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Does sexual selection influence population trends in European birds?

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ABSTRACT

Sexual selection may interact with anthropogenic impact and influence the population dynamics of bird species. First, there may be a trade-off between investment in traits under sexual selection and traits under natural selection. Thus, sexual selection may impede the response of species to anthropogenic changes of the natural selection regime within habitats. Second, sexual selection may reduce the effective population size. Thus, sexual selection may increase the risk of local extinction due to anthropogenic habitat fragmentation. We tested both hypotheses for Central European non-Passeriformes. We inferred sexual selection from sexual dimorphism of plumage and body size. These two surrogates of sexual selection were not correlated. We found no difference in the population trends between monomorphic and dimorphic species. Furthermore, we found no clear interaction between population size and the effect of dimorphism on population trends. We conclude that sexual selection had no negative effect on population trends.

Keywords: conservation, dimorphism, global change, macroecology, natural selection.

INTRODUCTION

Darwin (1871) appreciated the importance of sexual selection for the evolution of biodiversity. But sexual selection might also be a handicap (Fisher, 1930; Andersson, 1994). First, sexually selected organisms have to invest energy into traits which are advantageous during competition for partners. This energy is thus not available for investment in other traits. Some of these sexually selected traits are even disadvantageous under natural selection (Møller and Hedenstrom, 1999). This results in a trade-off between investment in traits under sexual selection and traits under natural selection (e.g. Fisher, 1930; Møller, 1989; for a review, see Andersson, 1994). Hence, if the regime of natural selection changes, species under strong sexual selection can invest less energy in their response to these changes than other species (McLain, 1993). Second, sexual selection reduces the effective size of a

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population, because parts of the population (usually males) do not contribute to reproduction (Møller and Birkhead, 1994). This increases the risk of extinction in small local populations (Foose *et al.*, 1995; Sorci *et al.*, 1998). Overall, sexual selection should have a negative effect on the abundance and distribution of species, in particular during environmental change and when local populations are small.

Sexual selection, however, is not necessarily always a handicap. First, sexual selection may reinforce natural selection if sexually selected traits signal the fitness of an individual (Møller *et al.*, 1998; Proulx, 1999; Katiaho, 2000), for example resistance to parasites (Hamilton and Zuk, 1982; but see Read and Harvey, 1989; Kurtz and Sauer, 1999). Second, sexually selected traits may facilitate communication between the sexes and thereby harmonize their reproductive efforts (Price, 1998). Third, sexual selection may reduce gene flow and thereby promote local adaptation (Owens *et al.*, 1999; but see Price, 1998).

Few studies have explored the relationship between sexual selection and the abundance or distribution of species. Badyaev and Ghalambor (1998) tested the hypothesis that sexual selection reduces a species' flexibility to cope with environmental changes associated with altitude. Sexually selected species should show a more limited altitudinal range than other species. However, for Cardueline finches, it was shown that species that are supposed to be under sexual selection (dimorphic species) occupy a wider altitudinal range than monomorphic species. But the pattern was more complicated. Dimorphic species occurred predominantly at low to intermediate altitudes (Badyaev, 1997), thereby avoiding the harsh environmental conditions at high altitudes. Three studies have tested the hypothesis that sexual selection increases the risk of extinction in small populations. Sorci *et al.* (1998) and McLain *et al.* (1995) analysed the success of introductions of temperate bird species to tropical islands. McLain and Vives (1998) studied the occurrence of beetle species on small tropical cays. All three studies found some support for the hypothesis.

In recent decades, humans have changed dramatically the natural selection regime within habitats (Noss and Csuti, 1997). As noted above, sexually selected species may have been less flexible to these changes than other species due to the trade-off between traits under sexual selection and traits under natural selection. Thus, we hypothesize that sexually selected species suffered more, or profited less, from anthropogenic changes than other species. We call this the 'trade-off hypothesis'. Humans have also dramatically changed the availability of habitats. Humans have decreased the size and increased the isolation of most natural habitats (Noss and Csuti, 1997). Such habitat fragmentation increases the risk of local extinctions, and species with a small total population size have a low probability of re-colonizing abandoned fragments (Hanski, 1999). Sexually selected species in particular may have suffered from this habitat fragmentation, as sexual selection also decreases the effective size of local populations. Thus, we hypothesize that, among species with a small total population size, sexually selected species have suffered more from anthropogenic habitat fragmentation than other species. We call this the 'effective population-size hypothesis'.

We test these two hypotheses about the effects of sexual selection by analysing large-scale population trends. Such trends reflect changes in the size of local populations and the frequency of local extinctions (Brown, 1995). We used published information on Central European birds (Bauer and Berthold, 1996). The 'trade-off hypothesis' predicts that population trends of sexually selected species are more negative or less positive compared with other species. The 'effective population-size hypothesis' predicts that the smaller the total population size, the more negative the impact of sexual selection on population trends.

MATERIAL AND METHODS

Surrogates of sexual selection

To infer sexual selection, we used plumage dimorphism (e.g. Lyon and Montgomerie, 1985; Scott and Clutton-Brock, 1990; for a review, see Andersson 1994) and body size dimorphism (males are larger than females; McLain and Vives, 1998; Székely *et al.*, 2000). We restricted our analysis to the non-Passeriformes. In Passeriformes, sexual selection often acts via acoustics rather than dimorphism in morphology (see Møller *et al.*, 2000).

We determined the presence or absence of sexual dimorphism in plumage from Bezzel (1985; with additional reference to Svensson *et al.*, 1999) and coded the results into a binary variable (McLain *et al.*, 1995; Sorci *et al.*, 1998). We also compiled a more detailed ranking of plumage dimorphism adopting the procedure of Badyaev and Ghalambor (1998). Because the two approaches provide similar results, we only report the results based on the binary variable. We believe using a binary variable is the most robust way of assessing plumage dimorphism. First, differences in plumage between males and females can result from qualitative as well as quantitative biochemical differences (Owens and Hartley, 1988; Kimball and Ligon, 1999); thus, there is no simple correlation between the amount of dimorphism and associated costs (Andersson, 1994). Second, the human eye may be a poor guide to the perception of plumage colours by a bird's eye (Burkhardt, 1989; Andersson, 1994).

We calculated body size dimorphism as male weight minus female weight divided by the average weight. This scales the difference between the sexes by their average, which permits a comparison of sexual dimorphism across a wide range of body weights. Body weights were taken from Bezzel (1985). When a range was reported, we used the midpoint.

Species traits

The population trend of a species is the outcome of many factors. In addition to sexual dimorphism, we considered three traits that have been suggested to be important in predicting population decline in birds (Bezzel, 1993; Bauer and Berthold, 1996; Böhning-Gaese and Bauer, 1996). First, we considered body size as it is correlated to many other life-history traits that affect population dynamics (Peters, 1983; Bezzel, 1993; Blackburn *et al.*, 1996). Body size was calculated as the average of maximum and minimum weights reported by Bezzel (1985). Before all analyses, body size was $\log_e$-transformed. Second, we analysed diet. We ranked species from primary consumers to top predators: 1 = mainly plants; 2 = plants + invertebrates; 3 = mainly invertebrates; 4 = mainly vertebrates. During our analyses, we treated this index of trophic position as a continuous variable. Third, we considered migratory behaviour using the information compiled by Bezzel (1985): 0 = residents; 1 = some populations migrate, while others are resident; 2 = short-distance migrants, which winter north of the Sahara; 3 = intermediate-distance migrants, which show a migratory behaviour between 2 and 4; 4 = long-distance migrants, which winter south of the Sahara. We treated this index of migratory behaviour as a continuous variable. Using ranks as continuous variables introduces some error into the statistical analysis. But there was no ambiguity in the results of our analyses. The effects of diet and migratory status were either clearly significant or clearly non-significant.

Population trends may also depend on a species' habitat use, because species with different habitat requirements show different responses to human impact (Bauer and Berthold, 1996). However, it is difficult to code habitat use across all Central European species in a meaningful way. In part, however, we account for the effect of habitat in our analysis by applying phylogenetically independent contrasts (see below). Most of these contrasts are calculated between closely related species; that is, species which use similar habitats in a similar way (for example, herons or diving ducks).

Population trends and population sizes

To quantify population trends of non-Passeriforme bird species, we used the ranking across 11 Central European countries (Austria, Belgium, Czech Republic, Germany, Hungary, Liechtenstein, Luxembourg, Netherlands, Poland, Slovakia, Switzerland) compiled by Bauer and Berthold (1996). For each country, these authors ranked the population trend on a scale from +2 to −2: increase in population size of >50% from 1970 to 1995 = +2; new establishment or increase of 20–50% during this period = +1; stable = 0; decline of 20–50% = −1; decline of >50% = −2. We found that the 162 non-Passeriforme species listed in Bauer and Berthold (1996) showed similar trends across countries: the average Spearman rank correlation between countries was 0.47 (55 correlations across 36–140 species). For each species, we calculated the average trend across all countries weighted by the population size in the respective countries (from Bauer and Berthold, 1996).

To quantify total population size of the species across Central Europe, we summed population sizes across countries. For all our analyses, we $\log_e$-transformed total population size.

Analysis

Our analysis proceeded along two lines. First, we used species as independent data points. Second, we calculated phylogenetically independent contrasts to control the analysis for phylogenetic relatedness among species and thus reduce the risk of phylogenetic bias (Burt, 1989; see also Kimball and Ligon, 1999). Using CAIC (Purvis and Rambaut, 1995; see below) we calculated contrasts across the hypothesized phylogeny of Sibley and Ahlquist (1990). Several authors have noted that the branch lengths reported by Sibley and Ahlquist (1990) may be imprecise or inconsistent (Sarich *et al.*, 1989; Harshman, 1994). Additionally, branch lengths have little impact on the results of analyses based on phylogenetically independent contrasts (Blackburn *et al.*, 1996). Hence, we set all branches to an equal length.

As a check of the performance of phylogenetically independent contrasts, the absolute value of a contrast should be independent of (1) the ancestral value at the phylogenetic node below that contrast (Freckleton, 2000) and (2) the square root of the expected variance of the unstandardized contrast (Purvis and Rambaut, 1995). To guarantee this, we transformed body-size dimorphism ($\log_e$), diet (x^2) and population trend ($x^{1.5}$). For consistency, we applied the same transformations when we used species as independent data points.

For univariate and multivariate tests of body-size dimorphism, we used the phylogenetically independent contrasts as implemented in CAIC's option 'Crunch' (Felsenstein, 1985; Pagel, 1992; Purvis and Rambaut, 1995). This option is appropriate for continuous variables. We analysed these contrasts by regression analysis with an intercept of zero (Purvis and Rambaut, 1995). For the univariate test of plumage dimorphism, we used the 'Brunch' option, which is appropriate for binary variables (Purvis and Rambaut, 1995; based on Burt, 1989). These 'Brunch' contrasts were tested against the null-expectation of zero by a *t*-test as well as a sign test (Purvis and Rambaut, 1995). For a multivariate test of plumage dimorphism, we applied the procedure suggested by Purvis and Rambaut (1995): First, we calculated the multiple regression of population trends against body size, migratory behaviour and diet using 'Crunch' contrasts. Second, we fitted this regression to the raw species data set and took the residuals from the line. Third, these residuals were tested against plumage dimorphism using CAIC's 'Brunch' option.

Our analysis of population trends may be confounded by population size. For small populations, the assessments of trends may be inaccurate, because a random change for only a few breeding pairs results in a high score. To tackle this problem, Böhning-Gaese and Bauer (1996) weighted a species' population trend by its logarithmic population size. However, the assessment of population trends may also be inaccurate for large populations. Their size can only be estimated, whereas the size of many small populations is known precisely. In our analysis, we found that weighting population trends by population size hardly changed the results. Thus we report only the unweighted analyses.

To test the 'effective population-size hypothesis', we compared the effect of sexual dimorphism on population trends across classes of increasing population size. We first ranked the species according to their population size. Then we repeated the above analyses for species with rank 1–15, 16–30, and so on. Each analysis yielded a β-value, or a t-value, describing the effect of sexual dimorphism on population trends. We correlated these values against the respective average population sizes using the Pearson correlation coefficient as well as the non-parametric Spearman correlation coefficient. An alternative approach to test the 'effective population-size hypothesis' would be to introduce an interaction term (population size × dimorphism) into a regression analysis. We only report the results of the above approach because it permits a simple graphical exploration of the results and because the two approaches generated the same results. We are not aware of any simple and straightforward method for correcting our analysis for phylogenetic relatedness among species. The problem is that our hypothesis refers to the effect of small versus large *absolute* population sizes. Methods that correct for phylogenetic relatedness test for the effect of *differences in* population size between sister taxa. This is basically a different hypothesis. The problem cannot be solved by sorting phylogenetically independent contrasts according to the reconstructed population sizes at the nodal values at which the contrasts were taken. This would sort contrasts according to higher taxa, given that higher taxa often differ with respect to population size (pigeons are much more common than eagles). Consequently, the sorting of contrasts would introduce the same phylogenetic bias as an analysis across species.

All P-values given in the text are one-tailed.

RESULTS AND DISCUSSION

Population trends

Species showed a wide range of population trends (Fig. 1). Overall, population increases occurred more often than decreases (Fig. 1). It is important to note that our hypotheses

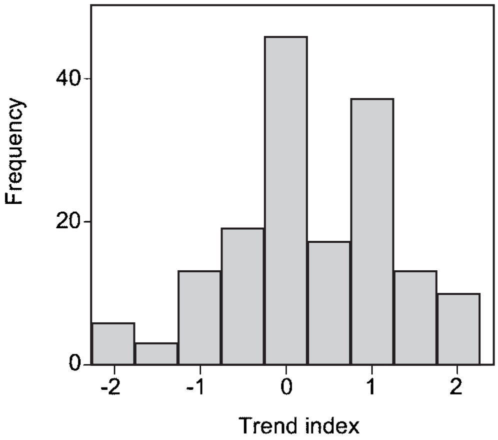

Fig. 1. Frequency distribution of the population-trend index across non-Passeriforme species from Central Europe. The index is a weighted average across 11 countries. It ranges from −2 (population decline of >50% from 1970 to 1995) to +2 (population increase of >50%). For details, see ‘Material and methods’.

apply for increasing as well as decreasing populations. Our hypotheses make predictions on population trends of dimorphic species compared with monomorphic species, not compared with zero.

Surrogates of sexual selection

We found no significant positive relationship between body-size dimorphism and plumage dimorphism for the cross-species analysis (t-test, $n = 162$, $t = -1.14$, $P > 0.50$) or for the analysis of contrasts (t-test, $n = 17$, $t = 0.040$, $P = 0.50$). On the one hand, this result may reflect the fact that in birds the association between body-size dimorphism (male size > female size) and sexual selection is less clear than initially supposed. In fact, sexual selection may sometimes favour small males: they may be more manoeuvrable in sexual contests (Andersson and Norberg, 1981) and females may prefer them because they are better at providing food (Mosher and Martray, 1974; Andersson, 1994). Moreover, natural selection may sometimes favour small females because they mature earlier than large females (Langston *et al.*, 1990; Andersson, 1994). Natural selection may also eliminate very large females (Colwell, 2000). On the other hand, even the association between plumage dimorphism and sexual selection may be ambiguous. For instance, during the breeding period, females may be more vulnerable to predators than males. Hence, natural selection by predators might favour plumage dimorphism by favouring the cryptic coloration of females (Andersson, 1994).

Our analysis may be biased by species with a plumage that is monomorphic to the human eye, but dimorphic to birds that are able to detect ultraviolet light (Burkhardt, 1989). However, among non-Passeriformes, such ‘pure UV dimorphism’ is rare (Andersson, 1996, 1999), except in parrots (Finger, 1995), which were not included in our data set. Moreover, ignoring UV dimorphism does not appear to introduce a systematic bias into studies of sexual selection. Such 'UV-blind' studies have given consistent results, even though they considered taxa with different frequencies of plumage dimorphism in UV light (Promislow *et al.*, 1992; Møller and Birkhead, 1994; McLain *et al.*, 1995; Bleiweiss, 1997; Sorci *et al.*, 1998).

The 'trade-off hypothesis'

The 'trade-off hypothesis' predicts that the mean score of population trends of dimorphic species is less than the mean score for the other species. We first considered body-size dimorphism as a surrogate of sexual selection and used species as independent data points. We found no relationship between dimorphism and population trends in univariate analyses (regression analysis, $n = 162$, $r = -0.07$, $P = 0.18$), but a significant negative relationship in the multivariate analysis (Table 1). However, with phylogenetically independent contrasts, this relationship disappeared (univariate regression analysis, $n = 107$, $r = 0.01$, $P = 0.50$; multivariate analysis in Table 1). When we considered plumage and used species as data points, we found the expected negative relationship between dimorphism and population trend in our univariate analysis (*t*-test, $n = 162$, $t = -2.09$, $P = 0.014$) and multivariate analysis (Table 1). However, when we used contrasts as data points the relationship became ambiguous in the univariate analysis ($n = 17$; *t*-test: $t = -2.01$, $P = 0.031$; sign test: negative relationship between dimorphism and trend in 65% of contrasts, $P = 0.17$) and clearly non-significant in the multivariate analysis (Table 1). Irrespective of the type of analysis, we found clear relationships between population trends and migratory behaviour as well as body size (Table 1).

Table 1. Multivariate analysis of population trends of Central European non-Passeriformes correlated with plumage dimorphism and body-size dimorphism, as well as several other variables

	Species ($n = 162$)		Contrasts ($n = 107$)		Contrasts ($n = 17$)			
Independent variable	β	P	β	P	t	P	%	P
Dimorphism								
Plumage	–0.16	0.015	–	–	–1.12	0.140	53	0.50
Body size	–0.13	0.038	–0.06	0.265	–	–	–	–
Control variables								
Migratory behaviour	–0.22	0.004	–0.263	0.007	–	–	–	–
$\mathrm{Log_e}$ (body size)	0.33	<0.001	0.245	0.013	–	–	–	–
Diet	0.11	0.119	–0.001	0.992	–	–	–	–
R^2/P	23/ < 0.001		17/ < 0.001		–		–	

Note: Data points are either species or phylogenetically independent contrasts. Variables were included simultaneously into the regression analysis. For the phylogenetically controlled analysis of plumage dimorphism, we calculated a *t*-test and a sign test. Both were based on residual population trends (see 'Material and methods'). β = standardized partial regression coefficient; P = error probability (one-tailed for dimorphism); R^2 = percentage of explained variance; t = *t*-value; % = percentage of contrasts with a negative relationship between dimorphism and residual population trend.

It is remarkable that our results supported the ‘trade-off hypothesis’ when we considered species as data points. This means that species within certain phylogenetic lineages exhibit strong sexual selection as well as negative population trends, whereas other lineages exhibit the opposite. Indeed, most Galliformes (8 of 10) and the two bustard species exhibit plumage dimorphism and negative population trends. On the other hand, the swan species, the cormorants, most gulls (7 of 8 species), most grebes (4 of 6) and most pigeons (3 of 4) exhibit no plumage dimorphism and a positive population trend. These differences between phylogenetic lineages in terms of plumage dimorphism and population trends correlate with differences in habitat use. The two lineages that exhibit plumage dimorphism and negative trends use agricultural landscapes, whereas most of the lineages with the opposite combination of traits use aquatic habitats. This difference in habitat use may be the real reason for the difference in population trends. Species in agricultural landscapes suffered from the industrialization of agriculture (Bauer and Berthold, 1996), whereas aquatic species profited from artificial water bodies and from increased water quality due to construction of waste-water plants (Bauer and Berthold, 1996). When we considered phylogenetically independent contrasts, we controlled for these differences between phylogenetic lineages.

Overall, our results provide no convincing support for the ‘trade-off hypothesis’. Either there was no trade-off between investment in traits under sexual selection and under natural selection because sexual selection actually reinforced natural selection, or an existing trade-off was fully compensated by the advantages of sexual selection, such as harmonization of reproductive behaviour or facilitation of local adaptation (see ‘Introduction’).

The ‘effective population-size hypothesis’

The ‘effective population-size hypothesis’ predicts that sexual selection negatively influences population trends, especially in species with small population sizes. However, we found only a single, marginally significant correlation between population size and the effect of sexual selection on population trends (Fig. 2). Mostly, the effect of sexual selection was distinctly more positive for the group of species with the smallest population sizes than for the next group of species (Fig. 2).

Overall, our results provide no clear support for the ‘effective population-size hypothesis’. This hypothesis assumes that sexual selection increases the risk of local extinction by reducing the effective size of local populations. Previous studies provided clear support for the ‘effective population-size hypothesis’ (McLain *et al.*, 1995; McLain and Vives, 1998; Sorci *et al.*, 1998), but they were restricted to island populations. There are two possible explanations for this difference between island studies and our mainland study. First, islands may differ from habitat fragments on a mainland (Rose and Polis, 2000). The risk of local extinction may be larger on islands because the local populations are smaller. Moreover, the chance of (re-)colonization may be smaller on islands. Hence, species under pressure of sexual selection may have a disadvantage, particularly under island conditions. In addition, many sexually selected species also exhibit a *K*-selected life history (McLain, 1991), which may also reduce their ability to colonize islands (Pianka, 1970). Second, many island studies differ from our mainland study in that they considered species introduced by humans. Humans usually introduced only very small founder populations. And humans preferred to introduce attractive (i.e. sexually selected) species, even those that had very little chance of surviving when they escaped from captivity. Hence the fondness of humans for attractive bird species may in part explain why many introductions failed.

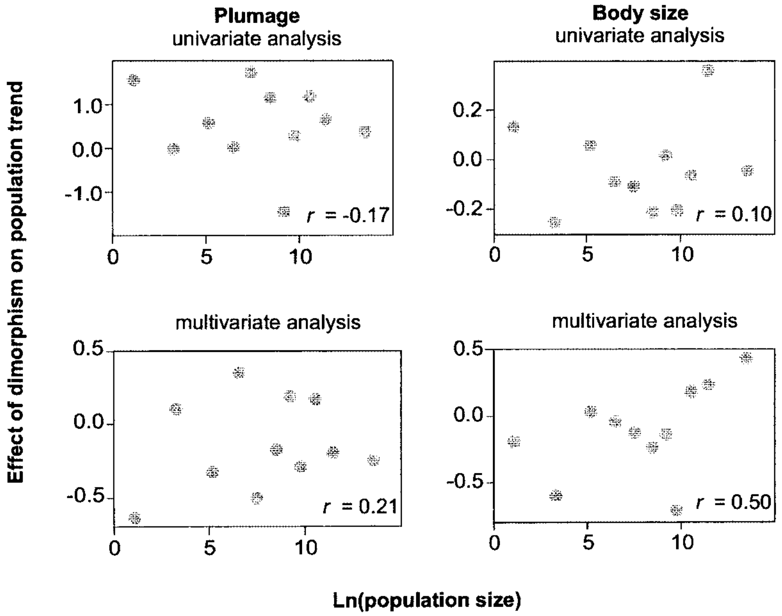

Fig. 2. Relationship between population size and the effect of dimorphism on population trends. We considered either plumage dimorphism or body-size dimorphism. Analyses were either univariate or multivariate (including migratory behaviour, body size and diet). The effect of dimorphism was measured as a β-value in a regression analysis or as a t-value in a t-test. The individual data points represent separate analyses across different sets of species. Only the Pearson regression coefficient (r) for body-size dimorphism in the multivariate analysis was marginally significant ($P = 0.06$). The analysis of rank correlations generated the same conclusions.

CONCLUSION

We conclude that, contrary to our naive hypotheses at the start of our project, sexual selection has little influence on population trends of birds in Central Europe. If sexually selected species do not suffer from the present period of habitat change and habitat fragmentation, they might not have suffered previously. Thus the notion of sexual selection as an ephemeral phenomenon that evolves and persists only during periods of constant habitat conditions (McLain, 1993) may not be correct. In fact, the persistent nature of sexual selection is already indicated by the strong phylogenetic conservatism of sexually selected traits (Andersson, 1994).

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