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The evolution of song repertoires and immune defence in birds

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Song repertoires (the number of different song types sung by a male) in birds provide males with an advantage in sexual selection because females prefer males with large repertoires, and females may benefit because offspring sired by preferred males have high viability. Furthermore, males with large repertoires suffer less from malarial parasites, indicating that a large repertoire may reflect health status. We hypothesize that sexual selection may cause a coevolutionary increase in parasite virulence and host immune defence because sexual selection increases the risk of multiple infections that select for high virulence. Alternatively, a female mate preference for healthy males will affect the coevolutionary dynamics of host–parasite interactions by selecting for increased virulence and hence high investment by hosts in immune function. In a comparative study of birds, repertoire size and relative size of the spleen, which is an important immune defence organ, were strongly, positively correlated accounting for almost half of the variance. This finding suggests that host–parasite interactions have played an important role in the evolution of song repertoires in birds.

Keywords: immune defence; sexual selection; song; spleen

1. INTRODUCTION

The evolution of bird vocalizations has been studied for more than 200 years, yet it is still poorly understood, with very little interspecific variation explained by ecological factors and hence selection pressures (Read & Weary 1992). This is the more surprising because comparative evidence provides ample evidence for morphological secondary sexual characters being associated with mating skew (Andersson 1994). Hamilton & Zuk (1982) hypothesized that secondary sexual characters have evolved to reveal the health status of males because only males in prime condition are able to produce the most exaggerated traits. Hence, parasite resistance should be associated with sexual display, and this prediction was supported for North American and European passerines using coloration and song complexity as display characters and infection status with haematozoans as health indicators (Hamilton & Zuk 1982). However, subsequent comparative analyses revealed little evidence for the hypothesis that song reflects parasite infection in birds (Read & Weary 1990).

Parasite-mediated sexual selection may account for the evolution of extravagant secondary sexual characters because males infected with parasites generally have less exaggerated displays than healthy males (Møller *et al.* 1999). This association between sexual display and health status is particularly strong if measures of general anti-parasite defence such as immune responses are investigated rather than infection with a particular parasite (Møller *et al.* 1999). Thus, comparative studies of the evolution of vocalizations in relation to parasitism should preferably be based on measures of immune function rather than the prevalence of specific parasites, because general parasite defences have evolved in response to past selection pressures by the entire community of parasites (Møller *et al.* 1998*b*).

We hypothesized that sexual selection may result in an increase in parasite virulence and host immune defence because (i) sexual selection promotes the risk of multiple infections that select for increased virulence (Bull 1994; Frank 1996), and (ii) a female mate preference for healthy males will affect the coevolutionary dynamics of host–parasite interactions by selecting for increased virulence and hence high investment in immune function by hosts (Van Baalen 1998). Thus we predicted a positive, interspecific association between immune function and sexual display. This prediction was tested by investigating the relationship between repertoire size and the relative size of the spleen in birds.

Intraspecific studies of song repertoires (the number of different song types sung by a male) in birds have demonstrated mating advantages to males with large repertoires because females prefer such males (Catchpole *et al.* 1984, 1986; Searcy 1984, 1988; Baker *et al.* 1986; Eens *et al.* 1991), and female great reed warblers *Acrocephalus arundinaceus* benefit because offspring sired by preferred males with large repertoires have high viability (Hasselquist *et al.* 1996). Males with large repertoires may survive better (McGregor *et al.* 1981; Lambrechts & Dhondt 1986) or may have high reproductive success (Catchpole 1980; Yasukawa *et al.* 1980; Hiebert *et al.* 1989), although these studies did not control for the effects of confounding variables such as age. However, Hasselquist *et al.* (1996) showed for the great reed warbler that offspring viability was positively related to paternal repertoire size, even when controlling for age and other potentially confounding variables. Furthermore, barn swallow *Hirundo rustica* males infected with parasites have

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low song rates independent of their age (Møller 1991), and sedge warblers *Acrocephalus schoenobaenus* with malarial infections have small repertoires (Buchanan *et al.* 1999). Males with large repertoires and high song rates also have low leucocyte counts and low concentrations of immunoglobulins (Saino *et al.* 1997; Buchanan *et al.* 1999). Thus, intraspecific studies of birds support the notion that health status is revealed by song features.

2. MATERIAL AND METHODS

(a) *Repertoire data*

Song repertoire size was estimated as the mean number of different song types produced by a male for 38 species of birds. Repertoire size is traditionally estimated using sonagrams and the cumulative number of different songs as more songs are analysed. We included all species for which spleen mass and repertoire size was available, with repertoire size being the limiting variable (we had information on spleen mass for an additional 314 species). Some studies report an infinite number of different songs, and in this case we assigned a value of 100 because the real number certainly is considerably larger. However, the conclusions of the analyses do not change if we assign a larger value to these species. We used the data set in Read & Weary (1992), supplemented with estimates of repertoire size for three other species (Todt 1971; Luschi 1993; Galeotti *et al.* 1997). The data set is given in an electronic appendix which can be found at the Royal Society Web site.

(b) *Spleen data*

The avian spleen is a secondary lymphoid organ that differentiates lymphocytes, which comprise more than 75% of the volume (Rose 1981; Alberts *et al.* 1983; Toivanen & Toivanen 1987; John 1994*a*). Intraspecifically, the size of the spleen is a direct measure of differentiation of lymphocytes and the amount of lymphocytes stored. Interspecifically, relative spleen size is positively correlated with relative levels of infection by haematozoans and helminths in birds (John 1994*b*; R. Poulin and S. Morand, unpublished results). Furthermore, residual spleen mass from a regression of spleen mass on body mass in 13 species of the family Hirundinidae was significantly positively correlated with T- and B-cell-dependent immune responses measured *in vivo* (A. P. Møller and S. Merino, unpublished data). Finally, the relative size of the spleen in different bird species (measured as residuals from a regression of log-transformed spleen mass on log-transformed body mass) was strongly positively correlated with the relative size of the thymus and the bursa of Fabricius, which are primary lymphoid organs responsible for the production of antibodies (A. P. Møller, unpublished data). This suggests that interspecific differences in spleen mass reflect interspecific differences in the importance of efficient humoral and cell-mediated immune responses *in vivo*, but also differences in the production of antibodies as reflected by the positive correlations with the relative size of the bursa and thymus.

We weighed on a micro-balance, to the nearest milligram, the mass of spleens from dead birds brought to J.E. The measurements were done without knowledge of the hypotheses under test and hence blindly with respect to the predictions being tested in this paper. Only adult males were used in this study since it is known that spleen size is reduced in adult relative to juvenile males (Møller *et al.* 1998*a*). The relative size of the spleen measured as residuals from a model I regression of $\log_{10}$-transformed spleen mass on $\log_{10}$-transformed body mass is highly repeatable, with differences among species being highly significant (one-way ANOVA: $F = 19.22$, d.f. $= 162, 835$, $p < 0.001$ (Møller *et al.* 1998*b*)). Hence, variation among species is considerable. A number of potential biases in the data set has been investigated, but found to be unimportant (Møller *et al.* 1998*b*). Information on body mass was obtained for exactly the same individuals. The data are reported in the electronic appendix.

(c) *Confounding variables*

Several variables are known to be related to repertoire size and spleen mass. Read & Weary (1992) reported associations between male parental effort and migration, respectively, and repertoire size. Møller and co-workers (Møller & Erritzøe 1996, 1998; Møller *et al.* 1998*b*) reported the evolution of relatively large spleens in sexually dichromatic species of birds, migratory birds, and hole nesting, and colonially nesting species. We classified all species with respect to these potentially confounding variables (migration: 0 if the breeding and the wintering range of the population in question overlapped, and 1 if there was no overlap; hole nesting: 1 if the species used a cavity or nest box for the nest, and 0 otherwise; coloniality: 1 if more breeding pairs were aggregated in small territories without food, and 0 otherwise) using information from a number of different sources (mainly Cramp & Perrins 1985–1994). The data are given in the electronic appendix.

(d) *Comparative analyses*

Species cannot be considered to be statistically independent observations because similarity of one or more variables may arise from common ancestry rather than convergent evolution. Hence, we used comparative analyses based on statistically independent linear contrasts (Felsenstein 1985). This comparative method is based on the assumption that differences among nodes of a phylogeny for two or more variables can be standardized by the length of branches and hence provide unbiased estimates of the rate of evolution of two or more variables of interest (Purvis & Rambaut 1995). We used the software CAIC for the tests (Purvis & Rambaut 1995), using the Crunch procedure that is well suited for continuous variables. We made the analyses based on the assumption that branch lengths were proportional to the number of species in a clade (a gradual mode of evolution (Purvis & Rambaut 1995)), but analyses based on the use of similar branch lengths (a punctuational mode of evolution (Purvis & Rambaut 1995)) gave very similar results. We used the phylogeny of Sibley & Ahlquist (1990) combined with information from other sources (Sheldon *et al.* 1992; Blondel *et al.* 1996; Leisler *et al.* 1997) to generate a phylogenetic hypothesis for the comparative analysis. The phylogeny is available from the authors upon request. Spleen mass, body mass and repertoire size were $\log_{10}$-transformed to achieve normally distributed variables. All regressions were forced through the origin as recommended for contrast analyses (Purvis & Rambaut 1995). We controlled for potentially confounding variables by using these as dummy variables (Sokal & Rohlf 1995). Residuals from these regressions were used to control both the dependent variable (repertoire size) and the independent variable (spleen mass) for the influence of the potentially confounding variables.

3. RESULTS

Spleen mass was strongly positively related to body mass across the 38 species (linear regression: $F = 68.84$,

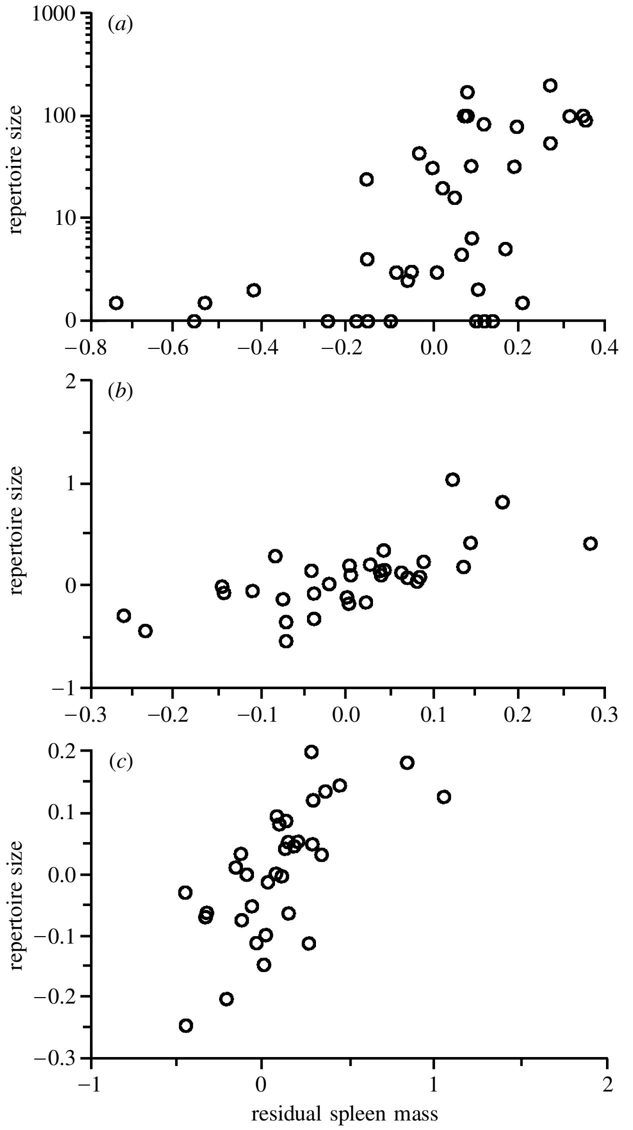

Figure 1. The relationship between repertoire size and relative spleen mass (measured as residuals from a regression of log-transformed spleen mass on log-transformed body mass) in birds, using (*a*) species, (*b*) contrasts and (*c*) residual contrasts, from a multiple regression analysis controlling for potentially confounding variables as data points.

d.f. = 1,36, $r^2 = 0.66$, $p < 0.0001$, slope (s.e.) = 0.99 (0.12)). Repertoire size was positively related to residual spleen mass from the regression of spleen mass on body mass, accounting for a third of the variance (figure 1*a*; linear regression: $F = 17.37$, d.f. = 1,36, $r^2 = 0.33$, $p < 0.0001$, slope (s.e.) = 1.87 (0.45)).

In a comparative analysis based on linear contrasts spleen mass was strongly positively related to body mass (linear regression: $F = 23.24$, d.f. = 1,32, $r^2 = 0.42$, $p < 0.0001$, slope (s.e.) = 1.04 (0.22)). Contrasts in repertoire size were positively related to contrasts in residual spleen mass from the regression of spleen mass on body mass, accounting for almost half of the variance (figure 1*b*; linear regression: $F = 26.18$, d.f. = 1,32, $r^2 = 0.45$, $p < 0.0001$, slope (s.e.) = 2.01 (0.39)).

The effect of potentially confounding variables on the size of the repertoire was assessed. Song repertoire size has been shown to be weakly associated with male parental care and migratory habits at some taxonomic levels, but not at others (Read & Weary 1992). All the species included in the present analysis provision their offspring causing relatively little variation for this confounding variable. However, we found no significant relationship between repertoire size and migration in the present study ($F = 2.02$, d.f. = 1,36, $p = 0.16$). Spleen size has been shown to be larger in sexually dichromatic species, hole nestling species, colonial species and migratory species of birds (Møller & Erritzøe 1996, 1998; Møller *et al.* 1998*b*). However, we found little evidence of these variables confounding the previous analyses (sexual dichromatism and spleen mass: $F = 0.05$, d.f. = 1,36, $p = 0.82$; hole nesting and spleen mass: $F = 0.09$, d.f. = 1,36, $p = 0.76$; coloniality and spleen mass: $F = 0.02$, d.f. = ,36, $p = 0.91$; migration and spleen mass: $F = 0.14$, d.f. = 1,36, $p = 0.71$). A linear regression analysis of residual repertoire size after correcting for migratory habits on residual spleen mass after correcting for sexual dichromatism, hole nesting, colonial nesting and migration, revealed similar conclusions to those in the simple regressions (figure 1*c*; linear regression: $F = 19.63$, d.f. = 1,36, $r^2 = 0.35$, $p < 0.0001$, slope (s.e.) = 1.91 (0.43); linear regression based on contrasts: $F = 29.25$, d.f. = 1,31, $r^2 = 0.49$, $p < 0.0001$, slope (s.e.) = 2.11 (0.39)).

4. DISCUSSION

In a comparative study of birds, repertoire size and relative size of the spleen, which is an important secondary lymphoid organ, were strongly, positively correlated (figure 1*a*), accounting for almost one-third of the variance among species. The conclusion was similar when the analyses were based on linear contrasts as statistically independent observations (figure 1*b*). Furthermore, a number of potentially confounding factors associated with the evolution of large repertoires or the evolution of large spleens did not affect these results (figure 1*c*). This conclusion suggests that host–parasite interactions have played an important role in the evolution of song repertoires in birds.

Comparative analyses are based on the assumption that observations representing a particular variable are similar in kind. This well-known 'comparability problem' (Kroodsma 1982) may arise from slight differences in definitions and/or measurement of variables. Obviously, any heterogeneity in the data set caused by this effect will render the findings conservative.

Comparative analyses of repertoire size have provided relatively little evidence of ecological factors accounting for large repertoires (Read & Weary 1992). Male parental effort during nestling rearing is weakly associated with large repertoires, and migratory birds also tend to have large repertoires (Read & Weary 1992). However, this was not the case for the species included in the present analyses. Similarly, several ecological factors have selected for increased investment in immune function, mainly via their effects on parasite virulence. These include enhanced opportunities for multiple infections in bird species reusing nest sites (hole nesters and colonially breeding birds (Møller & Erritzøe 1996)), migratory birds encountering several parasite faunas while residents only encounter one

(Møller & Erritzøe 1998), and sexual dichromatism being associated with increased investment in immune function (Møller *et al.* 1998*b*). Again, these variables were only weakly correlated with residual spleen mass in the present study, and a multiple regression controlling for these potentially confounding variables still revealed a strong, positive association between repertoire size and residual spleen mass (figure 1*c*).

Repertoires are costly at least in terms of brain space use. Bird song is associated with an increase in the number of neurons and greater synaptic and dendritic development in the higher vocal centre of the brain (Nottebohm *et al.* 1981, 1986; Canady *et al.* 1984). Annual cycles in the size of the higher vocal centre and the robust nucleus of the archistriatum used for song production suggest that the maintenance of these structures is costly in terms of brain space and/or energy (Nottebohm *et al.* 1986). Since the size of the higher vocal centre is positively related to repertoire size in interspecific studies of birds (DeVoogd *et al.* 1993; Székely *et al.* 1996), this implies that the magnitude of the cost increases with repertoire size. Repertoire size may be mechanistically linked to immune defence through the effects of parasitism and disease on song learning (see also Catchpole 1996). Several studies of rodents and humans have demonstrated impaired discrimination learning and spatial and non-spatial cognitive performance by individuals suffering from a range of parasitaemias, and parasitism may thus lead to a reduction in repertoire size (Kershaw *et al.* 1959; Stretch *et al.* 1960; Olson & Rose 1966; Dolinsky *et al.* 1981; Kvalsvik 1988; Kvalsvik *et al.* 1991; Nokes *et al.* 1992; Kavaliers *et al.* 1995). Given that discriminatory ability may be affected by disease status (Kershaw *et al.* 1959; Stretch *et al.* 1960; Olson & Rose 1966; Dolinsky *et al.* 1981; Kvalsvik 1988; Kvalsvik *et al.* 1991; Nokes *et al.* 1992; Kavaliers *et al.* 1995), it is possible that even the mate choice of females is affected by parasites.

The evolution of virulence is intricately associated with within-host and among-host dynamics (Bull 1994; Frank 1996). Sexual selection through sperm competition and the associated multiple matings by females gives rise to multiple contacts among hosts, and any directly transmitted parasite may thus change its levels of virulence in response to such altered transmission patterns (Van Baalen 1998). The predictions of the present study are based on the assumption that sexual selection in hosts is associated with an increase in parasite virulence. Although no specific tests of this prediction are available, previous comparative analyses of immune function and sexual selection in birds have also found an increased investment in immune function with increased intensity of sexual selection (Møller 1997; Møller *et al.* 1998*b*). Hence, the patterns described here may be of a general nature.

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