Extra-pair fertilizations contribute to selection on secondary male ornamentation in a socially monogamous passerine

T. ALBRECHT,*,† M. VINKLER*,†, J. SCHNITZER,† R. POLÁKOVÁ,* P. MUNCLINGER†
& J. BRYJA*

*Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Koněšín, Czech Republic
†Department of Zoology, Faculty of Science, Charles University in Prague, Praha, Czech Republic

Abstract

Despite considerable research effort, it remains unclear whether extra-pair fertilizations (EPF) drive the evolution of male secondary ornamentation in socially monogamous systems. In this study, we test the hypothesis that EPF contribute to the evolution or maintenance of male feather ornamentation in a sexually dichromatic passerine, the Scarlet Rosefinch, *Carpodacus erythrinus*. We show that the colouration of ornamental breast feathers is a good predictor of basic sources of variation in male annual reproductive output in rosefinches and that the annual realized reproductive success of males is positively associated with measures of ornamental colouration only when gains and losses because of EPF are considered. The results indicate that EPF in rosefinches may rely on absolute (good genes) rather than self referential (genetic complementarity) criteria of mate choice. Our study corroborates the potentially important role of EPF in the evolution and/or maintenance of elaborate male ornaments in socially monogamous taxa.

Introduction

Sexual selection has long been proposed as an explanation for the existence of elaborate male ornaments (Darwin, 1871). The opportunity (and strength) of sexual selection has traditionally been attributed to variance in the number of social mates among males, or the variance in the fecundity of social mates pairing with these males (Andersson, 1994; Shuster & Wade, 2003). However, with the advent of molecular tools, it has become apparent that there are other sources of variation in reproductive success. For example, it has been shown that female promiscuity occurs in mammals (Wolff & Macdonald, 2004), reptiles (Uller & Olsson, 2008) or amphibians (Liebgold *et al.*, 2006), and both males and females frequently mate outside their pair bonds in socially monogamous birds (Griffith *et al.*, 2002; West-neat & Stewart, 2003). The resulting extra-pair fertilizations (EPF) may represent an important process

leading to an increased variance in the reproductive success of males and the strength of sexual selection; if distributed unequally over individuals, EPF may contribute to the evolution of secondary ornaments even in strictly socially monogamous species (Webster *et al.*, 1995; Owens & Hartley, 1998).

Previous studies have demonstrated that in birds, extra-pair mating can contribute to variance in male reproductive success, or to the opportunity for sexual selection (OSS). However, whereas some intra-specific studies have suggested that this reproductive tactic significantly adds to variance in male fitness (reviewed in Whittingham & Dunn, 2005; see also Albrecht *et al.*, 2007), others reported slight or no increase of OSS because of EPF (e.g. Kraaijeveld *et al.*, 2004; Freeman-Gallant *et al.*, 2005). The contribution of EPF to OSS seems to be affected by inter-specific migration distance (Albrecht *et al.*, 2007) and mating system (polygyny or monogamy; Freeman-Gallant *et al.*, 2005; Whittingham & Dunn, 2005), but may also vary depending on the mechanism of mate choice, i.e. whether the extra-pair mate choice is mainly driven by self-referential or absolute criteria (Mays *et al.*, 2008). Similarly, rates of

Correspondence: Tomáš Albrecht, Institute of Vertebrate Biology Academy of Sciences of the Czech Republic, v.v.i., Studenec 122, CZ-675 02, Czech Republic.
Tel.: +420 608 237 158; fax: +420 543 211 346; e-mail: albrecht@ivb.cz

extra-pair paternity across species seem to correlate with degree of sexual dimorphism (Owens & Hartley, 1998) and testes size (Pitcher *et al.*, 2005), but apparently not with the OSS itself (Freeman-Gallant *et al.*, 2005).

Empirical studies that have attempted to evaluate the basic predictions of sexual selection theory, linking fertilization success of males with ornamental expression, have found that the occurrence of extra-pair paternity correlates with male size (Yezerinac & Weatherhead, 1997), song repertoire (Forstmeier *et al.*, 2002; Suter *et al.*, 2009), feather colouration (e.g. Foerster *et al.*, 2003; Safran *et al.*, 2005), structural ornaments (Kleven *et al.*, 2006), or a combination of several factors (e.g. Sundberg & Dixon, 1996). Yet other studies have found no selection via EPF acting on secondary male ornaments despite high contribution of EPF to OSS (Westneat, 2006). Thus, understanding the role of EPF in the process of evolution/maintenance of elaborate male ornamentation remains a challenging issue of evolutionary biology (Westneat & Stewart, 2003), particularly important for understanding the signalling function of various ornaments given the mainly indirect benefits that females gain from extra-pair mating (Griffith *et al.*, 2002).

Variance in total reproductive success of males [var (T_m)] can be partitioned between within- and extra-pair components (Webster *et al.*, 1995). To determine the evolutionary significance of EPF, it is necessary to identify (1) how the terms describing the ability of a male to avoid being cuckolded (within-pair fertilization success of males), and his ability to obtain extra-pair mate(s) contribute to overall variation in male fitness (Webster *et al.*, 2007) and (2) how phenotypic traits affect these components of male fertilization success. Although this information is crucial for understanding the mechanism by which promiscuity contributes to the process of sexual selection (Webster *et al.*, 2007), obtaining it is particularly challenging because to track the entire reproductive output of males, most if not all sires of extra-pair young (EPY) in nests must be identified (Freeman-Gallant *et al.*, 2005).

In this study, we evaluate the hypothesis that extra-pair mating drives selection on orange-to-red carotenoid-based feather male ornamentation in sexually dichromatic Scarlet Rosefinches (*Carpodacus erythrinus*, Pallas) by relating data on within- and EPF success of males with the extent of their sexual ornamentation in a population where most EPY can be associated with their biological fathers (Albrecht *et al.*, 2007). As in other related species, redness was expected to indicate a high level of expression of carotenoid-based ornamentation (for review see Hill, 2002). The data allowed us to link variation in sexual ornamentation to several components of fertilization success of males, in particular (1) the proportion of within-pair young (WPY) sired and (2) the number of extra-pair mates a male is able to obtain. Variation in these two fitness components (P_w and M_e *sensu* Webster *et al.*, 1995) has been shown to explain most (29% and 19%) variance in total annual reproductive output of male

rosefinches (Albrecht *et al.*, 2007). We also performed a pair-wise comparison of extra-pair males and males they cuckolded to elucidate whether sexual ornamentation affects female extra-pair mate choice. Finally, we test the hypothesis that sexual ornamentation *via* EPF success determines annual reproductive output in rosefinch males. While costly carotenoid-based sexual ornamentation plays a crucial role in mate choice decision in House Finches (*Carpodacus mexicanus*), where yellow males tend to be ignored by females and red males are preferred as mates (Hill, 2002; Oh & Badyaev, 2006), the speed of pairing between social mates in rosefinches appear to be unrelated to many male traits, including feather colouration (Björklund, 1990). However, thus far, data linking various components of EPF success and ornamentation have not been available for these species.

Methods

General procedures

Field work was carried out from May to July during the years 2001–2007 in the Šumava Mountains National Park, Czech Republic (48°49′N, 13°56′E). A detailed description of the study site and field procedures is presented in Albrecht *et al.* (2007). Briefly, the study was conducted in a shrubby wetland meadow of about 1 km² surrounded by a mosaic agricultural landscape hosting a colony of 10–20 breeding pairs of rosefinches per year (see also Albrecht, 2004; Albrecht *et al.*, 2007). The study site was searched systematically several times over each breeding season where there is vegetation suitable for nesting (mainly *Spiraea* bushes) so that nearly all nests were found during the egg-laying or incubation stages. Nests were visited regularly during the field season to estimate the exact day of egg hatching. Blood samples (~20 μL) were taken by venipuncture from adults and in 7-day-old chicks. Since nest survival in the study area was high (Albrecht, 2004), only a few broods (< 20%) were lost before it was possible to sample the chicks for blood. Adult birds were trapped using mist-nets either upon their arrival to the study area in May, or during the provisioning of chicks later in the season. Each adult bird was ringed with one aluminium ring (N MUSEUM PRAHA) and with an individual combination of 1–3 coloured plastic rings (AVINET). Individual females were assigned to a nest having either been flushed from that nests during the incubation period, or observed feeding and/or brooding the chicks in that nest. Males observed repeatedly feeding the female during incubation, and/or feeding chicks, were considered the social fathers of young in a particular nest.

Since the colour of ornamental patches in itself appears to be the most important feature in mate choice decision in several avian species (e.g. Hill, 2002; Safran *et al.*, 2005), and breast characteristics of rosefinch males seem to be of a particular importance during mate attraction (Stjernberg,

1979), we decided to concentrate on breast patch colour as the most relevant ornamentation in this species. In the analyses (see below), we thus omitted other potentially important parameters that might each convey further individual information, such as pigment symmetry, patch size or patch symmetry (Badyaev *et al.*, 2001) and also omitted ornamentation on other parts of the male body. Where possible, the breast patch of males in their 3rd year or older were photographed using a digital camera (Olympus Corp., Tokyo, Japan). Only photographed males were included in the analyses. All photographs were taken under standard lighting conditions in the dark room of a nearby field station using an electronic flash 40 cm from the colour patch, and colour swatches (grey card GC 18 and colour & grey chart Q 14; Danes-Picta, Praha, Czech Republic) were used to standardize measurements (Montgomerie, 2006). Each bird was placed directly on the grey card in a standardized position. Photographs were analysed using ADOBE PHOTOSHOP™ software (Adobe Systems Inc., San Jose, California). Hue, saturation and brightness (HSB colour space) were measured on 10 5×5 pixels points randomly distributed over the breast colour patch of males (also Kilner, 1997). There was a high repeatability in estimates for all three parameters within individual males (hue: $r = 0.996$; saturation: $r = 0.946$; brightness: $r = 0.987$). Increasing values of hue [range −9.1 (hue angle 350.9) to 23.17] indicate a yellower (less red) plumage, increasing values of saturation (range 42.75–85.45%) indicate more intensive colouration, and increasing values of brightness (range 35.08–95.30%) indicate lighter colouration (Montgomerie, 2006). Digital image analysis of avian ornaments and other methods based on human perception have been criticized (Bennett *et al.*, 1994) since birds are able to recognize reflectance in UV (320–400 nm) spectra. However, it has been argued that these methods can capture biologically relevant colour signal under certain conditions (reviewed in Andersson & Prager, 2006; Montgomerie, 2006). We compared measures obtained using the above method (not sensitive to UV wavelengths) with those received from spectrometer using a sample of 20 males trapped on the study plot or in nearby areas in the 2007 field season. Spectra were obtained using an Avantes Avaspec 2048 spectrometer with light source Avalight XE (Avantes BV, Eerbeek, The Netherlands). Standardized measurements were taken on ornaments with reflection probe (2 mm diameter). Colorimetric measures of the colour of the breast patch [spectral intensity (brightness), spectral location (hue) and spectral purity (saturation)] were assessed following equations given in Andersson & Prager (2006) using the average of five measurements per bird. There was a significant correlation between HSB obtained by both methods (hue: $r^2 = 0.847$, $F_{1,18} = 99.915$, $P < 0.0001$; saturation: $r^2 = 0.509$, $F_{1,18} = 18.687$, $P < 0.001$; brightness: $r^2 = 0.224$, $F_{1,18} = 5.197$, $P = 0.037$), indicating that our estimates based on digital photography can be used to describe colouration of ornamental feathers in rosefinches.

Delayed plumage maturation occurs in rosefinches, with males in their 2nd calendar year (SY males) resembling females (Stjernberg, 1979). Only five SY males (9%) were found to be breeding on our study plot, a situation also reported from other areas (Björklund, 1989). As there is no sexual ornamentation in SY males (Stjernberg, 1979), these males were excluded from analyses. Only six after-second-year (ASY) males on the study plot were identified as being unpaired (for criteria see Albrecht *et al.*, 2007). Sexual ornamentation was scored in five of these males, but these were excluded from all analyses since no data on within-pair fertilization success were by definition available for them (and in any case, inclusion of these males in potentially relevant analyses did not change the results). However, we were able to use one unpaired male in pair-wise comparisons of cuckolded and cuckolding males. Males trapped as ASY individuals in more than one season ($n = 13$) were used to evaluate how sexual ornamentation changes with age.

Identification of parentage

Parentage analysis was conducted using 15 microsatellite loci developed by screening genomic libraries of two *Carpodacus* finches and by cross-species amplification of loci from related species: CE207, CE165, CE150, CETC215, CE152, CE147, CM026, CM014, CM001 and CM008E (Poláková *et al.*, 2007), Hofi 17, Hofi 52, Hofi 24, Hofi 5 (Hawley, 2005) and LOX 1 (Piertney *et al.*, 1998). Primer details, PCR amplification conditions, fragment detection and analysis are described in Poláková *et al.* (2007). The loci used for parentage analyses were remarkably variable (4–95 alleles per locus; median = 18), had high heterozygosities for particular loci within adult individuals ($H_e = 0.39$–0.98, median = 0.86), and each adult individual possessed a unique genotype. The average probabilities of excluding a single randomly chosen unrelated individual from being a parent were calculated for all 15 loci (when the maternal genotype was known) using the program CERVUS 3.0 (Kalinowski *et al.*, 2007). These analyses were based (1) on all resident adult individuals genotyped in the course of the study and (2) separately for each year. The total exclusionary power exceeded in all cases 99%.

We did not find any genetic mismatches (i.e. evidence of a mutation) between an offspring and its social mother. The offspring's paternal alleles were subsequently compared with the alleles of its putative father (the female's social partner). Some offspring did not match their social father at 5–14 loci (mean = 9.44) and they were considered EPY. Sires of EPY were determined using the exclusion approach (Jones & Ardren, 2003); that is, we compared the paternal alleles of EPY with the genotypes of all males in the population using the CERVUS 3.0 software. Because we found no mismatches between WPY and their parents, we also used the same strict criteria when attempting to identify the EPY sires. If

no male matched a particular EPY at all loci (in fact, social fathers either matched at all loci or differed at least at three loci), the sire was categorized as unknown.

Estimating reproductive success

Apparent reproductive success for a given male was measured as the total number of chicks (including possible EPY) that survived until age 7 days in his nest, corresponding to the age when chicks are able to leave the nest unaided in response to a perceived threat (Björklund, 1990). As some mortality of young occurs after this age, the above method of measuring reproductive success may lead to an over-estimate; however, these random mortality events will not bias our estimates of relative reproductive output of males. Realized reproductive success of a particular male was measured as a sum of offspring sired in his nest and in nests of other males in the study area surviving to 7 days post-hatch. Although our estimate of realized reproductive success could be biased if males frequently sire young outside the study plot, and we cannot rule out the possibility that birds from the different breeding colonies encounter each other on a third site, this seems unlikely to occur with high frequency in our study animals considering the relative isolation of our study area (the nearest rosefinch colony is situated 3 km away; for further discussion see Albrecht *et al.*, 2007). Although the incomplete sampling of nests (e.g. because of predation, see above) may also affect estimates of EPF success in males, this would not significantly change the directions of ornamentation–reproductive success correlations as males that mono-polized fertilizations in sampled nests are also those more likely to fertilize eggs in nests we missed. Variation in male fitness can be partitioned into several components (Webster *et al.*, 1995), such as the variance in number of mates [within (M_w) and extrapair (M_e)], proportion of young sired in a nest (P_w and P_e), and mate quality expressed as mate productivity (N_w and N_e; Webster *et al.*, 1995). In this study, we relate variation in male ornamentation to components associated with EPF success of males that were previously shown to account for significant portion of variance in male fitness in rosefinches (M_e, P_w; Albrecht *et al.*, 2007).

Statistical analyses

All analyses were based on data from ASY males for which we had photographs of the breast patch to score sexual ornamentation ($n = 54$ males, 75 observations). To reduce the number of explanatory variables describing the sexual ornamentation to a minimum, we performed a principal component analysis (PCA) on tri-stimulus HSB measures of all resident males for which we had adequate data. First, we checked the distribution of HSB for normality using a Kolmogorov–Smirnov test which revealed a normal distribution in all cases (all $\chi^2 > 0.10$). The single PCA axis

(PC1, eigenvalue = 1.66) was strongly associated with hue ($r = -0.91$) and, albeit only to a lesser extend, also with saturation ($r = -0.67$) and brightness ($r = -0.64$), and explained 55.36% of variation in data. We interpreted scores from the PC1 axis (hereafter 'composite colouration' or 'overall sexual ornamentation') as the combined measure of ornamentation and assumed that the expression of sexual ornamentation (degree of carotenoid-based colouration, redness) in rosefinches was positively associated with PC1 values. However, we also present analyses based raw measures of HSB of ornamental feathers.

As some males were scored in more than 1 year ($n = 13$), in most analyses we used generalized linear-mixed effect model approach (GLMM) with male identity ($n = 54$) treated as a random effect to avoid pseudore-plications (Faraway, 2006). We chose link functions in the models following the nature of dependent variables. When modelling numbers (the number of offspring sired, the number of extra-pair mates obtained) we assumed a Poisson distribution of error terms and used log-link function. When modelling probabilities and proportions (the likelihood of being cuckolded, the proportion of young sired in a nest), logit-link function was applied instead, assuming a binomial distribution of error terms (Faraway, 2006). The onset of breeding, if included in the analysis, was standardized over years (1, the day a first egg in a season was laid) and log transformed to achieve normality. The significance of a particular term in models was based on the change in deviance between the full and reduced/null models, distributed as χ^2 with degrees of freedom equal to the difference in the degrees of freedom between the models with and without the term in question (Faraway, 2006). Minimal adequate models, i.e. models with all terms significant, are presented (Crawley, 2007). When modelling change in colouration of individual males over years, GLMM with an identity link function was applied, with year of male occurrence treated as the ordered categorical predictor, measures of sexual ornamentation as the dependent variables, and male identity as a random effect. Pair-wise comparisons of cuckolding and cuckolded males at the same nest were conducted using standard *t*-tests for dependent samples. In cases when more than one male was cuckolding in the nest of a single social male we considered these as independent events in the analysis. However, results (not shown) remained similar even when nests cuckolded by only a single male were evaluated. Analyses were performed using R 2.8.1 (http://www.r-project.org/) and STATISTICA 6.0 statistical packages. Estimates are presented ± SE unless stated otherwise.

Results

Patterns of paternity

Extra-pair young were identified in 24 of 75 (32%) broods for which we also obtained phenotypic traits of

social fathers. In most cases, broods with mixed paternity contained two EPY (mean 2.17 ± 0.214, range 1–5, $n = 24$), and three broods consisted exclusively of EPY. A total of 52 EPY were sired in these nests and the biological father was assigned to 39 (72.2%) of them. The number of genetic fathers siring young in nests varied from one (no EPY detected) to four (mean 2.30 ± 0.092, $n = 75$), and paired males obtained between zero and two extra-pair mates (mean 0.22 ± 0.052, $n = 75$) and sired zero to four EPY (mean 0.48 ± 0.12, $n = 75$). The overall probability of occurrence of at least one EPY in nests was not associated with the onset of breeding and year, though the slope of the relation between the occurrence of EPF and the onset of breeding in particular years differed (Table 1). Similarly, the onset of breeding was not correlated with the overall sexual ornamentation of males (Table 1).

Extra-pair paternity and male ornamentation

We found no systematic effect of age on hue (GLMM, $\chi^2_5 = 0.604$, $P = 0.989$) or brightness (GLMM, $\chi^2_5 = 9.639$, $P = 0.089$), but a positive effect of age on saturation (GLMM, $\chi^2_5 = 11.864$, $P = 0.038$) in a subset of males scored in more than 1 year ($n = 13$ males, 34 repeats in total). However, no effect of age on the composed measure of sexual ornamentation (PC1) was detectable (GLMM, $\chi^2_5 = 0.819$, $P = 0.976$). In models describing within-pair and EPF success of males ($n = 54$ individuals and 75 observations), the occurrence of at least one EPY in nests was not significantly associated with the composite colouration of social fathers (PC1: GLMM, binomial errors; $\chi^2_1 = 1.994$, $P = 0.158$, Fig. 1a), but was associated with hue (Table 2). On the other hand, overall sexual ornamentation was identified as an important predictor explaining variation in the proportion of young sired by a male in his nest [GLMM, binomial errors; $\chi^2_1 = 6.274$, $P < 0.05$ (slope: 0.701 ± 0.296)]; was strongly associated with the probability of obtaining at least one EPF [GLMM, binomial errors; PC1: $\chi^2_1 = 12.690$, $P < 0.001$ (slope: 1.303 ± 0.435); Fig. 1b]; and was also a good predictor of

Table 1 (a) Correlates of the occurrence of EPF, i.e. of at least one extra-pair young (EPY) found in nest ($n = 75$) as a function of the standardized timing of breeding (log transformed) and year, and (b) the onset of breeding as a function of male sexual ornamentation (PC1) and year.

(a)	d.f.	χ^2	P	(b)	d.f.	F	P
Timing	1	1.619	0.203	PC1	1, 67	0.129	0.721
Year	6	5.000	0.544	Year	6, 67	1.144	0.347
Year:timing	6	13.277	0.039	PC1:year	6, 61	0.651	0.689

Analyses are based on logistic regression (a) and general linear (b) models, respectively. Significances are based on Type III sums of squares. The total numbers of nests analysed in respective years are as follows (year in parenthesis): 10 (2001), 9 (2002), 10 (2003), 13 (2004), 13 (2005), 9 (2006) and 11 (2007).

the total number of EPY a male obtained in a season [GLMM, Poisson errors; $\chi^2_1 = 10.764$, $P < 0.001$ (slope: 0.867 ± 0.278)]. Again, specific components of colouration contributed unequally to these associations, with hue and brightness being the most important predictors of male fertilization success (Table 2). Finally, composite colouration was a parameter which allowed the discrimination between cuckolding and cuckolded males in nests containing EPY where both the social and cuckolding males were scored for sexual ornamentation ($n = 19$ male couples), indicating that cuckolding males were redder than the males they cuckolded (*t*-test for dependent samples, $t_{18} = -2.404$, $P = 0.027$, Fig. 2). Cuckolding and cuckolded males, however, did not differ in hue, saturation or brightness when these were treated separately (hue: $t_{18} = -1.931$, $P = 0.069$, saturation: $t_{18} = -1.698$, $P = 0.107$, brightness: $t_{18} = -0.820$, $P = 0.423$).

Sexual ornamentation and annual reproductive success of males

There was no relationship between apparent reproductive success of males and their overall sexual ornamentation
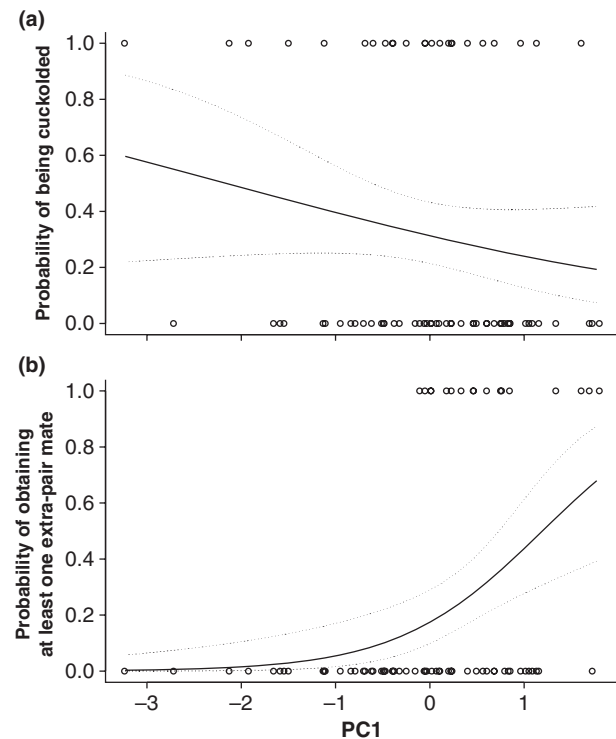

Fig. 1 Predicted probability of (a) being cuckolded and (b) obtaining at least one extra-pair mate for rosefinch males as a function of composite male ornamentation (PC1; higher values of PC1 indicate higher degree of ornamentation). Dotted lines are 95% confidence limits. Estimations on the figures are based on simple logistic regression models not adjusted for repeated sampling for several males (see the main text for results based on mixed-model effect approach).

Table 2 Results of mixed-effect models (GLMM) evaluating the effects of hue, saturation and brightness on (a) the probability of having at least one EPY in a nest (0 – no EPY, 1 – EPY); (b) the proportion of young sired by a male in his nest; (c) the probability of obtaining at least one extra-pair mate (0 – no mate, 1 – EP mate); and (d) the number of extra-pair offspring sired.

MAM	Term	Estimate	SE	χ	d.f.	P
(a) **Hue**	Intercept	−1.452	0.435			
	Hue	0.179	0.0932	4.311	1	0.038
(b) **Hue**	Intercept	3.327	0.481			
	Hue	−0.164	0.061	8.108	1	0.004
(c) **Hue + Brightness**	Intercept	2.720	1.899			
	Hue	−0.270	0.103	8.675	1	0.003
	Brightness	−0.069	0.034	4.895	1	0.027
(d) **Hue + Brightness**	Intercept	3.440	1.531			
	Hue	−0.205	0.079	8.101	1	0.004
	Brightness	−0.087	0.028	12.544	1	< 0.001

Minimal adequate models (MAM), i.e. models for which all terms are significant are presented in bold. Values of significance for particular terms are based on Type III sum of squares (adjusted for effects of other terms in a particular MAM). Analyses a, b and c are logistic regressions (logit link function), while analysis *D* is a Poisson regression (log link function).
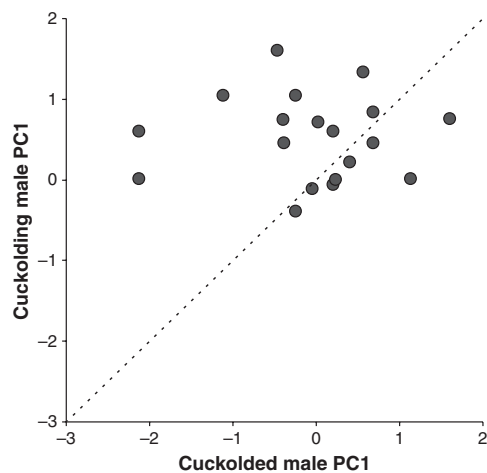

Fig. 2 The relationship between the PC1 scores (higher values of PC1 indicate higher degree of ornamentation) for cuckolded and cuckolding males at the same nests. Diagonal dashed line represents identical colouration of cuckolded and cuckolding males.

Fig. 3 The relationship between PC1 (higher values of PC1 indicate higher degree of ornamentation) and (a) apparent annual reproductive success of paired Scarlet Rosefinch males when no gains and losses because of extra-pair fertilizations (EPF) were considered; and (b) realized reproductive success for paired males with the effect of EPF taken into account. The line on the bottom graph (b) is based on the predictions from a simple Poisson regression model with the number of offspring as dependent variable. Calculations based on mixed-effect model (male identity included as random effect) assuming Poisson distribution of dependent variable showed that only realized reproductive success of males was associated with male colouration (see the main text for further details).

(GLMM, Poisson errors; $\chi_1^2 = 0.705$, $P = 0.401$, $n = 54$ individuals and 75 observations; Fig. 3a), and the same was true for particular components of sexual ornamentation (GLMM, Poisson errors; hue: $\chi_1^2 = 0.507$, $P = 0.476$; saturation: $\chi_1^2 = 0.607$, $P = 0.436$; brightness: $\chi_1^2 = 0.013$, $P = 0.910$). However, an increased number of extra-pair mates also increased annual reproductive success of males (Spearman Rank Correlation, $r_s = 0.508$, $P < 0.0001$, $n = 75$), and standardized variance in fitness (*sensu* Arnold & Wade, 1984) was 3.36 higher for realized than
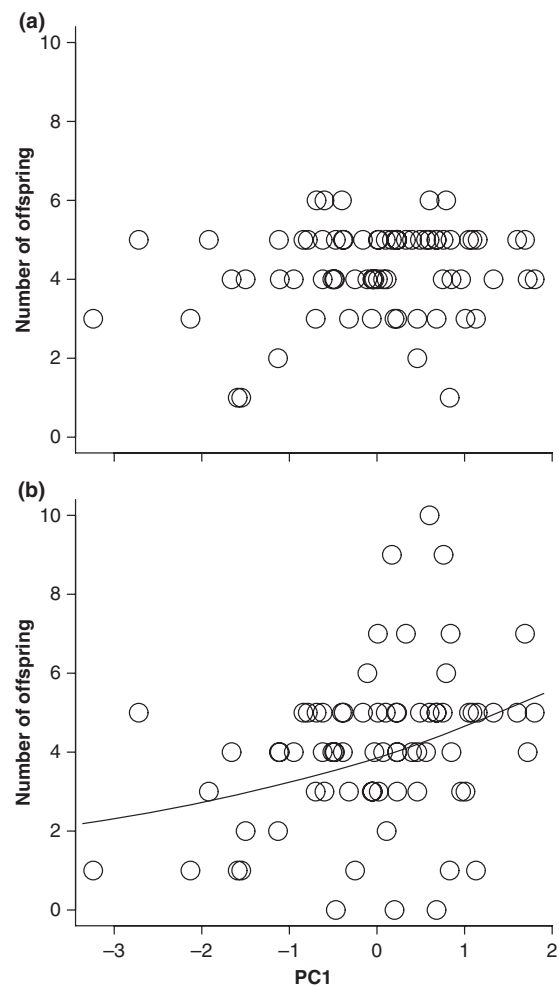
for apparent reproductive success (0.234 and 0.069, respectively) in a sample of males ($n = 54$ males, 75 observations, all years combined) used in the analyses. When the analysis accounted for gains and losses because of EPF, composite colouration was a significant predictor of annual reproductive success of males [GLMM, Poisson errors; PC1: $\chi_1^2 = 8.167$, $P < 0.01$ (slope: 0.172 ± 0.061), $n = 54$ individuals and 75 observations; Fig. 3b]. Of the three components of colouration, only hue was a significant predictor of total male reproductive output

[GLMM, Poisson errors; hue: $\chi_1^2 = 7.712$, $P < 0.01$ (slope: -0.036 ± 0.014); saturation: $\chi_1^2 = 0.874$, $P = 0.350$; brightness: $\chi_1^2 = 3.133$, $P = 0.077$].

Discussion

We found a positive association between the expression of ornamental feather colouration in rosefinch males and their annual reproductive success. Similarly, colouration was a good predictor of male ability to obtain extra-pair mates. Sexual ornamentation was only important as a predictor of male fitness when gains and losses because of EPF were taken into account; that is, when we considered the realized reproductive success. The fact that apparent reproductive success was unrelated to male ornamentation indicates that drab and bright males did not differ in their ability to attract high quality (fecund) females. We have shown elsewhere (Albrecht *et al.*, 2007) that variation in fecundity of social mate (N_w) contributes some 9% to the OSS in rosefinches, but this variation is apparently not related to male characteristics we measured. The onset of breeding, which may reflect pairing date and hence male attractiveness, was also not associated with male ornamentation. The lack of relationship between male secondary ornamentation, the onset of breeding, and female quality could be the outcome of the rapid, random and synchronous pairing in this long-distance migratory passerine (Stjernberg, 1979; Björklund, 1990; Albrecht *et al.*, 2007). Female promiscuity in rosefinches might thus have evolved as a 'compensatory' mechanism through which high-quality females paired socially to inferior (drab) males engage in extra-pair copulations to adjust for their inappropriate choice of social mate. In fact, a comparison of cuckolded and cuckolding males at the same nest showed that the latter were more colourful.

The idea of EPF as the outcome of female behaviour correcting for inappropriate or hasty choice of social males has been already advocated by several studies (e.g. Weatherhead & Yezerinac, 1998), and seems to be supported by some comparative studies. For example, long distance migration may be associated with hasty and apparently inappropriate choice of social mate. Correspondingly, rates of EPF are higher in migratory than sedentary species (Spottiswoode & Møller, 2004), and the OSS because of EPF is positively associated with migration distance in north-temperate zone breeding passerines (Albrecht *et al.*, 2007). An implicit assumption in this scenario is, however, that EPF represent a female strategy, a view that is not shared by all authors (e.g. Arnqvist & Kirkpatrick, 2005; but see Griffith, 2007). Moreover, other factors, such as breeding synchrony, can independently contribute to high contribution of EPF to OSS across species (Albrecht *et al.*, 2007; Macedo *et al.*, 2008).

Male sexual ornamentation could also serve as a dominance signal in male–male competition, or may signal the intensity of mate guarding, factors that may affect the variation among males in the ability to obtain EPF or loose paternity in own nests independently of direct female preferences (Qvarnstrom, 1997). However, in house finches, pale males tend to be dominant over red males and seem to invest more in obtaining mates, yet red males have a greater ability to attract females (McGraw & Hill, 2000). Similarly, attractive males devote less time guarding their mates in bluethroats, despite being more successful in both within- and EPF than drab males (Johnsen *et al.*, 1998). This indicates that, at least in some passerines, mate guarding is not a very effective paternity-assurance strategy (Johnsen *et al.*, 2003; but see Chuang-Dobbs *et al.*, 2001), and a negative relationship between male ornamentation and the intensity of mate guarding could even be the rule (Kokko & Morrell, 2005). Ornament colouration might also reflect quality of males not directly assessed by females. For example, health and oxidative state of an individual could affect both the male ornamentation (e.g. Alonso-Alvarez *et al.*, 2004) and ejaculate quality (Tremellen, 2008). Higher fertilization success of superiorly ornamented males in the process of extra-pair-mating-induced sperm competition may thus not be under direct behavioural control of females (Pizzari *et al.*, 2008), although post-copulatory cryptic female choice (e.g. Birkhead & Møller, 1998) cannot be ruled out. Although this possibility was not evaluated in our study, both within- and extra-pair success were associated with various components of sexual ornamentation of rosefinch males.

Traits associated with life history but not sexual selection *per se* could be another important factor affecting the distribution of EPF in a population. Young males are typically more prone to cuckoldry than older males, and age is associated positively with the ability of males to obtain EPF outside their pair bonds in birds (e.g. Richardson & Burke, 1999; Bouwman *et al.*, 2007). However, age itself is unlikely to bias the relationship between male ornamentation and reproductive success reported in our study. First, we have restricted our analyses to ASY males, thus decreasing the variance in age of males in the sample. In addition, there was either no (for hue and brightness) or only moderate (for saturation) association between male ornamentation and age in a group of males sampled repeatedly over several breeding seasons. It seems that hue in particular represents only a poor indicator of male age. We therefore conclude that this parameter of male ornamentation is a good predictor of annual realized success for rosefinch males independent of age.

The variation in realized reproductive success of males is affected by at least two processes: male ability to protect paternity in his own nest, and his ability to attract extra-pair mates (Webster *et al.*, 1995, 2007). These components have either a synergistic positive effect on male fitness, or there could be a trade-off when males loose paternity in own nests when seeking for EPF

(Webster *et al.*, 1995). High contribution of EPF to the OSS is typically associated with positive covariance between within-pair paternity and EPF, and seems to indicate absolute (good genes) rather than self-referential (genetic complementarity) criteria of female extra-pair mating preferences (Mays & Hill, 2004; Pialek & Albrecht, 2005; Mays *et al.*, 2008). We have demonstrated elsewhere that variance in realized reproductive success is about three times higher than in apparent reproductive success in rosefinches, with EPF accounting for a significant portion of variance in male fitness (Albrecht *et al.*, 2007). This figure corresponds to that reported for other long-distance migratory passerines (Albrecht *et al.*, 2007). In this study, we evaluated the effect of male sexual ornamentation on basic components of variation in reproductive output in male rosefinches. First, we demonstrate that variation in male ability to sire offspring in their own nests (P_w) is explained by ornamental expression. However, sexual ornamentation was also associated with the variance among males in the number of extra-pair mates obtained (M_e). These results imply that the selection on sexual colouration in rosefinches operates simultaneously through both within- and EPF success, in line with predictions of absolute criteria of female extra-pair mating preferences (e.g. Mays & Hill, 2004). Unfortunately, we were unable to measure the effect of colouration on the contribution of within- and extra-pair paternity to the life-time reproductive success of males, a common pitfall of many similar studies (but see Webster *et al.*, 2007).

Orange to red ornamentation of cardueline finches is caused by carotenoids (e.g. Hill, 2006), and although there have been other studies suggesting an important role of EPF in the evolution of carotenoid-based ornamentation in passerines (e.g. Sundberg & Dixon, 1996; Oh & Badyaev, 2006; Reudink *et al.*, 2009; but see Hill *et al.*, 1994), our study provides to our knowledge one of the first evidence of a link between carotenoid-based colouration and various components of male extra-pair and within-pair fertilization success in this taxon. Because female birds only obtain sperm from extra-pair mates, we can eliminate some alternatives often used to explain female preferences for brightly coloured males (e.g. the 'good parent' model). Similarly, the quality of territory and/or spatial distribution of nests were unlikely to affect our results (see discussion in Albrecht *et al.*, 2007). However, whether (and how) female rosefinches benefit from preferring coloured males as extra-pair mates awaits further study. Carotenoid-based colouration honestly reflects health status and condition of the bearer in a wide array of taxa, including fish (Magurran, 2005) and birds (reviewed in Hill, 2006), therefore, females might gain both direct and indirect benefits by preferring ornamented extra-pair mates, either through decreased probability of parasite/pathogen transfer (Poiani & Wilks, 2000), or through genetic quality reflected by ornamentation that can be inherited

by offspring (e.g. good immunocompetence genes are reflected by ornaments; Hamilton & Zuk, 1982). The expression of carotenoid-based ornamentation could be linked with immunocompetence genes via several pathways (e.g. Zelano & Edwards, 2002), but the evidence for any 'good genes' related to carotenoid-based colouration in birds, although substantial, is still only indirect (Hill, 2006). However, it has been unequivocally established that the expression of carotenoid-based colouration reflects the ability of an individual to cope with and liberate itself from experimentally-induced infection (Hill & Farmer, 2004); in addition, it has been suggested that the intensity of carotenoid-based colouration has a heritable component (Birkhead *et al.*, 2006).

Our measure of overall sexual ornamentation (PC1) was mainly based on hue, but was also positively correlated with saturation and brightness. It has been suggested that different colour parameters have different sensitivity to environmental stress given their different mechanisms of origin and development, and thus convey different information about the bearer (reviewed in Hill, 2006). For example, hue may be a function of the proportion of yellow xanthophylls and costly red keto-carotenoids deposited in feathers, whereas the saturation will be determined by total carotenoid concentrations (Inouye *et al.*, 2001; Andersson & Prager, 2006) and brightness reflects the structural properties of the feather surface (e.g. bacterial damage; Shawkey *et al.*, 2007). We can only speculate about the signalling function of HSB in rosefinches. However, it seems that hue of the ornament (redness) is a parameter extremely sensitive to condition and health status in related house finches (see Hill, 2002 for review). Hence, hue (perhaps better than other colour components) reflects either the indirect qualities males provide via EPF to females, or at least mirror variance in the general vigour of male rosefinches. Although hue was the most important predictor of male fertilization success in rosefinches, it is worth noting that compared with saturation and brightness, our photography-based estimates of hue were the least different from measurements taken by a spectrometer (also Hill, 1998). This may indicate that there was some variation among individuals in saturation and brightness that was not measurable using simple digital photographs. In any case, the brightness we measured was still a good predictor of male abilities to obtain an extra-pair mate, independent of hue.

In summary, our study demonstrates the propensity of brightly coloured males to gain both high within-pair paternity and EPF at the expense of drab males, resulting in a link between ornamental colouration of males and their total annual reproductive success. As our study is correlative, we cannot distinguish between alternative explanations of the observed pattern and to fully exclude the possibility that ornamentation and fertilization success of males may be correlated with a third, unmeasured variable, such as overall male com-

petitive abilities. Most importantly, the interpretation of the results is based on the understanding of the adaptive value of extra-pair behaviour for female birds (e.g. Westneat & Stewart, 2003; Arnqvist & Kirkpatrick, 2005; Albrecht et al., 2006). In any case, we show that EPF may significantly contribute to the evolution and/or maintenance of sexual ornamentation in rosefinches, and conclude that EPF not only represent an important process contributing to the increased OSS, but also promote the evolution of male secondary traits in socially monogamous systems, and at least in some passerine species.

Acknowledgments

References

Albrecht, T. 2004. Edge effect in wetland-arable land boundary determines nesting success of Scarlet Rosefinches (*Carpodacus erythrinus*) in the Czech Republic. *Auk* **121**: 361–371.

Albrecht, T., Kreisinger, J. & Pialek, J. 2006. The strength of direct selection against female promiscuity is associated with rates of extrapair fertilizations in socially monogamous songbirds. *Am. Nat.* **167**: 739–744.

Albrecht, T., Schnitzer, J., Kreisinger, J., Exnerova, A., Bryja, J. & Munclinger, P. 2007. Extrapair paternity and the opportunity for sexual selection in long-distant migratory passerines. *Behav. Ecol.* **18**: 477–486.

Alonso-Alvarez, C., Bertrand, S., Devevey, G., Gaillard, M., Prost, J., Faivre, B. & Sorci, G. 2004. An experimental test of the dose-dependent effect of carotenoids and immune activation on sexual signals and antioxidant activity. *Am. Nat.* **164**: 651–659.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.

Andersson, S. & Prager, M. 2006. Quantifying colours. In: *Bird Colouration*, Vol. I – *Mechanisms and Measurements* (G.E. Hill & K. McGraw, eds), pp. 41–89. Harvard University Press, Cambridge, MA.

Arnold, S.J. & Wade, M.J. 1984. On the measurement of natural and sexual selection: theory. *Evolution* **38**: 709–719.

Arnqvist, G. & Kirkpatrick, M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and

indirect selection on extrapair copulation behavior in females. *Am. Nat.* **165**: S26–S37.

Badyaev, A.V., Hill, G.E., Dunn, P.O. & Glen, J.C. 2001. Plumage colour as a composite trait: developmental and functional integration of sexual ornamentation. *Am. Nat.* **158**: 221–235.

Bennett, A.T.D., Cuthill, I.C. & Norris, K.J. 1994. Sexual selection and the mis-measure of colour. *Am. Nat.* **144**: 848–860.

Birkhead, T.R. & Møller, A.P. 1998. *Sperm Competition and Sexual Selection*. Academic Press, London.

Birkhead, T.R., Pellatt, E.J., Matthews, I.M., Roddis, N.J., Hunter, F.M., McPhie, F. & Castillo-Juarez, H. 2006. Genic capture and the genetic basis of sexually selected traits in zebra finch. *Evolution* **60**: 2389–2398.

Björklund, M. 1989. Is the absence of 1st-year males on breeding grounds in the Scarlet Rosefinch related to a male-biased sex-ratio. *Anim. Behav.* **38**: 1081–1083.

Björklund, M. 1990. Mate choice is not important for female reproductive success in the common rosefinch (*Carpodacus erythrinus*). *Auk* **107**: 35–44.

Bouwman, K.M., Van Dijk, R.E., Wijmenga, J.J. & Komdeur, J. 2007. Older male reed buntings are more successful at gaining extrapair fertilizations. *Anim. Behav.* **73**: 15–27.

Chuang-Dobbs, H.C., Webster, M.S. & Holmes, R.T. 2001. The effectiveness of mate guarding by male black-throated blue warblers. *Behav. Ecol.* **12**: 541–546.

Crawley, M.J. 2007. *The R Book*. John Willey & Sons, Chichester.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.

Faraway, J.J. 2006. *Extending the Linear Model with R*. Chapman & Hall/CRC, London.

Foerster, K., Delhey, K., Johnsen, A., Lifjeld, J.T. & Kempenaers, B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* **425**: 714–717.

Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. 2002. A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proc. R. Soc. Lond. B* **269**: 1479–1485.

Freeman-Gallant, C.R., Wheelwright, N.T., Meiklejohn, K.E., States, S.L. & Sollecito, S.V. 2005. Little effect of extrapair paternity on the opportunity for sexual selection in savannah sparrows (*Passerculus sandwichensis*). *Evolution* **59**: 422–430.

Griffith, S.C. 2007. The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. *Am. Nat.* **169**: 274–281.

Griffith, S.C., Owens, I.P.F. & Thuman, K.A. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**: 2195–2212.

Hamilton, W.D. & Zuk, M. 1982. Heritable true fitness and bright birds – a role for parasites. *Science* **218**: 384–387.

Hawley, D.M. 2005. Isolation and characterization of eight microsatellite loci from the house finch (*Carpodacus mexicanus*). *Mol. Ecol. Notes* **5**: 443–445.

Hill, G.E. 1998. An easy, inexpensive means to quantify plumage coloration. *J. Field Ornithol.* **69**: 353–363.

Hill, G.E. 2002. *A Red Bird in a Brown Bag: The Function and Evolution of Colourful Plumage in the House Finch*. Oxford University Press, Oxford.

Hill, G.E. 2006. Female mate choice for ornamental colouration. In: *Bird Colouration*, Vol. II – *Function and Evolution* (G.E. Hill & K. McGraw, eds), pp. 137–200. Harvard University Press, Cambridge, MA.

Hill, G.E. & Farmer, K.L. 2004. Carotenoid-based plumage colouration predicts resistance to a novel parasite in the House Finch. *Naturwissenschaften* **92**: 30–34.

Hill, G.E., Montgomerie, R., Roeder, C. & Boag, P. 1994. Sexual selection and Cuckoldry in a monogamous songbird - implications for sexual selection theory. *Behav. Ecol. Sociobiol.* **35**: 193–199.

Inouye, C.Y., Hill, G.E., Stradi, R.D. & Montgomerie, R. 2001. Carotenoid pigments in male House Finch plumage in relation to age, subspecies, and ornamental colouration. *Auk* **118**: 900–915.

Johnsen, A., Andersson, S., Ornborg, J. & Lifjeld, J.T. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves : *Luscinia s. svecica*): a field experiment. *Proc. R. Soc. Lond. B* **265**: 1313–1318.

Johnsen, A., Lifjeld, J.T. & Krokene, C. 2003. Age-related variation in mate-guarding intensity in the bluethroat (*Luscinia s. svecica*). *Ethology* **109**: 147–158.

Jones, A.G. & Ardren, W.R. 2003. Methods of parentage analysis in natural populations. *Mol. Ecol.* **12**: 2511–2523.

Kalinowski, S.T., Taper, M.L. & Marshall, T.C. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**: 1099–1106.

Kilner, R. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. R. Soc. Lond. B* **264**: 963–968.

Kleven, O., Jacobsen, F., Izadnegahdar, R., Robertson, R.J. & Lifjeld, J.T. 2006. Male tail streamer length predicts fertilization success in the North American barn swallow (*Hirundo rustica erythrogaster*). *Behav. Ecol. Sociobiol.* **59**: 412–418.

Kokko, H. & Morrell, L.J. 2005. Mate guarding, male attractiveness, and paternity under social monogamy. *Behav. Ecol.* **16**: 724–731.

Kraaijeveld, K., Carew, P.J., Billing, T., Adcock, G.J. & Mulder, R.A. 2004. Extra-pair paternity does not result in differential sexual selection in the mutually ornamented black swan (*Cygnus atratus*). *Mol. Ecol.* **13**: 1625–1633.

Liebgold, E.B., Cabe, P.R., Jaeger, R.G. & Leberg, P.L. 2006. Multiple paternity in a salamander with socially monogamous behaviour. *Mol. Ecol.* **15**: 4153–4160.

Macedo, R.H., Karubian, J. & Webster, M.S. 2008. Extrapair paternity and sexual selection in socially monogamous birds: are tropical birds different? *Auk* **125**: 769–777.

Magurran, A.E. 2005. *Evolutionary Ecology: The Trinidadian Guppy*. Oxford University Press, Oxford.

Mays, H.L. & Hill, G.E. 2004. Choosing mates: good genes versus genes that are a good fit. *Trends Ecol. Evol.* **19**: 554–559.

Mays, H.L., Albrecht, T., Liu, M. & Hill, G.E. 2008. Female choice for genetic complementarity in birds: a review. *Genetica* **134**: 147–158.

McGraw, K.J. & Hill, G.E. 2000. Plumage brightness and breeding-season dominance in the House Finch: a negatively correlated handicap? *Condor* **102**: 456–461.

Montgomerie, R. 2006. Analyzing colours. In: *Bird Colouration*, Vol. I – *Mechanisms and Measurement* (G.E. Hill & K. McGraw, eds), pp. 90–147. Harvard University Press, Cambridge, MA.

Oh, K.P. & Badyaev, A.V. 2006. Adaptive genetic complementarity in mate choice coexists with selection for elaborate sexual traits. *Proc. R. Soc. Lond. B* **273**: 1913–1919.

Owens, I.P.F. & Hartley, I.R. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond. B* **265**: 397–407.

Pialek, J. & Albrecht, T. 2005. Choosing mates: complementary versus compatible genes. *Trends Ecol. Evol.* **20**: 63.

Piertney, S.B., Marquiss, M. & Summers, R. 1998. Characterization of tetranucleotide microsatellite markers in the Scottish crossbill (*Loxia scotica*). *Mol. Ecol.* **7**: 1261–1263.

Pitcher, T.E., Dunn, P.O. & Whittingham, L.A. 2005. Sperm competition and the evolution of testes size in birds. *J. Evol. Biol.* **18**: 557–567.

Pizzari, T., Worley, K., Burke, T. & Froman, D.P. 2008. Sperm competition dynamics: ejaculate fertilizing efficiency changes differentially with time. *BMC Evol. Biol.* **8**: 332.

Poiani, A. & Wilks, C. 2000. Sexually transmitted diseases: a possible cost of promiscuity in birds? *Auk* **117**: 1061–1065.

Poláková, R., Vyskocilová, M., Martin, J.F., Mays, H.L., Hill, G.E., Bryja, J. & Albrecht, T. 2007. A multiplex set of microsatellite markers for the Scarlet Rosefinch (*Carpodacus erythrinus*). *Mol. Ecol. Notes* **7**: 1375–1378.

Qvarnstrom, A. 1997. Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proc. R. Soc. Lond. B* **264**: 1225–1231.

Reudink, M.W., Marra, P.P., Boag, P.T. & Ratclife, L.M. 2009. Plumage colouration predicts paternity and polygyny in the American redstart. *Anim. Behav.* **77**: 495–501.

Richardson, D.S. & Burke, T. 1999. Extra-pair paternity in relation to male age in Bullock's orioles. *Mol. Ecol.* **8**: 2115–2126.

Safran, R.J., Neuman, C.R., McGraw, K.J. & Lovette, I.J. 2005. Dynamic paternity allocation as a function of male plumage colour in barn swallows. *Science* **309**: 2210–2212.

Shawkey, M.D., Pillai, S.R., Hill, G.E., Siefferman, L.M. & Roberts, S.R. 2007. Bacteria as agent for change in structural plumage color: correlation and experimental evidence. *Am. Nat.* **169**: S112–S121.

Shuster, S.M. & Wade, M.J. 2003. *Mating Systems and Strategies*. Princeton University Press, Princeton.

Spottiswoode, C. & Møller, A.P. 2004. Extrapair paternity, migration, and breeding synchrony in birds. *Behav. Ecol.* **15**: 41–57.

Stjernberg, T. 1979. Breeding biology and population dynamics of the Scarlet Rosefinch *Carpodacus erythrinus*. *Acta Zool.* **157**: 1–88.

Sundberg, J. & Dixon, A. 1996. Old, colourful male yellowhammers, *Emberiza citrinella*, benefit from extra-pair copulations. *Anim. Behav.* **52**: 113–122.

Suter, S.M., Ermacora, D., Rieille, N. & Meyer, D.R. 2009. A distinct reed bunting dawn song and its relation to extrapair paternity. *Anim. Behav.* **77**: 473–480.

Tremellen, K. 2008. Oxidative stress and male infertility – a clinical perspective. *Hum. Reprod. Update* **14**: 243–258.

Uller, T. & Olsson, M. 2008. Multiple paternity in reptiles: patterns and processes. *Mol. Ecol.* **17**: 2566–2580.

Weatherhead, P.J. & Yezerinac, S.M. 1998. Breeding synchrony and extra-pair mating in birds. *Behav. Ecol. Sociobiol.* **43**: 217–219.

Webster, M.S., Pruett-Jones, S., Westneat, D.F. & Arnold, S.J. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution* **49**: 1147–1157.

Webster, M.S., Tarvin, K.A., Tuttle, E.M. & Pruett-Jones, S. 2007. Promiscuity drives sexual selection in a socially monogamous bird. *Evolution* **61**: 2205–2211.

Westneat, D.F. 2006. No evidence of current sexual selection on sexually dimorphic traits in a bird with high variance in mating success. *Am. Nat.* **167**: E171–E189.

Westneat, D.F. & Stewart, I.R.K. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annu. Rev. Ecol. Evol. Syst.* **34**: 365–396.

Whittingham, L.A. & Dunn, P.O. 2005. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. *Behav. Ecol.* **16**: 138–144.

Wolff, J.O. & Macdonald, D.W. 2004. Promiscuous females protect their offspring. *Trends Ecol. Evol.* **19**: 127–134.

Yezerinac, S.M. & Weatherhead, P.J. 1997. Extra-pair mating, male plumage colouration and sexual selection in yellow warblers (*Dendroica petechia*). *Proc. R. Soc. Lond. B* **264**: 527–532.

Zelano, B. & Edwards, S.V. 2002. A Mhc component to kin recognition and mate choice in birds: predictions, progress, and prospects. *Am. Nat.* **160**: S225–S237.