Immune defence, extra-pair paternity, and sexual selection in birds

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SUMMARY

Secondary sexual characters have been suggested to reliably reflect the ability of individuals to resist debilitating parasites, and females may gain direct or indirect fitness benefits from preferring the most extravagantly ornamented males. Extra-pair paternity provides an estimate of an important component of sexual selection in birds. Species with a high frequency of extra-pair paternity have a variance in realized reproductive success that is greater than the variance in apparent reproductive success, and extra-pair copulations and hence extra-pair paternity by females are often directly associated with the expression of male secondary sexual characters. If sexually dichromatic species have experienced a long period of antagonistic coevolution with their parasites, such species should have evolved larger immune defence organs than sexually monochromatic species. Bird species with sexual dichromatism had larger spleens for their body size than monochromatic species in a comparative analysis. Furthermore, species with a high frequency of extra-pair paternity were sexually dichromatic and had large spleens for their body size. These results are consistent with the hypothesis that females of dichromatic bird species seek extra-pair copulations to obtain indirect fitness benefits in terms of superior resistance of their offspring to virulent parasites.

1. INTRODUCTION

Parasite-mediated sexual selection has been suggested as a functional explanation for the evolution of extravagant secondary sexual characters (Hamilton & Zuk 1982; Møller 1990; Clayton 1991; Zuk 1992). If the most extreme expression of secondary sexual characters is costly in terms of time and energy, only individuals in prime condition not suffering from the debilitating effects of parasites will be able to produce extravagant ornaments. Females may prefer to mate with the brightest parasite-free males because such males are efficient parents, have a low probability of carrying infectious parasites, or carry genes for parasite resistance. Intraspecific evidence for parasite-mediated sexual selection is abundant although the kinds of benefits achieved by choosy females are controversial (reviews in Møller 1990; Clayton 1991; Zuk 1992). Interspecific evidence for parasite-mediated sexual selection is much less clear-cut (Hamilton & Zuk 1982; Møller 1990; Clayton 1991; Zuk 1992), and there are a number of reasons for an absence of apparent effects in comparative analyses. First, the parasite data used for the analyses may not provide reliable estimates of the abundance of virulent parasites currently affecting a group of hosts. Second, the extreme diversity of parasites affecting any metazoan host makes it unlikely that research efforts investigating the relationship between sexual displays and the abundance of any single group of parasites should commonly be successful.

If parasites are a diverse assemblage of species, host

responses to parasitism in general may be measured by means of host defences, such as immune defences (Møller & Erritzøe 1997). Several recent hypotheses suggest that secondary sexual characters may be reliable signals of genetic quality of hosts because the most extravagantly ornamented individuals are able to raise the most efficient immune defences. This could be due to the trade-off between sexual display, androgens and immune defence (Folstad & Karter 1992), or the effect of condition on the expression of both sexual display and immune defence (Møller 1995). Intra-specific studies have demonstrated positive relations between immune defences or experimentally elicited immune responses and the degree of sexual display (Saino *et al.* 1995; Zuk *et al.* 1995; Møller *et al.* 1996; Saino & Møller 1996; von Schantz *et al.* 1996). Comparative evidence from birds also demonstrates that sexually dichromatic species have larger bursa of Fabricius and spleen (immune defence organs that produce antibodies) for their body size than sexually monochromatic bird species (Møller *et al.* 1997). The fact that both bursae of Fabricius and spleens were larger in dichromatic species suggests that the costs of sexual selection appear even before sexual maturity because the bursa disappears completely during the juvenile stage.

The main objective of this paper is to investigate comparatively the relationship between immune defence, extra-pair paternity and sexual dichromatism in birds. I used the frequency of extra-pair paternity as a measure of the current intensity of sexual selection. This assumption is valid because the standardized

variance in apparent male reproductive success during one season (simply estimated from the number of offspring in the nest of a male) was consistently smaller than the standardized variance in realized reproductive success (estimated from the number of offspring sired; Møller 1997). Furthermore, the frequency of extra-pair copulations and extra-pair paternity of male birds is directly related to the degree of exaggeration of secondary sexual characters in a diverse array of bird species (review in Møller 1997). The efficiency of the immune system was estimated from the size of the spleen. I assumed that a larger spleen will be able to produce a better immune response than a smaller one. This is likely as most of the spleen (85 %) is composed of lymphocytes (Rose 1981; Alberts *et al.* 1983; Toivanen & Toivanen 1987; John 1994). The spleen produces lymphocytes responsible for a humoral antibody response and a cell-mediated immune response (Rose 1981; John 1994), and its size reflects the current level of parasite infection and genetic differences among individuals (reviewed in Arvy 1965; Keymer 1982; Molyneux *et al.* 1983; John 1994). The relationships between immune defence, extra-pair paternity and sexual dichromatism were investigated using two comparative methods.

2. MATERIALS AND METHODS

I obtained information on the frequency of extra-pair paternity based on DNA paternity analyses as the proportion of offspring that was sired by males other than the male mated to the female. The sources of this information were mainly reported in Møller & Birkhead (1994) and later primary literature. Information on body mass was obtained from Brough (1983). Volume of the spleen was obtained from J. Erritzøe, a taxidermist who has measured this organ in hundreds of species of birds during the past ten years. We found no evidence of consistent seasonal variation in spleen size across species (P. Christie and A. P. Møller, unpublished data), and individuals were therefore used independent of sampling date. Although sex differences in the size of the spleen have been reported (John 1994), this was not a general finding in our extensive studies of hundreds of species (Møller & Erritzøe 1997; Møller *et al.* 1997). Both sexes were therefore used in the analyses. Information on the composition of species, measurements, reliability and sources of error are discussed fully in Møller & Erritzøe (1997) and Møller *et al.* (1997).

Scores of sexual dichromatism were obtained by providing males and females of the species in question with a score from 1 to 5 (5 being most conspicuous and bright) based on illustrations in field guides. Two independent scorers unaware of the purpose of the study produced highly repeatable scores that were strongly positively correlated. The measure of sexual dichromatism was simply the difference between the mean score for males and females. (See Møller & Birkhead (1994) for further methodological details.) The use of colour differences in the visual spectrum neglects the ability of birds to see in the ultraviolet part of the spectrum. However, there are no cases of bird species being sexually dichromatic in the visual spectrum and monochromatic in the UV spectrum, or vice versa. There is a considerable amount of evidence for sexual selection being related to differences in coloration of male birds in the visible spectrum (review in Andersson 1994), and this is also the case for scores of coloration as those used in the present study (Møller & Birkhead 1994; Møller

Figure 1. Phylogeny of avian species used in the comparative analyses, mainly based on Sibley & Ahlquist (1990).

et al. 1997). Although future studies of UV vision may change our view of sexual selection in birds based on visual signals, this should not prevent us from studying sexual selection based on signals that represent parts of the visible spectrum of birds.

The predictions under test were investigated using two different comparative methods, the independent contrast method and pairwise comparisons between pairs of closely related taxa (Felsenstein 1985; Møller & Birkhead 1992; Purvis & Rambaut 1995). The independent contrast method is based on statistically independent differences for two or more variables at the nodes of a phylogeny. These contrasts are standardized dependent on the model of evolution underlying the phylogenetic hypothesis. I assumed that branch lengths in the phylogeny were related directly to the number of species in a clade (a gradual model of evolution). However, the conclusions were qualitatively similar when based on branches of equal length (a punctuated model of evolution), and only the former results are therefore reported. (See Purvis & Rambaut (1995) for further methodological details.) The phylogeny used in this study is based on those reported by Sibley & Ahlquist (1990), Gill *et al.* (1989) and Winkler & Sheldon (1992) (figure 1). Although this phylogenetic hypothesis is controversial, the use of two different models of evolution in the contrast comparative analyses and of two different comparative methods should render any conclusions derived from the analyses robust.

Extra-pair paternity was square root-arcsine-transformed and body mass and volume of spleen were log₁₀-transformed before analyses. The effect of body mass on the mass of immune defence organs was removed by using residuals from a regression of contrasts of volume of immune defence organs on contrasts of body mass. The relationship between a dependent variable and one or more independent variables was tested in simple or multiple linear regression analyses.

The pairwise comparative method is based on comparisons between pairs of closely related species that differ in the variable in question (the dependent variable; Møller & Birkhead 1992). We found pairs of closely related species using the phylogeny in figure 1. If more than two species were available for comparison, one was chosen randomly. Pairwise comparisons were subsequently made using a paired *t*-test. Pairwise comparisons are powerful because they automatically control for potentially confounding variables as closely related species generally have very similar ecology, physiology, anatomy and evolutionary past. The pairwise comparative method is also less dependent on phylogenetic information than the contrast method because the relationships of closely related species are often less disputed than the relationships of more distantly related taxa. This is certainly the case in birds (Sibley & Ahlquist 1990).

3. RESULTS

The relationship between extra-pair paternity and immune defence was investigated for the spleen. However, large species will, for simple allometry reasons, have larger immune defence organs than small species, and we therefore had to correct the size of immune defence organs for any effects of body size. Contrasts in the volume of the spleen increased with contrasts in body mass ($F = 20.65$, d.f. = 1,25, $r^2 = 0.430$, $p < 0.0001$). Therefore, subsequent analyses were based on residuals from this regression line.

The relative size of the spleen was significantly

Figure 2. Contrasts in extra-pair paternity in relation to relative spleen volume (corrected for body mass) across birds. Values are contrasts calculated by the CAIC package. The regression line has the equation $y = 0.002$ (s.e. = 0.013) $+ 0.371$ (s.e. = 0.099) x .

Table 1. *Relative size of the spleen (residuals from a linear regression of volume on body mass) in relation to sexual dichromatism of pairs of avian sister taxa*

(See figure 1 for phylogeny.)

monochromatic species		dichromatic species	
<i>Branta leucopsis</i>	-0.088	<i>Anas platyrhynchos</i>	-0.071
<i>Larus argentatus</i>	-0.166	<i>Falco tinnunculus</i>	-0.341
<i>Corvus monedula</i>	0.171	<i>Lanius collurio</i>	0.650
<i>Sturnus vulgaris</i>	0.010	<i>Ficedula hypoleuca</i>	0.291
<i>Delichon urbica</i>	-0.224	<i>Hirundo rustica</i>	0.011
<i>Prunella modularis</i>	-0.384	<i>Fringilla coelebs</i>	0.108
<i>Passer montanus</i>	0.064	<i>Passer domesticus</i>	0.197
<i>Junco hyemalis</i>	0.207	<i>Emberiza citrinella</i>	0.235

related to extra-pair paternity, with spleens being relatively larger in species with frequent extra-pair paternity (figure 2; $F = 14.05$, d.f. = 1,25, $r^2 = 0.334$, $p = 0.0009$). Similar conclusions were reached if the size of the spleen was compared for pairs of closely related species that differed in extra-pair paternity (paired *t*-test: $t = 2.29$, d.f. = 9, $p = 0.048$).

The relationship between sexual dichromatism and immune defence was not significant for the spleen when based on analyses of contrasts ($F = 0.84$, d.f. = 1,25, $r^2 = 0.033$, $p = 0.37$). However, in the pairwise analysis, spleen size was significantly larger in dichromatic than in monochromatic species of birds (table 1; paired *t*-test, $t = 2.62$, d.f. = 7, $p = 0.035$). This difference between the results of the pairwise analyses and the contrast analyses arose because of differences in patterns when only using contrasts at the tips of the phylogeny (the pairwise analyses), or when using all contrasts including those at deeper branches of the phylogeny (the contrast analyses).

Sexual dichromatism has previously been shown to be associated with extra-pair paternity (Møller & Birkhead 1994), and the independent effect of size of immune defence organs on extra-pair paternity after controlling for sexual dichromatism showed a highly significant independent effect of both variables, together explaining almost half the variance in extra-pair paternity (table 2).

If secondary sexual characters reliably reflect the ability of individuals of particular species to raise an immune response, relative spleen size should be predicted by extra-pair paternity rather than sexual dichromatism because there is no *a priori* reason to expect sexual dichromatism to covary with the size of immune defence organs after controlling for the intensity of sexual selection. This was, in fact, the case as only extra-pair paternity was a statistically significant predictor of the relative size of the spleen (table 2). This result supports the basic underlying assumption that sexual selection for parasite resistance is mediated through sexual dichromatism.

4. DISCUSSION

A comparative analysis of the covariation between immune defence, extra-pair paternity and sexual selection showed that sexually dichromatic birds, which have high levels of extra-pair paternity (as

Table 2. *Multiple regression models of the relationship between extra-pair paternity (dependent variable) and size of spleen and sexual dichromatism (independent variables), and between relative size of spleen (dependent variable) and extra-pair paternity and sexual dichromatism (independent variables)*

source	d.f.	MS	F	p	b(SE)
extra-pair paternity in relation to immune defence and sexual dichromatism					
model: $F = 12.82$, d.f. = 2,24, $r^2 = 0.476$, $p = 0.0002$					
spleen	1	0.045	13.35	0.0013	0.326(0.089)
dichromatism	1	0.026	7.78	0.0102	0.049(0.018)
residual	24	0.003			
immune defence in relation to extra-pair paternity and sexual dichromatism					
model: $F = 7.30$, d.f. = 2,24, $r^2 = 0.378$, $p = 0.0033$					
extra-pair paternity	1	0.153	13.93	0.0013	1.097(0.300)
dichromatism	1	0.008	0.76	0.406	-0.031(0.037)
residual	25	0.011			

shown in a previous comparative study; Møller & Birkhead 1994), also have relatively large-sized immune defence organs (as shown in another comparative study; Møller *et al.* 1997). The present study demonstrated that immune defence covaried with a measure of current sexual selection, the relative frequency of extra-pair paternity. A recent review has demonstrated that extra-pair paternity in sexually dichromatic species increases the variance in realized male reproductive success as compared to the variance in apparent reproductive success as estimated from the number of offspring in the nests of a male (Møller 1997). There is no such increase in sexually monochromatic species with no or little extra-pair paternity, and the intensity of sexual selection as estimated from extra-pair paternity thus increases with increasing dichromatism. Many studies have also demonstrated a direct link between male secondary sexual characters and success in acquisition of extra-pair copulations and/or extra-pair fertilizations (reviewed in Møller 1997).

Although the present study has supported a direct link between extra-pair paternity, sexual dichromatism and immune defence, the benefits obtained by choosy individuals from their mate choice remain a question for discussion. As the size of the spleen reflects both the current state of infection and genetic differences between species, it is possible that different levels of infection between species may result in a positive association between extra-pair paternity and relative spleen size. This explanation seems highly unlikely because the variance in relative spleen size (based on residuals from a regression of spleen size on body mass) among species was considerably larger than the variance within species (Møller *et al.* 1997). If the size of immune defence organs was determined mainly by exposure to parasites, intraspecific variation should be substantial, with relatively parasite-free hosts having very small spleens and repeatabilities being low. However, consistent differences between pairs of closely related species in relative size of the spleen (Møller & Erritzøe 1997; Møller *et al.* 1997; this study) suggest that the differences in spleen size are mainly caused by adaptations to an evolutionary history of parasite exposure.

Sexual selection may arise from either male-male competition or female choice, and individuals of the

choosy sex, usually females, may obtain direct or indirect fitness benefits from their mate choice (Andersson 1994). Most direct fitness benefits can be excluded when using extra-pair paternity as a component of sexual selection (reviews in Birkhead & Møller 1992; Møller 1997). The only exception is the fertilization function of female extra-pair copulations. However, there is no or little empirical evidence for a role of fertility insurance in extra-pair copulations (Birkhead & Fletcher 1995; Kempenaers *et al.* 1996). Even if ejaculate size or swimming speed of sperm was found to be positively associated with the size of a secondary sexual character, this does not imply that this effect plays any role in fertilization. Such effects will only be important determinants of fertilization when the number and timing of copulations by two males in sperm competition are similar. This suggests that females obtain indirect fitness benefits in terms of parasite resistance from their choice of extra-pair males; an interpretation that also is consistent with increasing evidence of females obtaining indirect fitness gains from extra-pair copulations (reviewed in Møller 1997).

Why should dichromatic bird species have evolved large immune defence organs? There are at least three different explanations for this relationship. First, host-parasite coevolution may be particularly intense in sexually selected species because good genes' sexual selection in hosts continuously selects for improved ability of parasites to exploit their hosts (Hamilton & Zuk 1982). This in turn should increase selection for better immune defences in hosts subject to intense sexual selection (Folstad & Karter 1992; Møller & Saino 1994; Møller 1995; Møller *et al.* 1997). This is the hypothesis traditionally associated with parasite-mediated sexual selection for indirect fitness benefits. Second, if sexual selection results in an increased frequency of horizontal transmission of parasites, because of repeated encounters between the most preferred males and females, this should result in an evolutionary increase in virulence being associated with sexual selection (Møller *et al.* 1997). The increased virulence in host species with frequent horizontal transmission of parasites should result in selection for large immune defence organs independent of the benefits of female choice. Third, secondary sexual characters are considered to be costly to produce and

maintain (Andersson 1994), and sexually selected hosts are therefore assumed to be subject to higher levels of stress than less sexually selected hosts (Parsons 1995; Møller 1996). High stress susceptibility and poor body condition will characterize sexually selected hosts during adverse environmental conditions, and they will therefore be particularly susceptible to the negative effects of parasites and other kinds of environmentally induced stress (Møller 1996). Body condition is a very important determinant of immune defence in a number of different organisms (Chandra & Newberne 1977; Gershwin *et al.* 1985). Sexually selected hosts are thus predicted to have evolved more efficient immune defences to counter the negative effects of high stress-susceptibility.

In conclusion, parasite-mediated sexual selection is an important feature of sexually dichromatic bird species because such species have relatively large spleens and high levels of extra-pair paternity. These patterns of covariation are likely to arise as a consequence of female choice of extra-pair males for indirect fitness benefits.

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APPENDIX

Table A1. *Information on extra-pair paternity, body mass, mass of spleen and sexual dichromatism in birds*

species	extra-pair paternity/%	body mass/g	spleen size /cm ³	sexual dichromatism
<i>Phasianus colchicus</i>	6.0	1100	0.791	4
<i>Branta leucopsis</i>	0.0	1750	1.251	0
<i>Anas platyrhynchos</i>	3.0	1079	0.844	2.5
<i>Apus apus</i>	5.0	25	0.026	0
<i>Accipiter nisus</i>	5.4	190	0.221	1
<i>Falco tinnunculus</i>	1.89	204	0.102	1
<i>Larus argentatus</i>	0.0	1020	0.644	0
<i>Gallinula chloropus</i>	0.0	340	0.619	0
<i>Columba livia</i>	1.0	393	0.256	0
<i>Corvus monedula</i>	0.0	246	0.393	0
<i>Pica pica</i>	5.0	220	0.391	0
<i>Lanius collurio</i>	8.22	29.9	0.180	1.5
<i>Sturnus vulgaris</i>	6.83	80	0.099	0
<i>Ficedula hypoleuca</i>	15.18	12.1	0.035	1.5
<i>Turdus merula</i>	14.0	106	0.254	1
<i>Oenanthe oenanthe</i>	7.58	24	0.028	1.5
<i>Phylloscopus trochilus</i>	0.0	8.8	0.002	0
<i>Riparia riparia</i>	15.7	14.4	0.009	0
<i>Hirundo rustica</i>	23.8	18.6	0.027	1
<i>Delichon urbica</i>	21.7	14.5	0.012	0
<i>Parus major</i>	16.2	18.8	0.025	1
<i>Parus caeruleus</i>	12.7	10.8	0.031	0
<i>Prunella modularis</i>	0.0	20.8	0.012	0
<i>Passer montanus</i>	10.0	22.4	0.036	0
<i>Passer domesticus</i>	12.85	28.2	0.060	1.5
<i>Fringilla coelebs</i>	17.0	22.7	0.039	2
<i>Junco hyemalis</i>	25.0	20.4	0.046	0
<i>Emberiza citrinella</i>	36.6	27.0	0.063	3