Extra-pair mating, male plumage coloration and sexual selection in yellow warblers (*Dendroica petechia*)

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SUMMARY

Extra-pair mating has been proposed as a source of sexual selection responsible for secondary sexual traits that are common among socially monogamous birds, although supporting evidence is scant. In the socially monogamous yellow warbler, males are larger than females, and unlike females, have extensive reddish streaking on their breasts. Using DNA fingerprinting we show that within-pair parentage was positively related to male size, and that extra-pair mating success was positively related to the amount of streaking on the breast. To our knowledge, this is the first intraspecific evidence of an association between a male plumage ornament and gains of extra-pair paternity that is apparently independent of age. This study confirms that extra-pair mating can be an important mechanism of sexual selection even when the most successful sires are commonly cuckolded, and refutes a previous hypothesis that the variation in plumage and behaviour among male yellow warblers is an example of alternative, equally successful, evolutionarily stable strategies (ESS). More generally, the demonstrated independence of within-pair and extra-pair success and their associated traits indicates that where animals have multiple secondary sexual traits, different traits may be selected by different mechanisms that contribute to total reproductive success.

1. INTRODUCTION

Sexually dimorphic traits, such as plumage ornaments and large body size, are generally thought to be the product of sexual selection. Indeed, since Darwin (1871) pointed to a positive relation between the development of secondary sexual characters and polygamy, comparative and intraspecific studies have repeatedly shown connections between secondary sexual characters, reproductive competition and mating success, particularly among polygamous species (reviewed in Andersson 1994). However, secondary sexual characters are not restricted to polygamous species. For example, most birds are socially monogamous, and they too exhibit plumage ornaments, vivid colours and size dimorphism, yet direct evidence that these traits are sexually selected is limited (see Andersson 1994). The reason for this lack of evidence may be that some of the ways in which reproductive success can vary have been overlooked.

Most studies of sexual selection have focused on differential success in territory or mate acquisition, and differences in mate quality as the causes of variation in reproductive success (Kirkpatrick *et al.* 1990; Andersson 1994). Although these factors can generate sexual selection (e.g. Price 1984; Norris 1990), recent attention has focused on sexual selection from extra-pair mating (Trivers 1972; Møller 1992; Webster *et al.* 1995; Weatherhead & Boag 1997). Indeed, DNA

profiling has shown that extra-pair fertilizations occur in many birds (reviewed in Birkhead & Møller 1992; Westneat & Webster 1994), and that they can significantly increase the variance in male mating success and thereby the opportunity for sexual selection (Webster *et al.* 1995; Yezerinac *et al.* 1995).

The most consistent phenotypic correlates of extra-pair mating success to emerge thus far have been male age and survival (e.g. Morton *et al.* 1990; Kempenaers *et al.* 1992; Weatherhead & Boag 1995; Wetton *et al.* 1995). However, correlations with secondary sexual characters have been inconsistent and mostly null. Where within-pair paternity has been compared to male plumage features or body size, null results outnumber positive ones for both traits (see Westneat 1990; Smith & Montgomerie 1991; Dunn *et al.* 1994; Hill *et al.* 1994; Ratti *et al.* 1995). Fewer studies have assigned paternity and measured extra-pair siring success, but null results again predominate for secondary sexual characters (Weatherhead & Boag 1995; Wetton *et al.* 1995). Recent exceptions include positive correlations between song and extra-pair success in the great reed warbler (*Acrocephalus arundinaceus*; Hasselquist *et al.* 1996), and between male age, plumage coloration and extra-pair success in the yellowhammer (*Emberiza citrinella*; Sundberg & Dixon 1996), although in the latter case it was not possible to separate the more commonly observed effect of age from that of plumage. Nevertheless, comparative evidence of a positive association between male plumage brightness and sexual dichromatism and levels of extra-pair paternity among socially monogamous species (Møller & Birkhead 1994), suggests that extra-pair

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mating may often create sexual selection on male plumage traits.

Here we investigate pair and extra-pair mating success in relation to male plumage, size and age in the socially monogamous yellow warbler, a small songbird that breeds throughout most of North America. Male yellow warblers are larger than females on average, and have conspicuous reddish streaking on their bright yellow breast feathers, with the amount of streaking varying greatly among males. Previous research found that variation in male plumage streaking was positively related to territorial behaviour and negatively related to paternal care in a way that resulted in equal apparent reproductive success across the continuum of plumage variation (Studd & Robertson 1985*a, b*, 1988, 1989). Because these patterns were not age-related and were consistent within individuals between years, the authors argued that this was an example of an evolutionarily stable strategy in which males with different plumage streaking allocated their reproductive effort differently to achieve the same reproductive success. Here we test the alternative hypothesis that sexual selection resulting from extra-pair paternity favours male yellow warblers with more plumage streaking.

2. METHODS

(a) *Study population and measurements*

We studied yellow warblers at three sites between 2 and 8 km apart near the Queen's University Biological Station in eastern Ontario, Canada (44° 34' N; 76° 20' W; described in Yezerinac *et al.* 1995). Colour banding and blood sampling of adults was begun in 1991, when 30–70% of territorial males at these sites were captured. During the 1992–94 breeding seasons, respectively, 90%, 95% and 100% of territorial males, and 32%, 61% and 78% of nesting females were banded and bled. Beginning in 1992, at capture we made video recordings of each male to measure the proportion of the breast covered by reddish streaking (figure 1). We measured the mass of birds to the nearest 0.1 g, tarsus length to the nearest 0.1 mm, and the length of the unflattened wing chord to the nearest 0.5 mm. Measurement error, calculated as the within-individual percentage of total variance, was low for all three measures (weight = 5.73%, tarsus = 2.06%, wing = 0.56%), and two repeated measures of each trait were averaged throughout the study (Yezerinac *et al.* 1992). We used PC1 scores from a principal component analysis of the variance-covariance matrix of tarsus, wing and weight (using residuals from annual means) as an index of body size. PC1 explained 45.2% of the variation and the respective character loadings for tarsus, wing and weight were 0.58, 0.58 and 0.57.

From banding we estimated the minimum ages of yellow warblers. The return rate for marked males between seasons was 32.5% ($n = 123$ male-years in fully censused sites) and territory fidelity was high (90.2% of 41 returned males occupied the same or an adjacent territory). Thus, we used the number of years banded as an estimate of age, and in areas where we had banded previously, we assumed new territory holders were one year old. Given high territory fidelity and low survival, if males generally acquire territories at the same age, this gives a good estimate of actual age.

(b) *Breeding pairs and offspring sampling*

In 1992 there were 30, 40 and eight pairs, respectively, at the three sites. We restricted field work to the two largest sites in 1993 (33 and 42 pairs) and only one of the sites in 1994 (26 pairs). Each breeding season (May–early July) we visited each territory every 1–4 days and mapped territorial boundaries (judged from male song perches and male–male chases) and nests. Nests were found by regular searches of vegetation and by following adults, and were checked every 2–4 days. We estimate that we failed to find fewer than 5% of nests. In 1992, we took blood samples from all nestlings that reached five days of age, although 61% of nests were depredated before reaching this stage. To increase the proportion of nests sampled in 1993 and 1994, we collected eggs from all nests (under permit from the Canadian Wildlife Service) after 5–7 days of incubation, and used the embryos as a source of DNA. Consequently, male success is measured in terms of fertilization success. Females remained with the same partners and always re-nested (until late June) following natural or artificial predation.

(c) *Parentage analysis*

We used DNA from adults and offspring to analyse parentage with multi-locus DNA fingerprinting. Laboratory methods, band sharing and linkage statistics are described in Yezerinac *et al.* (1995, 1996). Briefly, *Alu* I digested DNA from nestlings and their putative parents were run on the same gel along with neighbouring pairs. Southern blots were probed with *per*, *Jeffreys'* 33.15 and an in-lane lambda size marker. Bands not found in either social parent (novel genetic markers) and band-sharing coefficients between nestlings and the female and male were used to establish parentage as described in Yezerinac *et al.* (1995). These two criteria were never in contradiction. When only the male was sampled (30% of families), low band-sharing with offspring (≤ 0.27) was taken as evidence of extra-pair paternity because in all other families the mismatched parent was always the putative father. We identified true fathers of extra-pair sired offspring in 29 nests using the same criteria as for parentage exclusion (also see Yezerinac *et al.* 1995); extra-pair sires had band-sharing coefficients greater than 0.40 with offspring (range 0.43–0.71; mean number of bands scored per individual = 34.03 ± 0.40 s.e.), and for the 21 nests (72%) where the female had been sampled, extra-pair sires' genotypes also accounted for all novel bands in offspring (mean number of novel bands = 11.2 ± 0.3 s.e., range 8–22).

(d) *Data analysis*

We used multiple linear regression to determine the effect of male age, plumage streaking and size on within-pair parentage. We used multiple logistic regression to determine the effect of male age, plumage streaking and size on the likelihood that a male sired extra-pair offspring or not. We excluded data from 1992 when comparing extra-pair sires to other males because we had only fingerprinted males with sampled nests. This made our sample of potential extra-pair sires incomplete and hence our classification of males comparatively inaccurate. However, we did include the four known extra-pair sires from 1992 in pairwise comparisons of cuckolders and cuckoldees, and in analyses of male traits and the number of extra-pair young sired by extra-pair sires.

The 130 families for which parentage was analysed included 99 different male–female pairs and 91 different males. Twenty-one different males were the extra-pair sires at 29 nests, representing 26 unique cuckolder–cuckoldee dyads. One male was an extra-pair sire in two separate years.

Figure 1. Frequency distribution for male breast streaking ($n = 125$ male-years). Pictures show a relatively lightly and heavily streaked male. Each bird was videotaped with a Sony 8 mm camera, in shade, with the lens and a 30 watt halogen lamp 15–20 cm distant and perpendicular to the breast. Tapes were played into an Apple Computer (256 shades of grey [0 = white, 256 = black] using *Computer Eyes Video Digitiser & V1.5.8* software; Digital Vision, Inc.) and analysed using *NIH Image V1.44* (National Institutes of Health-USA) image analysis software. Using the ruler in each image to calibrate relative size, we calculated separately the area (mm^2) of streaking above greyscale values 55 (lowest greyscale value of streaking among ten randomly selected males), 65 and 70 within a rectangle extending 3.5 cm from the most anterior streaking and 2.5 cm wide. The three, highly correlated ($r \geq 0.96$) measures were averaged to calculate each male's breast streaking score. Measurement error (see §2) was 18.23%, and was reduced by averaging measures from two different images for each male. Raw values are plotted here, but residuals from annual means were used for analysis to control for yearly variation.

To avoid pseudoreplication yet still make use of all the data, we employed resampling; we performed 200 separate calculations of each analysis using a single, randomly selected value for each male. Occasional missing values produced sample sizes that varied slightly. Mean test statistics and minimum error degrees of freedom (when it varied due to missing values) were used to determine p values. Where appropriate, all higher order interactions were removed from final calculations if non-significant ($p > 0.05$). Where year could not be included as a main effect, we inspected the data to ensure the nature of the overall relationship did not vary between years. Because estimates of age were least accurate in 1992 (the second year of banding), we checked whether excluding these data qualitatively changed age-related results; it did not.

3. RESULTS

(a) *Within-pair parentage and male traits*

Over the three years combined, 53.8% of the 130 clutches contained extra-pair young and 33.1% of 484 offspring were sired by extra-pair males. Variation in parentage (the proportion of the brood sired by the social father) was independent of clutch size and changes in clutch size of renests (Yezerinac *et al.* 1995,

1996). Parentage increased with male size, but was unrelated to plumage streaking or estimated age (table 1), consistent with results from 1992 and 1993 only, that showed parentage and estimated age were unrelated (Yezerinac *et al.* 1995, 1996).

Table 1. *Results of a multiple linear regression model relating estimated male age, male plumage streaking and size, and year of study (1992–94) to within-pair parentage*

(Response variable is arcsin ($\sqrt{\text{proportion of brood sired by putative father}}$). The analysis used resampling of 116 clutches from 86 different males each represented once. The overall multiple regression is statistically significant. $F_{5,80} = 3.15$, $p = 0.01$, $r^2 = 0.10$.)

independent variable	d.f.	F	p	partial regression coefficient
estimated age	1	0.15	0.70	−0.01
plumage	1	0.33	0.57	−0.52
size	1	4.62	0.03	0.12
year	2	1.86	0.16	

Table 2. Results of a logistic regression relating estimated male age, male plumage streaking and size, and year of study (1993–94) to whether a male sired extra-pair young

(The analysis used resampling of 65 male-years from 61 different males each represented once. The overall multiple logistic regression is statistically significant. $G = 11.01$, d.f. = 4, $p = 0.03$, $r^2 = 0.16$.)

independent variable	d.f.	G	p	partial regression coefficient
estimated age	1	2.21	0.14	0.55
plumage	1	6.20	0.01	9.47
size	1	1.05	0.31	0.33
year	1	0.05	0.83	−0.06

(b) *Extra-pair success and male traits*

Paternity was assigned, respectively, to 17%, 43% and 57% of extra-pair sired young from 4 of 19, 14 of 34 and 11 of 16 nests that contained extra-pair offspring in 1992, 1993 and 1994. We sampled 33, 57 and 40 clutches in the three years. The percentage of territorial males known to be extra-pair sires was 8.8%, 25.6% and 26.9%, respectively, over the three years. Paternity assignment and the percentage of males identified as extra-pair sires were lower in 1992 because of sampling differences (see §2). Paternity assignment was incomplete in 1994, despite all territorial males on the study area being fingerprinted, indicating that some extra-pair sires did not reside within the study area. Non-resident males and perhaps the 5% unsampled territorial males accounted for unassigned young in 1993 (Yezerinac *et al.* 1995).

The likelihood that a male sired extra-pair young increased with his plumage streaking, but was unrelated to his estimated age or size (table 2). Just among extra-pair sires, the number of extra-pair young sired increased with plumage streaking of the sire ($r = 0.38$, $n = 21$, one-tailed $p = 0.045$), but was unrelated to estimated age or size (respectively, $r = 0.10$, $n = 21$, $p = 0.67$; $r = 0.19$, $n = 21$, $p = 0.41$).

In pairwise comparisons, the extra-pair sire had more plumage streaking than the cuckolded male in 13 dyads, less in 12 dyads and the same in one dyad (Wilcoxon Matched Pairs test, $T^+ = 129.5$, $z = 0.89$, $p = 0.37$). The extra-pair sire was larger than the cuckolded male in 12 dyads, and smaller in eight dyads (Wilcoxon Matched Pairs test, $T^+ = 130$, $z = -0.93$, $p = 0.35$). The extra-pair sire was older than the cuckolded male in nine dyads, the same age in 17 dyads and never younger, which is more extreme than expected by chance based upon the frequencies of each age class in the population ($\chi^2 = 8.14$, d.f. = 2, $p = 0.017$). Thus, while age does not provide an absolute advantage, it may provide a relative advantage.

(c) *Inter-trait correlations*

The multiple regression analyses indicate the relations between size and parentage, and between plumage and extra-pair success were independent of

Figure 2. Frequency distribution for the total number of offspring sired in a season ($n = 66$ males). Extra-pair sires (black bars) had higher total success (ANOVA, $F_{1,65} = 46.81$, $p < 0.001$, $r^2 = 0.41$). Only males from 1993–94 that had within-pair parentage determined for at least one brood are included, and only one brood per male is considered at once because pairs raise no more than one brood to independence per year.

the other measured traits. Additional results support this conclusion. First, size, plumage streaking and estimated age were not correlated with one another, either among all territorial males (size and plumage $r = 0.06$, $n = 85$, $p = 0.58$; age and size $r = 0.17$, $n = 86$, $p = 0.12$; age and plumage $r = 0.07$, $n = 87$, $p = 0.52$), nor among extra-pair sires (size and plumage $r = -0.28$, $n = 18$, $p = 0.26$; age and size $r = 0.42$, $n = 18$, $p = 0.08$; age and plumage $r = 0.02$, $n = 21$, $p = 0.93$). Also, we can corroborate Studd & Robertson's (1989) result that plumage streaking of males measured in two successive breeding seasons neither consistently increased ($n = 14$) nor decreased ($n = 10$; Wilcoxon Matched Pairs test, $T^+ = 173$, $z = 0.66$, $p = 0.51$), and showed moderate repeatability (22.21%).

(d) *Total mating success*

Total annual success (sum of young sired with social mate and with extra-pair mates) was expected to be correlated with size and plumage streaking because size contributed positively to the former and plumage streaking to the latter. However, total success was not significantly related to year of study, or to size, plumage streaking or estimated male age, ($F_{4,56} = 1.38$, $p = 0.25$). The absence of statistically significant relations was not a consequence of males trading off within-pair and extra-pair success. Extra-pair sires were as likely (nine of 20) as other males (43%) to have lost parentage (Binomial test $p = 0.97$). They sired a similar proportion of their partner's eggs (mean $\pm$ s.e. = 0.78 ± 0.07) as other males (0.74 ± 0.04 ; ANOVA of arcsin $\sqrt{\text{data}}$, $F_{1,98} = 0.08$, $p = 0.77$). Their gains of extra-pair paternity exceeded their losses of within-pair parentage (mean difference in number of offspring = 1.68 ± 0.45 s.e.; matched pairs t -test, $t = 3.68$, $p = 0.002$, $n = 20$). Therefore, they had higher total mating success, and they comprised the upper 17% of males in the population for total success (figure 2). Rather, the

null relations resulted from the sample size being reduced (males without comparable measures of within-pair parentage, extra-pair success and traits had to be excluded), and the sample variance increased (within-pair success and extra-pair success were summed, yet size was correlated with only the former and plumage with only the latter).

4. DISCUSSION

Larger male yellow warblers had higher within-pair parentage and males with more streaking on their breast plumage had higher extra-pair mating success. These effects were independent of one another and of estimated age. Thus, in the yellow warbler, extra-pair mating creates sexual selection on two common male secondary sexual traits. Higher within-pair parentage with male size has been noted in other species (e.g. Kempenaers *et al.* 1992; Weatherhead & Boag 1995). This is the second species for which there is genetic evidence that a plumage trait is related to extra-pair success, though it is the first in which the effect is apparently independent of age (see Sundberg & Dixon 1996).

The different ways in which extra-pair paternity was related to size and plumage indicate that both within-pair parentage and extra-pair success need to be measured for a full perspective of how extra-pair mating affects sexual selection. More generally, these results have implications for the evolution of multiple secondary sexual traits. Because the effects of size and plumage variation on extra-pair mating were independent, it seems unlikely that the same factor (e.g. female choice) underlies both patterns. The independent evolution of different secondary sexual traits via different components of sexual selection may explain the evolution of multiple secondary sexual traits, without requiring multiple female preferences (see Møller & Pomiankowski 1993; Andersson & Iwasa 1996). Thus, yellow warblers and other species with extra-pair mating could be useful for testing hypotheses about the evolution of multiple secondary sexual traits.

Extra-pair success increased with plumage streaking, and although the relation between plumage streaking and total mating success was not significant, the higher total mating success of extra-pair sires as a group implies that more streaked males had higher annual mating success. Moreover, because males with more plumage streaking have higher annual survival (S. M. Yezerinac, unpublished data), lifetime reproductive success of highly streaked males is likely to exceed that of less streaked males. Thus, Studd & Robertson's (1985*b*, 1988) ESS hypothesis that the variation in plumage and behaviour among male yellow warblers is a case of alternative, equally successful strategies appears incorrect. Rather this variation seems more likely to be an example of alternative reproductive tactics with unequal fitnesses (see Gross 1996).

Variation in sexually dimorphic plumage ornaments is common in birds. These results have implications for two different interpretations of plumage variability. One view is that variable plumage traits function as

badges of status used as arbitrary signals in settling social disputes (see Owens & Hartley 1991). Johnstone & Norris (1993) have proposed that contest-independent benefits to badge size, such as increased mating success, are one way to maintain honest status signalling. Our results indicate that plumage streaking of yellow warblers satisfies this requirement of being a reliable badge of status (also see Studd & Robertson 1985*a*). Another view is that plumage ornaments are honest indicators of intrinsic quality, with honesty maintained by the costliness of traits (Hill 1994). For example, both the black throat patch of house sparrows (Veiga & Puerta 1996) and the red carotenoid plumage pigmentation of house finches (Hill & Montgomerie 1994) are apparently costly to produce, their expression being dependent on nutritional condition during the molt. Breast streaking in yellow warblers may also be a condition-dependent signal of male quality, particularly if the streaking is carotenoid based (Hill 1996). In support of this interpretation, male streaking appears to be positively related to inter-annual survival (S. M. Yezerinac, unpublished data).

Although male size and plumage streaking were related to within-pair and extra-pair mating success, respectively, extra-pair sires were not consistently more streaked or larger than the males they cuckolded. Moreover, although the estimated age of males was not related to extra-pair mating overall, cuckolders were never younger than the males they cuckold. Thus, although we have identified targets of sexual selection associated with extra-pair mating, the fact that male success was not a simple function of plumage brightness, size or age, means that both the proximate and ultimate factors promoting extra-pair mating in yellow warblers are not resolved fully.

We thank NSERC (Canada) for financial support, Queen's University for use of the Molecular Ecology Lab (P. Boag, Director) and Biological Station, P. Boag, D. Michaud-Freeman, R. Montgomerie and T. Taylor for assistance with various aspects of the study, the Murray and Curtis families for access to land, and R. Gibson, R. Heinsohn, G. Hill, S. Legge, W. Rendell and R. Robertson for comments that improved the paper.

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Received 13 November 1996; accepted 27 November 1996