

REPORT

No evidence that sexual selection is an ‘engine of speciation’ in birds

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Abstract

Sexual selection has been implicated as having a role in promoting speciation, as it should increase the rate of evolution of reproductive isolation, and there is some comparative evidence that sexual selection may be related to imbalances in clade size seen in resolved phylogenies. By employing a new comparative method we are able to investigate the role of sexual selection in explaining the patterns of species richness across birds. We used data for testes size as an index of post-mating sexual selection, and sexual size dimorphism and sexual dichromatism as indices of pre-mating sexual selection. These measures were obtained for 1031 species representing 467 genera. None of the variables investigated explained the patterns of species richness. As sexual selection may also increase extinction rates, the net effect on species richness in any given clade will depend on the balancing effects of sexual selection upon speciation and extinction rates. We suggest that variance across clades in this balance may have resulted in the lack of a relationship between species richness and sexual selection seen in birds.

Keywords

Species richness, sexual conflict, sexual selection, testes size, dichromatism, dimorphism, MacroCAIC.

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INTRODUCTION

Darwin (1859) first recognized the potential role for natural selection in providing a mechanism of speciation in adaptive radiations. A wealth of empirical evidence demonstrating how populations may diverge ecologically through natural selection, and subsequently reproductively, has since accumulated (see Schluter 2000). One of the suggested selective forces that may facilitate speciation, via the prezygotic isolation of either allopatric or sympatric populations, is sexual selection (West-Eberhard 1983; Turner & Burrows 1995; Payne & Krakauer 1997; Price 1998; Higashi *et al.* 1999; reviewed by Turelli *et al.* 2001; Kirkpatrick & Ravigné 2002). Related to this is the suggestion that sexual conflict should promote speciation (Rice 1996, 1998; Rice & Holland 1997; Parker & Partridge 1998; Gavrillets 2000; Gavrillets *et al.* 2001).

There are few empirical studies which support the hypotheses that sexual selection or sexual conflict has a direct role in speciation (Rice & Hostert 1993), but a number of comparative studies are broadly supportive. Among birds for instance, species richness has been

found to covary positively not only with mating system (Mitra *et al.* 1996) and sexual dimorphism (Barraclough *et al.* 1995; Møller & Cuervo 1998; Owens *et al.* 1999); but also with various ecological factors (Owens *et al.* 1999; Hawkins & Porter 2001). In plants, the length of sexually selected floral nectar spurs of *Aquilegia* species was found to be related to subspecific diversity (Hodges & Arnold 1995). Arnqvist *et al.* (2000) found evidence that polyandrous clades of insects were more speciose than their monandrous sister clades, which was attributed to the effect of post-mating sexual conflict. Species richness in Syrphid hoverflies was found to be positively correlated with two hypothetical indices of sperm competition intensity (spermathecal width and testes length) (Katzourakis *et al.* 2001). However, most recently a large comparative study of mammals (480 genera), butterflies (105 genera) and spiders (148 genera) found no evidence that sexual selection influences patterns of clade richness (Gage *et al.* 2002).

The majority of these comparative studies have examined sister clades in order to determine whether differences in species number between these clades is attributable to variation in the intensity of sexual selection. This approach

has advantages (Barracough *et al.* 1998) and disadvantages (see Harvey & Pagel 1991; Panhuis *et al.* 2001 for discussions). An alternative comparative method, that is both powerful and well-established, is to examine the relationship between phylogenetically independent contrasts (Felsenstein 1985; Pagel 1992). This method attempts to control for the possible confounding effects of shared phylogenetic history by comparing species and nodes that share a common ancestry. However, unlike other continuous characters, measures of species richness at these nodes within the phylogeny cannot be calculated as a mean of the associated higher nodes. Instead, species richness at each node must be calculated from the sum of the higher nodes (for details see Agapow & Isaac 2002; Isaac *et al.* in press). Several papers have now employed this method when searching for correlates of species richness (Gittleman & Purvis 1998; Desdevises *et al.* 2001; Orme *et al.* 2002a, b) including two studies investigating the role of sexual selection in explaining patterns of speciosity (Katzourakis *et al.* 2001; Gage *et al.* 2002).

As sexual selection and sexual conflict are predicted to lead to more frequent speciation events, then genera that have experienced higher intensities of sexual selection or conflict should be more species rich. Birds are an ideal taxa with which to test these hypotheses as they are monophyletic (Sibley & Ahlquist 1990) and as data are available for indices of sexual selection such as testes size, sexual size dimorphism and sexual dichromatism for a great number of species.

We use relative testes size as a measure of the intensity of post-mating sexual selection (Parker 1998; Hosken & Ward 2001), because this trait is widely accepted to be a reliable predictor of the rate of extra-pair paternity and as such the intensity or risk of sperm competition (Møller & Briskie 1995). We also use two measures of pre-mating sexual selection – sexual size dimorphism and sexual dichromatism (Dunn *et al.* 2001). Using these indicators of pre- and post-mating sexual selection we are able to test the predictions made by current theories that as the intensity of sexual selection or sexual conflict increases so does the frequency of speciation events.

MATERIALS AND METHODS

Sexual size dimorphism

Data on total body mass was obtained from museum specimens (see Acknowledgements) and from the literature (Ridgeway 1901–1946; Cramp & Simmons 1977, 1980 & 1983; Cramp 1985, 1988 & 1992; Cramp & Perrins 1993, 1994a & 1994b). Where the literature reported a range of body masses for each sex, midpoints of these ranges were used. Dimorphism in size was then calculated from residuals

of a regression between \log_{10} male body mass and \log_{10} female body mass. Dimorphism is known to vary geographically within the range of a species (e.g. Mayr 1942) and we thus attempted to use data from the same location where possible. The mean dimorphism for each genus was then calculated from these species values.

Sexual dichromatism

Plumage dichromatism was scored on a scale from 0 (monomorphic) to 10 (maximum dichromatism) following Owens & Bennett (1994). For each species, the difference in plumage between the sexes was scored over five regions of the body (head, nape-back-rump, throat-belly, tail and wings) using three scores (0, no difference between the sexes; 1, difference in shade or intensity; 2, difference in colour or pattern). Average dichromatism was then obtained for each species from the scores of two observers. The mean dichromatism for each genus was then calculated from these species values.

Testes mass

Testes mass for each species was obtained from published compilations (Møller 1991; Møller & Briskie 1995; Stutchbury & Morton 1995; Dunn *et al.* 2001) or from museum specimen tags (see Acknowledgements), which consisted of testis length and width measurements for fresh material. Testes mass was estimated from these measurements using Møller's (1991) corrected formula: testis mass (g) = $2 \times 1.087 \text{ g cm}^{-3} 1.33\pi[a(\text{cm})]^2 b(\text{cm})$, where a and b are the width and length of each testis (see also Møller & Briskie 1995). In cases where more than one estimate was available for the same species we used the average of available estimates. Testes mass was calculated as the mean testes value from at least 10 breeding males, and up to 2500 in some cases (e.g. Møller 1991; Møller & Briskie 1995). As a result of extreme seasonal variation in testes size (Murton & Westwood 1977; Wingfield 1984), testis size was recorded for adult specimens that were in breeding condition or collected during the appropriate breeding season (see Dunn *et al.* 2001, for details). Mean testes mass for each genus was then calculated from these species values.

Species richness

The numbers of species within each genus were obtained from Sibley & Monroe (1990).

Comparative methods

Phylogenetic relationships, together with estimates of branch lengths, were obtained from Sibley & Ahlquist

(1990). Although this phylogeny has been criticized (see for example Barker *et al.* 2002) it has been validated by several independent data sets (Sibley 1994) and is the most widely used working hypothesis of the true phylogeny of birds. The effects of phylogenetic inertia were controlled for using MacroCAIC (Agapow & Isaac 2002), which is based on CAIC (Purvis & Rambaut 1995) and also implements the comparative method developed by Pagel (1992) and Felsenstein (1985). MacroCAIC is available as a Macintosh binary executable from <http://www.bio.ic.ac.uk/evolve/software/macrocaic/index.html> (examples in Gittleman & Purvis 1998; Desdevises *et al.* 2001; Katzourakis *et al.* 2001; Gage *et al.* 2002). Species richness cannot be treated as other continuous variables are, because the species richness at any particular node in a phylogeny is not calculated from the mean of the richness of the higher nodes, but is the sum of the richness of these higher nodes (Agapow & Isaac 2002). MacroCAIC produces a phylogenetically independent measure of species richness [relative rate difference (RRD)] that is calculated as the natural logarithm of the species richness of the clade with the largest value of X (the value of the contrasted independent character) divided by the species richness of the contrasted clade. Thus, when this ratio is smaller than 1 (negative natural logarithm) the clade with the lowest value of the trait has more species, conversely when this ratio is greater than 1 (positive natural logarithm) the clade with the largest value of the trait has more species. The RRD is therefore assumed to evolve at a constant rate (following a Markovian model), an assumption which we checked in our data by examining the relationship between RRD and clade size for each predictor variable. All these indicated equal variance in RRD as clade size varied. The RRD can be examined in two ways. First, a one-sample t -test may be employed to compare the mean value of RRD against the null hypothesis that this ratio will not differ from 1 (as $\ln 1$ is 0). Secondly, RRD at each node may be regressed against standardized contrasts of any traits examined (here: dimorphism, dichromatism and testes size). Such regressions are forced through the origin following Garland *et al.* (1992).

RESULTS

There were 1031 species, representing 467 genera, for which data on testes size and dichromatism were available. This data represents just over 10% of extant species of birds and over 20% of all extant bird genera. A total of 4240 species were included in the count of species richness within these 467 genera, representing just under 44% of the world's bird fauna. However, the number of contrasts generated by MacroCAIC is reduced from the number of clades for which data are available because of polytomies or unresolved parts of the phylogeny.

Species richness varied greatly across genera and the distribution of species across all genera included in this study was strongly non-random – the observed distribution of species was significantly different from a Poisson distribution ($\chi^2 = 5657.1$, d.f. = 2, $P < 0.001$). This distribution was found to be very similar to that found for the number of species per family (Owens *et al.* 1999), with many more species-rich and species-poor genera than expected by chance. Eighty-five genera were monospecific whereas the genus *Nectarinia* included 79 different species. However, there was no significant difference from zero in the species richness (calculated as RRD) over all nodes when contrasts in either size dimorphism, sexual dichromatism or residual testes size were examined (Table 1).

Furthermore, regression analyses revealed that none of the three estimates of sexual selection intensity showed a significant association with species richness (Table 2). However, because of the non-normal distribution of the predictor variables (dimorphism, dichromatism and testes size) the assumptions of a linear regression were violated. It was also not possible to normalize these distributions with any of the transformations attempted and so the regressions were randomized following Manly (1991) using PopTools, a Microsoft Excel Addin available from <http://www.cse.csiro.au/CDG/poptools> (Version 2.3). This follows a random pairing of x and y -values from the data set from which a new regression coefficient is calculated. This was reiterated 9999 times, to obtain a normal random distribution of regression

Table 1 The t -tests examining whether species richness, measured as relative rate difference (RRD), at all nodes differed from 0 for the three measures of sexual selection (n = number of contrasts. This varies across tests as data could not be obtained for character from all genera)

| Character | n | t | P -value |
|--------------|-----|-------|------------|
| Dimorphism | 133 | -0.31 | 0.8 |
| Dichromatism | 180 | 1.25 | 0.2 |
| Testes size | 178 | 0.35 | 0.7 |

Table 2 Estimates of the slopes (\pm SE) in regressions, forced through the origin, of species richness [relative rate difference (RRD)] on the three estimates of sexual selection. Given are also the 95% confidence intervals of t from a randomization test of $H_0: \beta = 0$

| Character | b | t | 95% CI of t | P -value |
|--------------|--------------|-------|---------------|------------|
| Dimorphism | -5.40 (6.82) | -0.79 | -2.15 to 1.87 | 0.27 |
| Dichromatism | -0.20 (0.47) | -0.43 | -1.28 to 2.64 | 0.14 |
| Testes size | 0.36 (0.96) | 0.38 | -1.80 to 2.18 | 0.57 |

coefficients and their associated t (the constant being excluded from the model). None of the t -statistics from the original regressions obtained for testes size, dimorphism and dichromatism fell outside the corresponding 95% CI of t from these randomized regressions (Manly 1991) (Table 2). All the above analyses were also performed using family level data (rather than genus), but in no case did these analyses yield results which were qualitatively different from those above in terms of our ability or inability to reject null hypotheses.

DISCUSSION

Species richness varies considerably across the 467 genera included in this study. However, it is clear that none of our measures of pre- or post-mating sexual selection explained any of the variation in species richness. This result is likely to be robust given the substantial size of our dataset and the power of the comparative method employed. There is also no reason to suppose that any of our three measures of sexual selection are inherently unreliable.

Verbal and mathematical theories addressing how sexual selection may promote speciation abound (reviewed by Turelli *et al.* 2001; Kirkpatrick & Ravigné 2002). Recent interest in sexual conflict has also generated a clutch of theoretical papers showing the strong potential for sexually antagonistic coevolution to be an 'engine of speciation' (Parker & Partridge 1998; Rice 1998; Gavrillets 2000; Gavrillets *et al.* 2001). All these theories predict a positive relationship between the intensity of either pre- or post-mating sexual selection and the richness of species within clades.

Our results do not match the theoretical predictions or most of the several previous comparative studies that have examined patterns of species richness among birds. All these former studies used a different methodology (sister group comparison) on smaller data sets. The first attempt to investigate how sexual selection influenced patterns of speciation in birds was carried out by Barraclough *et al.* (1995). They found a positive association between clade richness variation and an estimate of sexual dichromatism (estimated using the method we adopted here) in 20 sister tribes (the taxonomic level slightly higher than genera) of passerine birds. However, Price (1998) subsequently found, using a subset of the same data used by Barraclough *et al.* (1995), that there was no evidence for greater numbers of sympatric species in clades that were more dichromatic. Mitra *et al.* (1996) also claimed a positive association between their measure of sexual selection (social mating system) and clade richness, using 14 sister taxa. But their results were somewhat equivocal, as the statistical significance of the result depended solely upon the inclusion or exclusion of a single species. More recently, Møller &

Cuervo (1998) again attempted to test the hypothesis that sexual selection promoted speciation. In addition, using sister group comparisons ($n = 68$ pairs), species richness was found to be greater in ornamented genera relative to non-ornamented genera. Finally, Owens *et al.* (1999) examined which of the six competing hypotheses best fitted patterns of species diversity across 28 unambiguous sister taxa. Increases in species diversity were found to correlate with dispersal potential, range size and fragmentation, together with sexual dichromatism. However, they found no significant association between mating system or size dimorphism and species richness.

As already mentioned, all previous studies used comparisons between sister taxa in relation to various correlates of sexual selection. However, designating as to which groups are true sister groups is not without problems (an exception being Owens *et al.* 1999). The method we have employed here (phylogenetically independent contrasts) is potentially more powerful because it uses information from as many taxa for which there is data available, and incorporates the full phylogeny. To our knowledge there have been three studies that have looked for a relationship between species richness and sexual selection in animals other than birds: insects (Arnqvist *et al.* 2000), hoverflies (Katzourakis *et al.* 2001), and mammals, butterflies and spiders (Gage *et al.* 2002). The first two studies found positive relationships, in agreement with theories of speciation via sexual selection, whereas the last (examining three separate taxa) found no evidence of a relationship.

We suggest that our analysis is more powerful and more representative of the variation in the parameters investigated when compared with previous sister group analyses in birds. The lack of a positive relationship between sexual selection intensity and speciosity in our analyses could, of course, reflect a true absence of any promoting effect of sexual selection on speciation. However, we consider this unlikely. Instead, we suggest that the lack of a relationship may be the result of a simultaneous increase in the rate of extinction. All models and forms of sexual selection predict that both sexes, in one way or the other, become more or less maladapted as they accumulate traits which are costly in terms of natural selection (Andersson 1994), even if certain sexual selection processes may increase the rate of fixation of various beneficial alleles (Whitlock 2000). This sexual selection 'load' increases the risk of extinction in theory (Dawkins & Krebs 1979; Tanaka 1996), and at least some support for this suggestion comes from three different sources. First, comparative studies of birds have shown that survival rates of males are lower in sexually dimorphic species compared with sexually monomorphic species (Promislow *et al.* 1992; Promislow *et al.* 1994). Secondly, artificial selection experiments in insects have directly demonstrated that absolute fitness increases when sexual

selection is relaxed or removed (Holland & Rice 1999; Pitnick *et al.* 2001). Thirdly, a number of introductions of bird species to islands have shown that extinction rates are higher for sexually dimorphic compared with sexually monomorphic species (McLain *et al.* 1995, 1999; Sorci *et al.* 1998). Thus, sexual selection may be a double-edged process: while increasing the rate of evolution of reproductive isolation, it could also increase the probability of extinction in diverging lineages by lowering absolute fitness (see also Møller 2000). The net effect of sexual selection on extant species richness is thus unclear, because this is a product of both speciation and extinction events, and the promoting effect of sexual selection on speciation found in some comparative studies should thus be seen as a minimum estimate of this promoting effect (Arnqvist *et al.* 2000). Therefore, comparative tests of the hypothesis that sexual selection increase the likelihood of extinction are clearly needed.

Given the possible opposing effects of sexual selection on speciation and extinction, we suggest that predictions regarding the correlation between species richness and indices of sexual selection (see Panhuis *et al.* 2001 and above) may have to be revised. The net effects of sexual selection on species richness may actually vary greatly from clade to clade, depending on its relative roles in speciation and extinction in the past. The fact that we failed to find an overall correlation in birds may reflect a pattern where sexual selection is indeed positively related to net species richness in some clades, but negatively related in some and not at all in others. Understanding how and why the relative roles of sexual selection in elevating extinction and speciation rates vary across clades will pose a real challenge in the future.

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