failure to understand mate

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choice in this species. First, the influential "polygyny threshold model" of Orians (1969) focused much of the early attention on territory quality as the basis for female choice. That model assumed that males acquired territories according to competitive ability. Thus, the relative quality of a male's territory was assumed to be a reflection of his own quality, and females only needed to assess territory quality to choose the right male. We now know that territory acquisition in red-winged blackbirds is largely independent of male competitive ability (Eckert and Weatherhead 1987a, b; Beletsky and Orians 1989; Shutler and Weatherhead 1991, 1992), so if male traits are important in mate choice, female blackbirds (and students of mate choice) must assess those traits directly.

The second potential impediment to understanding mate choice in red-winged blackbirds was the assumption that social mating patterns reflected genetic mating patterns. Although the possibility that extra-pair fertilizations (EPFs) might be common in red-winged blackbirds was recognized 2 decades ago (Bray et al. 1975), it is only the recent availability of DNA-based methods of paternity analysis that has allowed accurate estimation of the occurrence of EPFs. Gibbs et al. (1990), Westneat (1993) and Gray (1994) all found that more than one quarter of all red-winged blackbird nestlings are sired by males other than the females' social mates. These results have two important implications for mate choice in blackbirds. First, they indicate that a female's decision as to which male will sire her offspring is at least partially independent of her nesting decision (i.e. in whose territory she nests; Weatherhead 1994). Second, these results indicate that EPFs are sufficiently common that any study of mate choice must use true measures of paternity if the relative success of different males is to be assessed reliably.

Our principal objective in this study was to use DNA-based measures of male reproductive success to test the hypothesis that males with the most elaborate secondary sexual characters were most successful. We attempted to include a fairly comprehensive set of morphological and behavioural characters in our analyses. We also had several subsidiary aims. One aim was to determine whether the same male traits contributed to male success on and off their territories. We know that females fledge fewer young as the proportion of extra-pair young in their nests increases, apparently because males defend nests less vigorously when they contain illegitimate young (Weatherhead et al. 1994). Therefore, EPFs can only benefit females if they result in superior offspring, which would require that extra-pair males differ in some consistent fashion from the males they cuckold. To determine whether genetic quality might underlie male reproductive success, we tested the hypothesis that the relative success of an individual should remain fairly constant across years. While evidence showing year-to-year consistency does not necessitate that variation in male quality is genetically based, lack of consistency in individual male performance across years would be strong evidence against a genetic basis for male quality. Finally, because some evidence from our study population (Weatherhead 1990a; but see Weatherhead et al. 1993) indicates that haematozoa prevalence covaries with secondary sexual traits as predicted by Hamilton and Zuk (1982), we assessed male reproductive success relative to whether males were infected with blood parasites.

Methods

General

Our data were collected from 1986 through 1991 as part of a study of red-winged blackbirds initiated in 1984 at sites 10 km from the Queen's University Biological Station in eastern Ontario. Each of the three sites is a spring-fed beaver pond surrounded by habitat inappropriate for red-winged blackbird nesting. The closest unstudied marsh with breeding blackbirds was 0.25 km from the nearest study area, and the study areas were 0.5–1 km from each other. We were able to capture, band, and collect 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 we only analysed paternity in 1988 and 1989, although we did monitor nesting activity throughout, so the age of the males present in 1988 and 1989 could be estimated.

Males were individually colour-banded as they returned and began defending territories in April. Territories were mapped through the breeding season using male movements, displays and interactions to determine boundaries. Once nesting began in early May the marshes were searched for nests every 2nd day. Active nests were monitored until they failed or the young fledged. Nestlings were banded when they were 5 or 6 days old. Females were captured and colour-banded once they were associated with a nest. We collected blood samples from males, females and nestlings at the time we banded them (Hoysak and Weatherhead 1991).

We defined harem size as the maximum number of females nesting on a male's territory at any time during the breeding season (Weatherhead and Robertson 1977). Another measure of harem size that has been used in studies of red-winged blackbirds is the number of different females that nest on a male's territory over the course of a breeding season. In this study our preference for the first measure of harem size made little difference because the two measures were highly correlated ($r_s = 0.95$, $n = 103$, $P < 0.0001$).

Male traits

Male red-winged blackbirds are substantially bigger than females and they have jet-black plumage with scarlet epaulets fringed with yellow, in contrast to the females' predominantly "sparrow-like" brown plumage. Males also engage in a variety of aggressive and courtship displays while defending territories and attracting mates. Both body size and the length of the red portion of the epaulet have been shown to be correlated with social dominance among captive male blackbirds (Searcy 1979; Eckert and Weatherhead 1987a). When we captured males for banding we measured the length of their wing, tarsus and bill and used PC1 scores from a principal component analysis (PCA) of the three measurements as our index

Table 1 Principal component (PC) loadings for the variables scored in male model presentations. PC1 is used as the "attack" score and PC2 is used as a "display" score

Variable	PC1	PC2	PC3
Time > 10 m	−0.813	−0.297	0.092
Time 5–10 m	−0.522	0.400	−0.475
Time 1–5 m	0.455	0.559	0.493
Time < 1 m	0.748	−0.482	−0.013
Song spread rate	0.318	0.773	−0.125
Song spread intensity	0.603	0.180	0.224
Time with epaulets exposed	0.705	0.382	−0.083
Flight song rate	−0.379	0.375	−0.130
Bill up rate	0.630	−0.361	−0.061
Attack rate	0.455	−0.581	−0.371
Alarm call rate	−0.365	−0.228	0.728
% Variance explained	32.3	20.3	11.3

Table 2 Principal component loadings for the variables scored in female model presentations. PC1 is used as the "courtship" score

Variable	PC1	PC2	PC3
Time > 10 m	−0.762	−0.740	−0.508
Time 5–10 m	−0.323	0.647	0.632
Time 1–5 m	0.572	−0.010	−0.203
Time < 1 m	0.618	0.251	−0.180
Song spread rate	0.019	−0.543	−0.620
Song spread intensity	0.679	−0.130	0.397
Time with epaulets exposed	0.753	−0.272	0.255
Flight song rate	0.778	0.021	−0.145
Time in crouch	0.613	0.441	0.092
Alarm call rate	0.039	0.519	−0.622
% Variance explained	28.3	18.8	17.5

of body size. PC1 explained 46.1% of the variation and the respective character loadings for wing, tarsus and bill were 0.70, 0.81 and 0.48. We also recaptured and remeasured most banded males each year that they returned and used the estimate of body size from a given year for that year's analyses. From 1986 to 1989 we measured the length of both the red and yellow portions of the epaulets for indices of epaulet size (Searcy 1979; Eckert and Weatherhead 1987c). We scored epaulet color by matching a male's epaulets with standardized color chips (Smithe 1975).

In 1988 and 1989, male responses to male and female models placed in their territories were recorded as part of a study investigating male behaviour relative to blood parasite status (Weatherhead 1990a). Trials lasted 15 min and were conducted between territory establishment and the initiation of nesting. For both models we recorded the amount of time the male spent > 10 m, 5–10 m, 1–5 m and within 1 m of the model, the time the male spent with his epaulets exposed, the rate of flight songs, alarm calls and song spreads, and the mean intensity of song spreads (a combination of posture and exposure of the epaulets; Eckert and Weatherhead 1987c). With the male model we also recorded the bill-up rate and attack rate, and with the female model we recorded the crouch rate (bill-up and crouch are aggressive and courtship displays, respectively). We only used the first trial with each model for males tested more than once. All the variables were arcsine transformed to normalize the data and then subjected to PCA. For male models, the first three components explained 63.8% of the variation. Strong positive loadings of time spent close to the model, bill-up rate and attack rate suggested that PC1 could be considered an "attack" score (Table 1). Strong loadings of time spent at intermediate distances and of rates of song displays suggested that PC2 provided a "display" score (Table 1). We did not use PC3 because it appeared to reflect alarm rather than courtship. For female models the first three components explained 64.6% of the variation. Strong positive loadings of time spent close to the model and display rates suggested that PC1 provided an index of "courtship" (Table 2). The other two components were not easily interpreted and were not used. Note that although the details of how trials were conducted and variables were scored differed from those of Eckert and Weatherhead (1987c), in general the results of the PCAs were quite similar, with the exception that components 1 and 2 for males were reversed.

Haematozoa were sampled by taking a blood smear from each male, fixing them in ethanol and sending them for scoring to the International Reference Centre for Avian Haematozoa at Memorial University of Newfoundland (Weatherhead and Bennett 1991). Blood smears were collected from 1987 to 1990. Smears were only identified by species, sex and band number when sent for scoring. Haematozoa were quantified by counting the number of parasites per 100 fields under oil ×40 for leucocytozoids and ×100 for *Haemoproteus* and *Plasmodium*.

Male red-winged blackbirds are generally more aggressive than females when defending nests. In our study population nest defence is the principal form of paternal care, and nests defended more vigorously by males are more likely to be successful (Weatherhead 1990b). On most visits to nests the response of the male to the observer was recorded for the first 2 min at the nest. Scores ranged from 0 (no response) to 7 (physical contact) (see Weatherhead 1990b for details). We used the mean score of all trials between days 4 and 10 of the nestling period as a male's defence score for a particular nest, and the mean of all nest scores for a male's overall nest defence score. Because males defend nests with illegitimate nestlings less vigorously (Weatherhead et al. 1994), we excluded nests with illegitimate nestlings from our analyses once paternity had been determined.

Because this study was part of an ongoing project on the same red-winged blackbird population, we were able to estimate male ages with reasonable accuracy. A small number of breeding adult males was banded on the study area as nestlings, and others were banded as floaters when they were in subadult plumage (Shutler and Weatherhead 1994). Therefore, we knew the exact ages of these males, and by following the population beyond the end of this specific study, we also knew how long they lived. The majority of breeding males established territories as unknown adults. For these males we only know the number of years they had been breeding at any given time, and how many years they ultimately remained in the population. Because most males first establish territories when they are 2 years old (Shutler and Weatherhead 1994), the number of years breeding is a reasonable index of age. Therefore, the two indices of male age that we use here are "age" (the number of years breeding at a point in time) and "longevity" (the number of breeding years in a male's lifetime).

Paternity analysis

Parentage analysis was conducted using standard techniques, summarized in detail for this study in Weatherhead et al. (1994). In brief, we analysed paternity for the 1st year of the study using both single and multilocus probes as described by Gibbs et al. (1990), and used only multilocus probes for the remaining 5 years. Southern blots of AluI–digested blackbird DNA were hybridized with Jeffreys' 33.15 (Jeffreys et al. 1985) and Per (Shin et al. 1985) 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). The resulting fingerprints were scored by hand or computer to produce estimates of band sharing and novel fragments as described in Weatherhead et al. (1994). Note that here we include data from 1986–1991 while Weatherhead et al. (1994) excluded data for 1987. That year no parentage analyses were conducted for nestlings that did not fledge, and because the focus of that study was an analysis of survival relative to paternity, 1987 provided no relevant information.

We assessed parentage of the 617 nestlings sampled in this study generally following methods described by Westneat (1993) using band-sharing coefficients (D_f-sharing between nestling and female; D_m-sharing between nestling and male) and novel fragments for diagnosis. Other studies using our scoring method (e.g. Hill et al. 1994) 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 and scoring errors), i.e. bands not occurring in the fingerprints of either genetic parent (see also Westneat 1993). Using these criteria, we concluded that the females at all but one of the nests we studied were the genetic mothers of the nestlings in the nests they attended. (Because neither of the two nestlings in the other nest were the offspring of the attendant female, this was more likely a case of our misidentifying the female than of brood parasitism). Omitting the nestlings which did not match their female attendant, D_f for the remaining 615 nestlings averaged 0.51.

In the analyses of paternity we assumed nestlings with $D_m \geqslant 0.40$ and $\leqslant 3$ novel bands with respect to the attending male were the offspring of that male. These analyses identified 459 nestlings as the genetic offspring of the attending male. Average D_m for these nestlings was 0.50. The remaining 158 nestlings were excluded by these criteria and were considered to be the result of extra-pair matings by the attending female.

To find the genetic fathers of the 158 excluded nestlings, we calculated D_m between each nestling and all other males resident on the marsh (1986 assignments also made use of a single-locus probe, see Gibbs et al. 1990). 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 158 extra-pair nestlings, 34 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 were virtually identical ($D_m = 0.51$; $D_f = 0.52$), and almost double that between extra-pair nestlings and their putative fathers ($D_m = 0.27$; see Weatherhead et al. 1994 for statistical details).

Data analysis

Because many males were present for multiple years in this study we have analysed the data in several ways. All our analyses assess variation in annual reproductive success. In our overall analysis each male is represented in the analysis separately each year he was present. From a statistical perspective this approach violates the assumption that each entry in an analysis is independent. However, this approach better reflects an evolutionary perspective, where a male's contribution each year would be weighted equally, and males present for more years have greater potential to influence selection. We also analysed each year separately to determine whether any overall patterns were consistent within years. A third approach was to restrict the analysis to the 1st year each male was present, so each male is represented once in the analysis and the effects of morphological traits on reproductive success can be assessed in the absence of any potential effect of age or experience. All of our major results were consistent between the three analyses. Note that because we did not measure all the male traits every year (see Methods), and because there were occasional missing values for various reasons, sample sizes vary among analyses.

Results

General

Over 6 years we monitored 341 nests, 155 of which were successful (fledged at least one young). We sampled blood from all nestlings in successful nests and from all nestlings in 54 nests that failed late in the nestling period. The total sample analysed was 617 nestlings from 203 nests in 103 male territory-years (each year a male was present is a territory-year). Elsewhere we have shown that EPF rates were higher among the sampled nestlings that failed to fledge (Weatherhead et al. 1994). Unless otherwise specified, analyses are restricted to young that fledged.

The proportion of EPFs was 25.6% for all nestlings sampled, 20.1% for young that fledged and 39.2% for sampled nestlings that did not fledge. We were able to assign the paternity of 124 of the illegitimate nestlings to males resident on the same study area. Another four illegitimate nestlings were from a territory adjacent to an unsampled male. Assuming those nestlings were sired by that unsampled male (Gibbs et al. 1990; Westneat 1993), and given that in most years we had sampled all the resident males, we estimate that approximately 19% of all illegitimate nestlings were sired by nonterritorial floaters. This represents 4.9% of all nestlings sampled and 4.3% of all nestlings that fledged.

There were no strong year effects. Annual nest success only varied from 41 to 50%, legitimacy among fledged young varied from 73 to 85%, and in every year legitimacy was higher among young that fledged than among sampled young that did not fledge. Analysis of variance indicated no significant variation among years for any of the variables we measured for males (number of legitimate young, number of extra-pair young, total young sired, mean nest success, harem size, number of nests; all $F_s < 1.44$, $df = 5.97$, all $P_s > 0.22$). Similarly, in the 2 years for which data were included from three marshes, there were no significant differences among marshes in the variables measured for males (ANOVA; all $F_s < 1.12$, $df = 2{,}100$, all $P_s > 0.31$).

Morphology and reproductive success

There are several ways one might measure male success. These include the total number of nestlings sired, the total number of fledglings sired, and the total number of females with which a male was known to have sired at least one nestling. Here we use the total number of fledglings sired as our measure of male reproductive success. This value is highly correlated with both the total number of nestlings sired (Spearman rank correlation, $r_s = 0.78$, $P < 0.0001$) and the number of females with which a male sired a nestling ($r_s = 0.74$, $P < 0.0001$). The total number of fledglings sired is simply the sum of all fledglings a male sired on his territory and all fledglings he sired on other males' territories.

The only morphological variable that was correlated with male reproductive success on their own territories over all years was body size (Table 3). Larger males sired more young (Fig. 1). Body size was also positively correlated with male success on their own territories in each year, although the relationship was only significant in 2 of the 6 years. Among the 35 first-time breeders, body size was also the only significant correlate of on-territory success ($r_s = 0.44$, $P = 0.01$; P_s for plumage variables all > 0.34).

Although success at obtaining extra-pair fertilizations was positively correlated with the success of males on their own territories, the relationship was not significant ($r_s = 0.25$, $P = 0.12$). Therefore, different attributes might affect the two modes of male reproduction. Success at EPFs was not correlated with male morphology over all years combined (Table 3). Within years there were no significant relationships and the sign of the correlation coefficients switched from positive to negative between years. For first-time breeders all the correlations were also not significant (all $P_s > 0.17$).

Total reproductive success (on territory + EPFs) over all years increased significantly with body size Table 3), reflecting the higher success realised by large males on their own territories. Body size was also positively correlated with total reproductive success within years, although the relationship only approached significance ($P = 0.07$) in 2 of the 6 years. For first-time breeders, total reproductive success increased significantly with body size ($r_s = 0.45$, $P = 0.009$). None of the plumage variables was significantly correlated with total reproductive success over all years (Table 3). Within years the relationships between plumage variables and total reproductive success were inconsistent and not significant in all but one case (reproductive success increased with the length of the yellow portion of the epaulet in 1986: $r_s = 0.57$, $P = 0.05$). Plumage variables were not significantly correlated with total reproductive success for males breeding for the first time (all $P_s > 0.32$).

Having determined that larger males produced more offspring on their own territories (and as a consequence also had higher total reproductive success), it is possible to identify the proximate factors that underlie that relationship. Using data for all years combined, larger males had significantly larger harems ($r_s = 0.29$, $P = 0.004$) and the mean success of nests on their territories tended to be higher ($r_s = 0.18$, $P = 0.09$). Larger males also tended to sire proportionately more of the young fledged on their territories ($r_s = 0.18$, $P = 0.10$). Increased harem size was clearly the most important factor responsible for the higher reproductive success of larger males. Analyses restricted to males breeding for the first time support this conclusion. Larger males obtained significantly larger harems ($r_s = 0.45$, $P = 0.009$) but did not have higher nest success on their territories ($r_s = 0.12$, $P = 0.49$) or sire a higher proportion of the young produced on their territories ($r_s = 0.11$, $P = 0.57$).

It is possible that bigger males obtained larger harems because they had larger territories. To assess this possibility we analysed our data for the largest marsh, which was also the site included in all 6 years of the study. Because different assistants contributed to the mapping of territories in different years, we reduced any effect of idiosyncrasies in mapping style by ranking the territories by area within years rather than estimating actual areas. Over all years there was a significant increase in harem size with territory area rank ($r_s = 0.30$, $P = 0.008$, $n = 81$), but larger males did not obtain larger territories ($r_s = 0.16$, $P = 0.16$), so the relationship between male size and harem size did not appear to be attributable to a relationship with territory area. Restricting the analysis to the 26 males for which we had data for their 1st year breeding on this marsh, we found no significant relationship between territory area and either harem size ($r_s = 0.21$, $P = 0.30$) or male size ($r_s = 0.01$, $P = 0.97$).

It is also possible that larger males acquired larger harems because they had higher quality territories. Females in this population forage almost exclusively off the breeding marsh, so the only territory characteristic likely to be of importance would be related to predation risk. On the marsh studied for 6 years, nest success on territories (the percent of nests that fledged at least one young) did not vary significantly with harem size (all territory years: $r_s = -0.10$, $P = 0.36$, $n = 82$; first time breeders: $r_s = -0.03$, $P = 0.87$, $n = 26$). Therefore, it does not appear that the variance

Table 3 Spearman rank correlations between male reproductive success (no. fledglings sired) on their own territories, by extra-pair fertilization and overall with male morphology, for all territory-years combined

Trait	n	Own territory		EPF		Overall	
		r_s	P	r_s	P	r_s	P
Body size	96	0.41	<0.0001	0.02	0.87	0.36	0.0004
Epaulet size							
– Red	69	0.08	0.53	−0.03	0.83	0.05	0.66
– Yellow	68	0.18	0.14	0.13	0.27	0.18	0.15
Epaulet colour[a]	66	−0.13	0.28	−0.08	0.54	−0.13	0.29

[a] The red portion of one epaulet was scored for colour (see Methods) and these scores were ranked by intensity

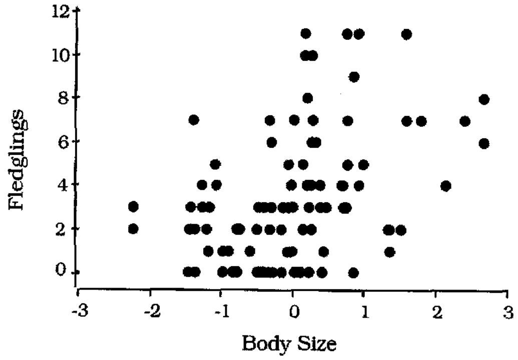

Fig. 1 Male reproductive success on their own territories relative to body size (PCI scores) for all territory-years combined

in harem size among males can be attributed to variance in territory quality.

Behaviour and reproductive success

We only scored the response of males to male and female models in 1988 and 1989, so we only present an analysis for the data from those 2 years combined. How males responded to a male model ($n = 40$) was not significantly related to their reproductive success on their own territories (attack: $r_s = -0.06$, $P = 0.73$; display: $r_s = 0.09$, $P = 0.57$). More aggressive males tended to be less successful at siring young on other males' territories (attack: $r_s = -0.28$, $P = 0.09$; display: $r_s = -0.23$, $P = 0.16$). Total male reproductive success was not significantly correlated with male aggression toward a male model (attack: $r_s = -0.12$, $P = 0.47$; display: $r_s = 0.04$, $P = 0.82$).

Males that were more vigorous in their courtship of the female model did not sire more young on their own territories ($r_s = 0.21$, $P = 0.18$, $n = 42$) or on other males' territories ($r_s = 0.20$, $P = 0.19$), nor did they have higher total reproductive success ($r_s = 0.24$, $P = 0.12$).

There were 43 male territory-years for which we had nest defence scores for males defending nests with exclusively legitimate nestlings. The intensity with which males defended these nests had little influence on male reproductive success on their territories ($r_s = -0.05$, $P = 0.71$), on other males' territories ($r_s = -0.16$, $P = 0.31$) or overall ($r_s = -0.06$, $P = 0.70$). Nest defence was not significantly correlated with the number of females that nested in a male's territory ($r_s = -0.07$, $P = 0.64$). However, because nest success was not higher on territories of males that defended their nests more vigorously ($r_s = 0.03$, $P = 0.84$), there would have been no advantage to females that preferred more aggressive males. The lack of relationship between nest success and male nest defence found here is contrary to that found in a previous study of this population (Weatherhead 1990b). However, that study included all nests regardless of nestling legitimacy, and nests with illegitimate young are both defended less vigorously and are less successful (Weatherhead et al. 1994) than nests with entirely legitimate broods.

Reproductive success and age and longevity

Neither age (the number of years a male had been breeding at a given time) or longevity (the total years a male bred) was significantly correlated with the males' reproductive success on their own territories ($r_s = 0.15$ and 0.10, $P = 0.14$ and 0.32, $n = 103$ and 102, respectively). Those overall results were reflected by the annual results, where age was never significantly correlated with reproductive success on the males' own territories ($P_s > 0.18$), and longevity was significantly associated with success in only one year ($r_s = 0.57$, $P = 0.04$; all other $P_s > 0.40$). Among males breeding for their first time, individuals that ultimately survived longer were not more successful in that first year ($r_s = 0.10$, $P = 0.55$). Note that longevity was not significantly correlated with size ($r_s = 0.02$, $P = 0.90$, $n = 48$) among the males included in this study, and our earlier analyses indicated that size was the best predictor of male success on their own territories.

In contrast to the lack of an effect of age on male success on their own territories, older males and males that lived longer sired more young on other males' territories ($r_s = 0.18$ and 0.28, $P = 0.07$ and 0.006, respectively; Fig. 2). An alternative approach for assessing the effect of age on extra-pair mating is to compare directly the ages of the cuckolding and cuckolded male in each instance of extra-pair mating for which both males are known. For this analysis we treat nests as our sample unit, so each comparison involves one nest, regardless of the number of young sired by the cuckolder. If the same pair of males was involved in cuckoldry at more than one nest, each instance was entered once in the analysis. There was also one case of reciprocal cuckoldry, where two males cuckolded each other. Both instances were included in the analysis, with the respective roles of the two males reversed in the two entries. We had a total of 57 cases of cuckoldry for this analysis. Cuckolders were older (Wilcoxon test, $Z = -3.31$, $P = 0.0009$, Fig. 3) and lived longer ($Z = -2.46$, $P = 0.01$) than the males they cuckolded. Repeating this analysis for the morphological and behavioral variables (see above) produced no results that approached significance.

The data in Fig. 3 suggest that age *per se*, rather than familiarity, accounted for the relation between age and cuckoldry success. Because of high male site fidelity, only males in their first breeding season were unfamiliar with the older males that cuckolded them. Although these young males were heavily cuckolded, males breeding for at least their 2nd year were also disproportionately cuckolded by older males, and they would have been familiar with the males that cuckolded them.

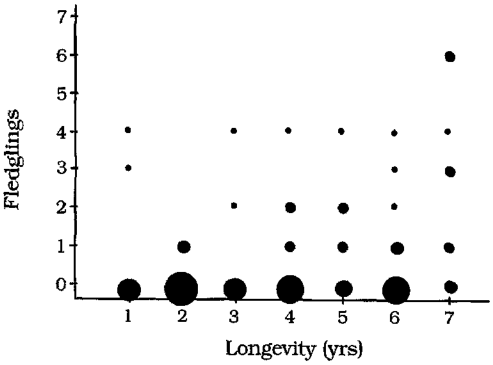

Fig. 2 Number of young sired by extra-pair fertilizations relative to estimated male longevity for all territory-years combined. *Dot size* reflects the number of entries with equal value (range = 1–16)

The combined effect of age having no effect on the success of males on their own territories but a strong effect on success at gaining EPFs was that there was a positive, but not significant association of male age and longevity with overall success ($r_s = 0.18$ and 0.13, $P = 0.07$ and 0.18, respectively).

To explore the factors that might contribute to higher extra-pair mating success by older males, we looked for other correlates of age. Older males and males that lived longer obtained larger territories ($r_s = 0.34$ and 0.50, $P = 0.002$ and < 0.0001, respectively) and among males breeding for the first time, those that lived longer obtained larger territories in their first year ($r_s = 0.46$, $P = 0.02$). However, there was only a weak association overall between territory area and success at siring young on other territories ($r_s = 0.20$, $P = 0.07$). It is also unclear how ownership of a large territory might influence extra-pair mating success. Interestingly, older males and males that lived longer had larger harems overall ($r_s = 0.26$ and 0.29, $P = 0.009$ and 0.003, respectively), although harem size was not significantly associated with longevity among first-time breeders($r_s = 0.18$, $P = 0.28$). There was also a tendency for males with larger harems to be more successful siring young off their territories ($r_s = 0.19$, $P = 0.06$). Again, it is not clear how possession of a larger harem could enhance a male's ability to mate with other males' mates.

Parasites and reproductive success

To assess the effect of parasites on reproductive success we classified males as either parasitized (infected with either one or more species of haematozoan) or unparasitized. We also excluded four males that held territories when they were 1 year old because males this age are less likely than older males to be parasitized (Weatherhead and Bennett 1991). Over all males and years, the mean number of young fledged for parasitized ($n = 26$) and unparasitized ($n = 34$) males did not differ significantly (4.31 vs. 4.21, Mann-Whitney test, $U = 443$, $P = 0.99$). Among first-time breeders, the difference between parasitized ($n = 8$) and unparasitized ($n = 17$) males was greater but still not significant (5.00 vs. 2.94, Mann-Whitney test, $U = 41.5$, $P = 0.12$). In a previous study involving this population (in fact, many of the same individuals) it was determined that parasitized and unparasitized males could be discriminated with reasonable accuracy on the basis of their morphology and their responses to male and female models (Weatherhead 1990a). Using the same discriminant function here for the males sampled in 1988 and 1989 (the only years in which all the necessary variables were measured), we found that a male's reproductive success on his own territory tended to increase as his discriminant function score increased ($r_s = 0.30$, $P = 0.08$, $n = 35$), but there was no evidence of a relationship between a male's success on other males' territories and his discriminant function score ($r_s = 0.06$, $P = 0.73$), or between overall reproductive success and his discriminant function score ($r_s = 0.25$, $P = 0.15$). In 1988 and 1989 there was also no difference in overall reproductive success between males known to have been parasitized and those known not to have been parasitized (Mann-Whitney test, $U = 180$, $P = 0.78$). Thus, haematozoa appear not to have had much effect on male reproductive success, despite the potential for females to discriminate between infected and uninfected individuals.

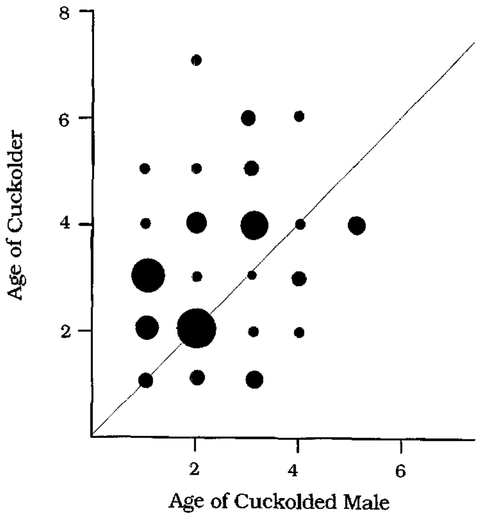

Fig. 3 Estimated ages of cuckolders and the males they cuckolded. Each entry is based on a nest where the cuckolder was identified, regardless of the number of young sired by the cuckolder. *Dot size* reflects the number of entries with equal value (range = 1–10). *Diagonal* is the line of equality

Male performance between years

To determine whether some males were consistently successful or unsuccessful when they were present for more than 1 year, we compared male performance each year with their performance the subsequent year (i.e. year x vs. year $x + 1$). Male reproductive success on their own territories was significantly positively correlated from year to year ($r_s = 0.30$, $P = 0.03$, $n = 52$). Male success at extra-pair fertilizations was not significantly correlated from year to year ($r_s = 0.09$, $P = 0.51$). A potential weakness in this analysis is that most males achieved few or no EPFs in a given year, so while their performances were consistently low from year to year, their exact number of EPFs did vary. However, if we just consider whether a male sired any extra-pair young or not, male performance was consistent from year x to year $x + 1$ about as often as it was inconsistent (29 cases vs. 23 cases). Overall reproductive success was significantly correlated from year to year ($r_s = 0.30, P = 0.03$, Fig. 4), reflecting the consistency of male success on their own territories.

The preceding analyses includes all males that were present for at least 2 years. By combining all males, the analyses tend to mask the consistently high success realised by a few individuals. One male in particular, YRRS, was consistently successful and sired far more offspring than any other male in the study. In our analysis of lifetime reproductive success (Weatherhead and Boag, unpublished work), YRRS produced twice the number of the young in his lifetime of the second-best male in the population. Based on an average of 16.5 males studied in each year of the study, YRRS was ranked in the top two in 3 of the 6 years for young sired on his territory (mean rank = 3.4), the top two in 5 of the 6 years for extra-pair fertilizations (mean rank = 2), and in the top two in 4 of the 6 years for overall success (mean rank = 2.6). In the 18 analyses (6 years × 3 measures of success), YRRS had nine number 1 ranks. Thus, the most productive male in the population was far more consistent than the average male in the population. It may be noteworthy that YRRS was in the top quartile of body size and was the longest-lived of the males included in this study.

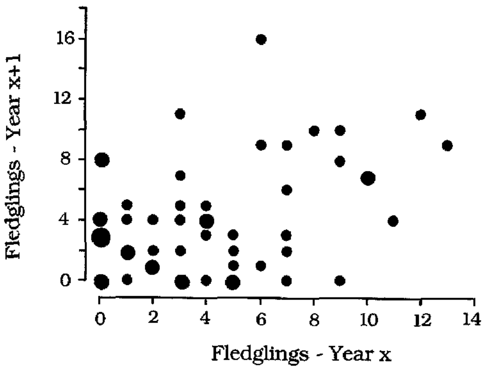

Fig. 4 Overall male reproductive success in year x relative to overall success in year x+1. *Dot size* reflects the number of entries with equal value (range 1–3)

Discussion

We investigated a substantial number of variables in our attempt to determine the factors that contribute to variation in male reproductive success both on and off their territories. Because many of the variables either had no effect or inconsistent effects on male success, the results are reasonably straightforward. To first summarize the main results, body size was the only male secondary sexual trait that affected reproductive success. Larger males sired more young on their own territories, and as a consequence, more young overall. Larger males were more successful primarily because more females nested on their territories, although larger males also tended to sire more of the young produced on their territories. The higher success by large males on their territories was not a consequence of larger males acquiring either larger or higher quality territories. Variation in male plumage and behavior was not correlated with variation in male reproductive success, and parasite status, measured either directly or predicted from behavior and morphology, was also unrelated to reproductive success.

Male success was also independent of male parental quality, which for this population of red-winged blackbirds is principally nest defence (Weatherhead 1990b). This result seems reasonable given that when variation in nest defence is assessed exclusively at nests for which all nestlings are legitimate, nest success no longer varies with nest defence. The other non-secondary sexual male quality we considered was age. Success at obtaining extra-pair fertilizations increased with both relative age and ultimate longevity, but because age did not appear to influence the success of males on their own territories, age was only weakly related to overall reproductive success. Westneat (1993) assessed the effect of male age on success obtaining extra-pair fertilizations by comparing the performance of 21 males studied in 2 consecutive years. Although he found no significant pattern between the 1st and 2nd year, the small sample size and limited variance in age made this a rather weak test, so it is premature to conclude that his population differs from ours with regard to the importance of age on male extra-pair mating success.

A principal goal of our study was to test the hypothesis that the males with the most elaborate secondary sexual traits would have the highest reproductive success. While the importance of body size to male success supports the hypothesis, the lack of importance of all the plumage and behavioural traits raises important questions. Male red-winged blackbirds have striking red and black plumage (in contrast to the drab brown plumage of females) which they display when interacting with other males or with females (Orians and Christman 1968). Variation in these traits appears unrelated to whether males are successful acquiring territories (Eckert and Weatherhead 1987a; Shutler and Weatherhead 1991a, b) or to the quality of territories that they acquire (Eckert and Weatherhead 1987b; Shutler and Weatherhead 1991b). How do we explain these elaborate traits if they are unrelated to reproductive success stemming from either direct competition among males for territories, or from indirect competition attracting females?

It is possible that we did not measure these traits correctly. For example, the behaviours were all measured as responses to male and female models placed on males' territories. Perhaps because inanimate models do not interact with males, the responses become entirely unnatural and variation in responses is therefore meaningless. This possibility warrants investigation because, although the use of inanimate models to elicit responses is well established in behavioural ecology, little is known about how well responses to models reflect natural interactions. In the case of plumage features, we know that if the epaulets are altered either directly (e.g. Peek 1972; Smith 1972) or indirectly (e.g. Metz and Weatherhead 1992), interactions of the altered males with other males or with females may be negatively affected. Therefore, normal plumage appears to be important for reproduction. It is possible that the bright plumage of males evolved via sexual selection but is no longer subject to directional selection (Grafen 1988). It is also possible that the quality of the plumage, and hence the male, is reflected, not by the absolute size or color of the epaulets, but by their symmetry (Møller 1990). Therefore, we can only conclude from our study that variation in the absolute size and color of male plumage is unrelated to male reproductive success.

Finally, what implications do our results have for the question of whether or not the acquisition of good genes underlies female mate choice in red-winged blackbirds? There are theoretical reasons to expect substantial heritable variation in male quality in polygynous species (Petrie and Lipsitch 1994). Empirical evidence consistent with female red-winged blackbirds selecting good genes is provided by our result showing year-to-year consistency in individual male reproductive success. This consistency was particularly pronounced for the most successful individual in the population. However, potentially problematic for the good genes proposition is the result showing that females preferred different traits in males siring their offspring through pair fertilizations from those siring young through extra-pair fertilizations. Large males were more successful at pair fertilizations while older males were more successful at extra-pair fertilizations. If females were selecting good genes to compensate for the cost of extra-pair copulation (EPC; Weatherhead et al. 1994), then we would have expected that females would prefer the same male traits regardless of how the genes were acquired. It is possible that females are not willing participants in EPCs, so that only offspring sired by pair matings reflect female choice. However, the best observations currently available (Monnett et al. 1984; Westneat 1992) provide no evidence that EPCs are either forced or coerced by males. By the same token, there is also no evidence, at least for eastern red-winged blackbirds, that females actively choose to mate with extra-pair males. However, recent evidence from a study in Washington found that female red-winged blackbirds in that population do seek EPCs (Gray 1994).

An alternative explanation that may reconcile our observations with the good genes hypothesis is suggested by a recent study investigating the relationship between body size and survival in red-winged blackbirds. Weatherhead and Clark (1994) found that larger males survived better than smaller males. One of the data sets demonstrating this relationship included the males that were the focus of the present study. The smaller sample of males that we included in this study, combined with a relatively weak relationship between body size and survival, might explain the lack of a significant relationship between age and size among the males that we studied here. Kempenaers et al. (1992) found that male blue tits (*Parus caeruleus*) that gained paternity through extra-pair mating were less likely to lose their mates and were larger and survived better than males that were cuckolded. Thus, in blue tits, size and longevity are positively correlated in males and were the male traits preferred by females. Petrie (1992, 1994) has shown that peahens (*Pavo cristatus*) prefer larger (and more ornamented) peacocks and that these males survive better and produce offspring that survive better. Alatalo et al. (1991) also showed that male black grouse (*Tetrao tetrix*) preferred by females had higher survival. Even if this explanation applies to red-winged blackbirds, and large males are preferred by females because they are, on average, longer-lived, we must still explain why females choose age directly when selecting extra-pair mates, and indirectly via body size when selecting pair mates.

We propose the following hypothesis. First, females prefer longer-lived males because they are genetically superior. Because a male's potential longevity cannot be assessed directly, it must be assessed by a correlated morphological variable, specifically body size. Thus, females prefer larger males as mates. Second, although females are willing participants in extra-pair matings, these matings do not arise purely as a function of female choice, but are influenced to a large extent by opportunity. For example, to be successful, an extra-pair male must not only have the female's acquiescence, but must have created the opportunity for a copulation by avoiding the mate guarding behavior of the female's mate. Older males may be better at creating or exploiting these opportunities by virtue of experience, so age rather than size would be a better predictor of EPF success.

We recognize that our hypothesis is speculative, including our assumption that females willingly participate in extra-pair matings, but the hypothesis is at least broadly consistent with our observations. Whether one tests this hypothesis or other alternatives that might be suggested by our results, however, there will be an obvious problem involving the key variables. Unlike traits such as plumage color or elaboration, body size and age or longevity cannot be modified, which will make experimentation difficult. Therefore, experimentation may be limited to manipulating which males are present on a study area by selective removals. Another problematic issue, but one much in need of research, concerns the circumstances under which extra-pair mating occurs. Where does it occur? Do males or females initiate the interaction? Although the new molecular techniques for assessing paternity have certainly moved forward our knowledge of mating patterns in red-winged blackbirds, our understanding of those patterns remains far from complete.

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References

Alatalo RV, Hoglund J, Lundberg A (1991) Lekking in the black grouse – a test of male viability. Nature 352:155–156

Beletsky LD, Orians GH (1989) Territoriality among red-winged blackbirds. III. Testing hypotheses of territorial dominance. Behav Ecol Sociobiol 24:333–339

Bray O, Kennelly JJ, Guarino JL (1975) Fertility of eggs produced on territories of vasectomized red-winged blackbirds. Wilson Bull 87:187–195

Darwin C (1871) The descent of man and selection in relation to sex. Modern Library, New York

Eckert CG, Weatherhead PJ (1987a) Ideal dominance distributions: a test using red-winged blackbirds (*Agelaius phoeniceus*). Behav Ecol Sociobiol 20:43–52

Eckert CG, Weatherhead PJ (1987b) Owners, floaters and competitive asymmetries among territorial red-winged blackbirds. Anim Behav 35:1317–1323

Eckert CG, Weatherhead PJ (1987c) Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (*Agelaius phoeniceus*). Behav Ecol Sociobiol 20:35–42

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

Grafen A (1988) On the uses of data on lifetime reproductive success. In: Clutton-Brock TH (ed) Reproductive success. Chicago University Press, Chicago, pp 454–471

Gray EM (1994) The ecological and evolutionary significance of extra-pair copulations in the red-winged blackbird (*Agelaius phoeniceus*). PhD thesis, University of Washington, Seattle

Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? Science 218:384–387

Hill GE, Montgomerie R, Roeder C, Boag PT (1994) Sexual selection and cuckoldry in a monogamous songbird: implications for sexual selection theory. Behav Ecol Sociobiol 35:193–199

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

Jeffreys AJ, Wilson V, Thein SL (1985) Hypervariable "minisatellite" regions in human DNA. Nature 314:67–73

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

Kirkpatrick M, Ryan MJ (1991) The evolution of mating preferences and the paradox of the lek. Nature 350:33–38

Metz KJ, Weatherhead PJ (1992) Seeing red: uncovering coverable badges in red-winged blackbirds. Anim Behav 43:223–229

Møller AP (1990) Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. Anim Behav 40:1185–1187

Monnett C, Rotterman LM, Worlein C, Halupka K (1984) Copulation patterns of red-winged blackbirds (*Agelaius phoeniceus*). Am Nat 124:757–764

Orians GH (1969) On the evolution of mating systems in birds and mammals. Am Nat 103:589–603

Orians GH, Christman GM (1968) A comparative study of the behavior of red-winged, tricolored, and yellow-headed blackbirds. Univ Calif Publ Zool 84:1–81

Peek FW (1972) An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (*Agelaius phoeniceus*). Anim Behav 20:112–118

Petrie M (1992) Peacocks with low mating success are more likely to suffer predation. Anim Behav 44:585–586

Petrie M (1994) Improved growth and survival of offspring of peacocks with more elaborate trains. Nature 371:598–599

Petrie M, Lipsitch M (1994) Avian polygyny is most likely in populations with high variability in heritable male fitness. Proc R Soc Lond B 256:275–280

Searcy WA (1979) Morphological correlates of dominance in captive male red-winged blackbirds. Condor 81:417–420

Shin H-S, Bargiello TA, Clark BT, Jackson FR, Young MW (1985) An unusual coding sequence from a *Drosophila* clock gene is conserved in vertebrates. Nature 317:445–448

Shutler D, Weatherhead PJ (1991) Owner and floater red-winged blackbirds: determinants of status. Behav Ecol Sociobiol 28:235–241

Shutler D, Weatherhead PJ (1992) Basal song rate variation in red-winged blackbirds: sound and fury signifying nothing? Behav Ecol 2:123–132

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

Smith DG (1972) The role of the epaulets in the red-winged blackbird social system. Behaviour 41:251–268

Smithe FB (1975) Naturalist's color guide. American Museum of Natural History, New York

Weatherhead PJ (1990a) Secondary sexual traits, parasites, and polygyny in red-winged blackbirds, *Agelaius phoeniceus*. Behav Ecol 1:125–130

Weatherhead PJ (1990b) Nest defence as shareable paternal care in red-winged blackbirds. Anim Behav 39:1173–1178

Weatherhead PJ (1994) Mixed mating strategies by females may strengthen the sexy son hypothesis. Anim Behav 47: 1210–1211

Weatherhead PJ, Bennett GF (1991) Ecology of red-winged blackbird parasitism by haematozoa. Can J Zool 69:2352–2359

Weatherhead PJ, Clark RG (1994) Natural selection and sexual size dimorphism in red-winged blackbirds. Evolution 48:671–678

Weatherhead PJ, Robertson RJ (1977) Harem size, territory quality and reproductive success in the red-winged blackbird (*Agelaius phoeniceus*). Can J Zool 55:1261–1267

Weatherhead PJ, Metz KJ, Bennett GF, Irwin RE (1993) Parasite faunas, testosterone and secondary sexual traits in male red-winged blackbirds. Behav Ecol Sociobiol 33:13–23

Weatherhead PJ, Montgomerie R, Gibbs HL, Boag PT (1994) The cost of extra-pair fertilizations to female red-winged blackbirds. Proc R 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 (1993) Polygyny and extra-pair fertilisations in eastern red-winged blackbirds (*Agelaius phoeniceus*). Behav Ecol 4:49–60

Zuk M, Thornhill R, Ligon JD, Johnson K, Austad S, Ligon SH, Thornhill NW, Costin C (1990) The role of male ornaments and courtship behavior in female mate choice of red jungle fowl. Am Nat 136:459–473

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