THE ROYAL SOCIETY

Received 4 February 2003
Accepted 8 May 2003

Sexual selection and the risk of extinction in birds

Edward H. Morrow[1]* and Trevor E. Pitcher[2]

[1]*Uppsala University, Evolutionary Biology Centre, Department of Animal Ecology, Norbyvägen 18D, SE-752 36 Uppsala, Sweden*
[2]*Department of Zoology, University of Toronto, Toronto, Ontario M5S 3G5, Canada*

The relationship between sexual selection and extinction risk has rarely been investigated. This is unfortunate because extinction plays a key role in determining the patterns of species richness seen in extant clades, which form the basis of comparative studies into the role that sexual selection may play in promoting speciation. We investigate the extent to which the perceived risk of extinction relates to four different estimates of sexual selection in 1030 species of birds. We find no evidence that the number of threatened species is distributed unevenly according to a social mating system, and neither of our two measures of pre-mating sexual selection (sexual dimorphism and dichromatism) was related to extinction risk, after controlling for phylogenetic inertia. However, threatened species apparently experience more intense post-mating sexual selection, measured as testis size, than non-threatened species. These results persisted after including body size as a covariate in the analysis, and became even stronger after controlling for clutch size (two known correlates of extinction risk). Sexual selection may therefore be a double-edged process—promoting speciation on one hand but promoting extinction on the other. Furthermore, we suggest that it is post-mating sexual selection, in particular, that is responsible for the negative effect of sexual selection on clade size. Why this might be is unclear, but the mean population fitness of species with high intensities of post-mating sexual selection may be especially low if costs associated with multiple mating are high or if the selection load imposed by post-mating selection is higher relative to that of pre-mating sexual selection.

Keywords: species richness; biodiversity; testis size; dichromatism; dimorphism; conservation status

1. INTRODUCTION

The role that sexual selection plays in determining patterns of species richness has been of great interest during the past 20 years. Patterns of species richness are of course the result of two processes—speciation and extinction. Of these two processes, sexual selection's effect upon speciation has received the greater share of attention from investigators (reviewed by Panhuis *et al.* 2001). Most of this work has been theoretical, with many models predicting that sexual selection should promote speciation by generating prezygotic isolation (e.g. West-Eberhard 1983; Turner & Burrows 1995; Payne & Krakauer 1997; Price 1998; Higashi *et al.* 1999; reviews by Turelli *et al.* 2001; Kirkpatrick & Ravigné 2002). Furthermore, sexual conflict is also predicted by theory to stimulate cladogenesis (Rice 1996, 1998; Rice & Holland 1997; Parker & Partridge 1998; Gavrilets 2000; Gavrilets *et al.* 2001). Several comparative studies provide some support for these theories by using data collected from birds (see Barraclough *et al.* 1995; Mitra *et al.* 1996; Møller & Cuervo 1998; Owens *et al.* 1999) and insects (see Arnqvist *et al.* 2000; Katzourakis *et al.* 2001). However, other studies using data from mammals, butterflies and spiders (see Gage *et al.* 2002), as well as birds (see Morrow *et al.* 2003) failed to find any evidence.

In contrast to speciation, sexual selection's impact on rates of extinction has rarely been investigated, either theoretically or empirically. This is unfortunate because imbalances in clade size observed today are the product of both past speciation and extinction events. Several authors have suggested that the selection load, generated by the evolution of extravagant traits via sexual selection, is higher in species with more intense sexual selection, thereby increasing the risk that these species will go extinct (Dawkins & Krebs 1979; Lande 1980; Kirkpatrick 1982; McLain 1993; Tanaka 1996; Møller 2000). Darwin was probably the first to allude to this idea when he framed his model of trait evolution via sexual selection (Darwin 1871) as directly opposing the evolution of traits via natural selection (Darwin 1859). In simple terms, ornamental traits could never evolve by natural selection alone, owing to their inherent extravagance. Although there is theoretical evidence that sexual selection may increase the likelihood that beneficial alleles will become fixed (Whitlock 2000), there is empirical evidence that sexual selection does not affect the rate of adaptation to a novel environment (Holland 2002), and that the selection load is real. For example, in *Drosophila melanogaster*, Wilkinson (1987) elegantly showed, experimentally, that there exists an equilibrium between the opposing forces of natural and sexual selection. Subsequently, several artificial selection experiments in the same species have directly demonstrated that absolute population fitness increases significantly when sexual selection is relaxed or removed (Rice 1996; Holland & Rice 1999; Pitnick *et al.* 2001). There are also several other lines of evidence that suggest sexual selection may relate positively to extinction risk. For example, two comparative studies of birds have shown that male survival rates are lower in sexually dimorphic species compared with sexually monomorphic species (Promislow *et al.* 1992, 1994). Several introductions of

*Author and address for correspondence: Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, CA 93106, USA (morrow@lifesci.ucsb.edu).

DOI 10.1098/rspb.2003.2441

bird species to islands have also indicated that extinction rates are higher for sexually dimorphic compared with sexually monomorphic species (see McLain *et al.* 1995, 1999; Sorci *et al.* 1998). A comparative study in mammals (Moore & Wilson 2002) found that the level of male-biased parasitism is positively associated with the intensity of sexual selection (measured as the degree of sexual size dimorphism or mating system). Finally, in the guppy, Brooks (2000) recently demonstrated experimentally that there exists a negative genetic correlation between the sexual attractiveness of males and their probabilities of survival. In addition, problems caused when populations become very small (such as inbreeding depression; Saccheri *et al.* 1998; Keller & Waller 2002) will be compounded in species with intense sexual selection, owing to the stronger reproductive skew, because only a subset of the population actually contributes to the genetic variance of the next generation (Sorci *et al.* 1998).

The combined weight of this theoretical, experimental and comparative evidence suggests that sexual selection may be double-edged: increasing the evolutionary rate of reproductive isolation, but also increasing the probability of extinction of the same lineages. It is therefore unclear what the net effect of sexual selection may be on patterns of species richness, and tests of the hypothesis that sexual selection increases the likelihood of extinction are clearly needed (Kokko & Brooks 2003). The aim of this study, therefore, was to examine whether species of birds that are currently under a high potential risk of extinction also undergo a greater intensity of sexual selection than species that are at a lower risk. Risk of extinction was inferred from the conservation status of each species as stated in the *IUCN Red List of Threatened Species* (IUCN 2002). Species present on this list were classified as facing a perceived threat of extinction, whereas those that were absent from the list were deemed to be at a lower risk—all known species of birds having been assessed by the IUCN for inclusion or exclusion on this list (see Hilton-Taylor 2000 (compiler)).

First, we investigated whether the conservation status of each species was related to their social mating system. Second, we employed a comparative method to examine how patterns of extinction risk across birds relate to three measures of the intensity of sexual selection. We used two surrogate indices of pre-mating sexual selection: (i) sexual dichromatism in plumage; and (ii) sexual size dimorphism; and one measure of post-mating sexual selection—testis size. All three are presumed to be good measures of the intensity of sexual selection that a species experiences (Møller & Briskie 1995; Owens & Hartley 1998; Dunn *et al.* 2001). A previous comparative study in birds has shown that extinction risk is positively correlated with body size and negatively correlated with clutch size (Bennett & Owens 1997). We therefore also examined how these covariates influenced the patterns of extinction risk in relation to the three sexual selection indices.

2. MATERIAL AND METHODS

Data on social mating systems, body size, sexual size dimorphism and sexual dichromatism were largely collated from Dunn *et al.* (2001).

(a) *Social mating system*

Following the methods of Dunn et al. (2001), species were assigned to one of six mating system categories: (i) polyandry; (ii) monogamy (less than 5% polygyny); (iii) mostly monogamy but occasional polygyny (5–15% polygyny); (iv) mostly polygyny (more than 15% polygyny); (v) cooperative breeding; and (vi) lek or promiscuous. This last category includes lekking species as well as lyrebirds, bowerbirds and most birds of paradise. These assignments were made according to standard references (see Dunn *et al.* 2001 and references therein).

(b) *Body size and sexual size dimorphism*

Data on total body mass were 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, 1994*a*,*b*). 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 on $\log_{10}$ 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 wherever possible.

(c) *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.

(d) *Testis mass*

Testis 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. Testis mass was estimated from these measurements by using Møller's (1991) corrected formula: testis mass (g) $= 2 \times 1.087\ \mathrm{g\ cm^{-3}}\ 1.33\pi[a(\mathrm{cm})]^2 b(\mathrm{cm})$, 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. Testis mass was calculated as the mean testis value from at least 10 breeding males, and up to 2500 in some cases (e.g. Møller 1991; Møller & Briskie 1995). Owing to extreme seasonal variation in testis 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).

(e) *Clutch size*

Data on the median number of eggs per nest for each species were obtained from the literature (Cramp & Simmons 1977, 1980 & 1983; Cramp 1985, 1988, 1992; Ehlrich *et al.* 1988; Stiles & Skutch 1989; Cramp & Perrins 1993, 1994*a*,*b*; Madge & Burn 1994; Harrap & Quinn 1995; Kaufman 1996; Rising 1996; Baicich & Harrison 1997; Harrsion & Castell 1998; Jaramillo & Burke 1999; Clement 2000).

Table 1. The distribution of threatened and unthreatened species divided into six social mating systems (21 species had an unknown mating system).

mating system	*n* unthreatened species	*n* threatened species	proportion threatened
polyandry	17	0	0.00
monogamy	741	22	0.03
5–15% polygyny	33	0	0.00
polygyny	42	3	0.07
cooperative breeding	49	5	0.09
lek or promiscuous	96	1	0.01
total	978	31	0.03

(f) *Conservation status of species*

The conservation status of each species was determined according to whether the species did or did not appear on the *IUCN Red List of Threatened Species* (IUCN 2002), which is available as a Web-based searchable database at http://www.redlist.org/. The compilers of this list have assessed all known species of birds, so species not appearing there can be reasonably assumed to be at a lower risk (Hilton-Taylor 2000 (compiler)). The list also gives additional information about how severe the threat is (on a six-point scale from 'Lower Risk' to 'Extinct' based upon the IUCN Red List categories and criteria; IUCN 1994). Subdividing the threatened species into these categories reduced the sample size considerably and so we were not able to use this potentially more fine-scaled measure of threat in our present analyses.

(g) *Comparative methods*

We analysed our data by using both raw species values and phylogenetically independent contrasts. To calculate the phylogenetically independent standardized contrasts we used the computer program Comparative Analysis of Independent Contrasts (CAIC) (Purvis & Rambaut 1995). This controls for the effects of shared evolutionary history by using the methods developed by Pagel (1992) and Felsenstein (1985). We assumed equal branch lengths, representing a punctuated model of evolution (Harvey & Pagel 1991). The phylogeny used was based upon the molecular phylogeny developed by Sibley & Ahlquist (1990). We used the BRUNCH procedure within CAIC because our measures of the conservation status of species is a binary variable (threatened or non-threatened). The null hypothesis, that the mean of the contrasts does not differ from zero, was then tested using a *t*-test. All means below are given ±1 standard error.

3. RESULTS

A *G*-test (with the William's correction; Sokal & Rohlf 1995) examining the distribution of 1009 threatened or unthreatened species among the six mating system categories was not significant ($G_{\text{adj}} = 9.61$; d.f. = 5; $p = 0.087$), suggesting that whether a species is threatened or not is unrelated to the social mating system of the species (table 1). When species were treated independently, there was no significant difference in mean testis size, plumage dichromatism or size dimorphism between species that are recorded as being threatened, versus those that are not (table 2). However, when controlling for phylogenetic inertia, species that are currently under a higher risk of extinction were found to have a larger residual testis size than non-threatened species (contrast mean = 0.094 ± 0.045, d.f. = 25, $t = 2.09$, $p = 0.047$), but there was no difference in the degree of sexual dichromatism or sexual dimorphism between the threatened or non-threatened groups (see table 3). Note that it was possible to obtain a significant result from the contrasts despite the raw species data not giving a significant result, because the variance around the contrast mean became reduced (whereas the difference between the threatened and non-threatened groups from the raw species data, and the difference between the contrast mean of the threatened group and 0, remained similar). Body size and clutch size have both previously been shown to be related to extinction risk (Bennett & Owens 1997). We therefore repeated these latter analyses by using body mass and clutch size as covariates (both variables were $\log_{10}$ transformed before analysis). Although we did not find that extinction risk was greater for species with larger bodies (mean = 0.006 ± 0.007, d.f. = 25, $t = 0.87$, $p = 0.39$), it was positively related to smaller clutch sizes (mean = −0.033 ± 0.013, d.f. = 20, $t = -2.51$, $p = 0.02$). None of our results changed qualitatively when body mass was included as a covariate alongside each of the indices of sexual selection (see table 3). However, the significance of the relationship between risk of extinction and testis size became stronger after including clutch size as a covariate (the power of this test was 0.81; table 3). Including clutch size as a covariate had no effect upon the significance of the relationship between extinction risk and sexual dimorphism or dichromatism (table 3). Finally, we checked what relationship, if any, our measures of pre-mating sexual selection had with that of post-mating sexual selection. We found that neither the contrasts of sexual dichromatism (Pearson's $r = -0.05$, $n = 461$, $p = 0.27$) nor dimorphism ($r = -0.03$, $n = 300$, $p = 0.63$) were related to testis size.

4. DISCUSSION

We have shown that species experiencing a greater threat of extinction are also those with a greater intensity of post-mating sexual selection, but that the intensity of pre-mating sexual selection does not significantly relate to whether a species is threatened or not. These results become stronger when a known ecological correlate of extinction risk (clutch size) was included in the analyses as a covariate, although body size (another known correlate of extinction risk; Bennett & Owens 1997) did not alter our results. The distribution of threatened versus non-threatened species was found to be even for the kind of mating system that predominates in a species, although this test was rather weak. Theoretical studies showing that sexual selection should promote speciation are numerous (reviewed by Kirkpatrick & Ravigné 2002), and although the number of studies demonstrating this empirically is limited (both in number and in taxonomic breadth; see § 1); at present the general view is that sexual selection promotes cladogenesis. By contrast, our results suggest that the intensity of sexual selection is also linked to the

Table 2. Using raw species data, there were no significant differences in the mean trait values (±1 s.e.m.) for unthreatened and threatened species (sample sizes given in parentheses).

trait	unthreatened	threatened	t	d.f.	p
testis size	0.00 ± 0.01 (980)	0.11 ± 0.08 (30)	−1.31	1008	0.19
dichromatism	1.79 ± 0.09 (999)	2.28 ± 0.11 (31)	−0.92	1028	0.36
dimorphism	0.00 ± 0.04 (505)	0.02 ± 0.01 (14)	−0.94	517	0.35

Table 3. Phylogenetically independent contrast means generated by CAIC, either with or without a covariate (body size or clutch size) were examined by using t-tests (where H_0: mean = 0).

analysis	trait	contrast mean (± s.e.m.)	t	d.f.	p
without covariates					
	testis size	0.094 ± 0.045	2.09	25	0.047
	dichromatism	−0.040 ± 0.252	−1.16	25	0.870
	dimorphism	0.005 ± 0.007	10.64	13	0.540
body size as a covariate					
	testis size	0.094 ± 0.045	2.09	25	0.047
	dichromatism	0.012 ± 0.226	0.05	25	0.960
	dimorphism	0.005 ± 0.007	0.64	13	0.540
clutch size as a covariate					
	testis size	0.129 ± 0.043	2.96	20	0.008
	dichromatism	−0.019 ± 0.306	−0.06	22	0.950
	dimorphism	0.003 ± 0.008	0.40	11	0.700

likelihood that a lineage will become extinct. Although this suggestion was explicitly made some time ago (Lande 1980; Kirkpatrick 1982), theoretical models in support of it are limited, partly because this question has been largely neglected by theoreticians. None the less, Tanaka (1996) showed that population extinction is more likely during environmental change if sexual selection is more intense. Specifically, Tanaka (1996) showed that an additional natural selection load exists when the model population had a sexual or social communication system, making the population more likely to go extinct owing to the cumulative or long-term effect of this load. There is good evidence that this load exists (e.g. Wilkinson 1987), and it has been shown experimentally that removal of sexual selection has a profound effect upon mean population fitness (Rice 1996; Holland & Rice 1999; Pitnick *et al.* 2001). A handful of other empirical studies indicate that sexually selected species face a higher risk of extinction (but see Prinzing *et al.* 2002). Several studies have shown that monomorphic birds introduced onto islands are more successful at establishing a stable population than dimorphic species (McLain *et al.* 1995, 1999; Sorci *et al.* 1998), perhaps because of the apparent cost of feather ornamentation (Møller & Hedenström 1999). In plants, species richness in dioecious clades is much lower than in hermaphroditic and monoecious ones (Heilbuth 2000). A possible explanation is that the extinction risk of more showy dioecious plants is higher, as pollinators will tend to visit the showy plants (males) more often, thereby increasing the likelihood that female plants will remain unpollinated (Vamosi & Otto 2002).

Clearly, the question of how sexual selection relates to extinction risk needs closer attention from both theoreticians and empiricists, but considering all the available evidence, a cautious conclusion is that sexual selection may have a double-edged effect upon patterns of species richness—encouraging both the conception and termination of species. This balancing effect could explain why some recent comparative studies have failed to find any relationship between species richness and the intensity of sexual selection, despite having large sample sizes and using powerful comparative methodologies (Gage *et al.* 2002; Morrow *et al.* 2003).

Given the apparent differences in how extinction risk relates to our indices of either pre- or post-mating sexual selection, our results also suggest that pre- and post-mating sexual selection may operate in different ways with respect to patterns of extinction. We can see three possible explanations for this difference. First, it is possible that there is no difference between the impact of pre- and post-mating sexual selection upon extinction risk, instead residual testis size is simply a better surrogate measure of sexual selection intensity than sexual dimorphism or dichromatism. We believe this is unlikely because although these traits indicate different components of sexual selection (Møller & Briskie 1995; Owens & Hartley 1998; Dunn *et al.* 2001) and are unrelated to one another in our dataset (see § 3), there is no reason to expect that data collected on the degree of sexual dimorphism or dichromatism are any less reliable than those for testis size.

A second possible explanation of why species with higher intensities of post-mating sexual selection, as opposed to pre-mating sexual selection, are under a greater threat of extinction, is that species with higher intensities of post-mating sexual selection (such as sperm competition) may also experience higher costs associated with multiple mating, such as the incidence of socially or sexually transmitted diseases (STDs), or that they may be more sensitive to inbreeding depression than more monogamous species (a problem that will be compounded at small population sizes). Species with high levels of sperm competition typically copulate more frequently and with many more partners (Birkhead & Møller 1998; Simmons 2001). This behaviour could be immunologically or energetically costly for both females and males. Alternatively, frequent multiple mating could increase the rate of horizontal transfer of pathogens between individuals in a population (see discussions in Møller 1998; Thrall *et al.* 2000). This latter argument is intuitively appealing, but higher infection rates may not necessarily translate into a lower population fitness, because there is likely to be host–parasite coevolution, with selection favouring the evolution of less virulent STDs (Knell 1999). None the less, when population sizes are small, those with higher rates of multiple mating may be more vulnerable to the spread of novel infectious agents than those populations that mate more monogamously. Empirical evidence that STD transmission rates and copulation frequency are related is somewhat limited (see Møller 1998), but a recent comparative study in primates has shown that female white blood cell counts are positively related to the degree of female promiscuity, across 41 species (Nunn *et al.* 2000). Thus, although there is limited evidence that post-mating sexual selection magnifies the incidence of disease, very few studies have specifically looked into this question.

Third, there could be a fundamental difference in the size of the selection load imposed by pre- and post-mating sexual selection. One possible scenario is that the energetic, immunological and/or developmental costs generated by testes or sperm production, high copulation frequencies, or of traits involved in female cryptic choice or post-mating sexual antagonism, may be considerably greater than those arising from traits associated with pre-mating sexual selection. Although it is broadly accepted that mate acquisition and mating are costly, despite any direct or indirect benefits that females may accrue by mating multiply (Andersson 1994; Arnqvist *et al.* 2000; Jennions & Petrie 2000), we know of no studies that have attempted to quantify the relative costs of pre- and post-mating sexual selection. Kotiaho (2001) recently questioned whether there existed any good evidence that sexually selected traits are costly, but most, if not all of the sexual traits reviewed were involved in pre-mating selection. A recent model of the dynamics of the coevolution between mate choice and display trait by Houle & Kondrashov (2002), indicates that under some apparently realistic circumstances, exaggeration of the display trait may continue indefinitely—even up to the point of extinction. It seems possible then, that the cost of traits under post-mating sexual selection may rise to similarly high levels, assuming the benefits accrued are similarly large. However, there does not seem to be any *a priori* reason why the cost of traits under pre-mating sexual selection versus those under post-mating selection would differ quantitatively in terms of the magnitude of these costs. We suggest that in species with more intense post-mating relative to pre-mating sexual selection, either the absolute population fitness is lower, or the overall selection load is higher. Either of these mechanisms could then have a bearing on how vulnerable a population is to becoming extinct.

The authors are extremely grateful to Göran Arnqvist, Urban Friberg, Ian Owens and Joseph Tomkins for many helpful ideas; to Dominique Mazzi and Caroline Pollock for technical assistance; and to the curators and managers of the following collections for access to specimens: Australian National Wildlife Collection (Canberra); Burke Museum, University of Washington (Seattle); Canadian Museum of Nature (Ottawa); Centennial Museum of Natural History (El Paso); Cornell University Museum of Vertebrate Zoology (Ithaca); Carnegie Museum of Natural History (Pittsburgh); Field Museum of Natural History (Chicago); Museum of Natural History, University of Kansas (Lawrence); Museum of Natural History, Smithsonian Institution (Washington, DC); Museum of Natural Science, Louisiana State University (Baton Rouge); Slater Museum of Natural History (Tacoma) and Royal Ontario Museum (Toronto). This work was funded by the Swedish Natural Science Research Council (to E.H.M. via Göran Arnqvist) and the Natural Science and Engineering Council of Canada.

REFERENCES

Andersson, M. 1994 *Sexual selection*. Monographs in behavior and ecology. Princeton University Press.

Arnqvist, G., Edvardsson, M., Friberg, U. & Nilsson, T. 2000 Sexual conflict promotes speciation in insects. *Proc. Natl Acad. Sci. USA* **97**, 10 460–10 464.

Baicich, P. J. & Harrison, C. J. O. 1997 *A guide to the nests, eggs, and nestlings of North American birds*. London: Academic Press.

Barraclough, T. G., Harvey, P. H. & Nee, S. 1995 Sexual selection and taxonomic diversity in passerine birds. *Proc. R. Soc. Lond.* B **259**, 211–215.

Bennett, P. M. & Owens, I. P. F. 1997 Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. Lond.* B **264**, 401–408. (DOI 10.1098/rspb.1997.0057.)

Birkhead, T. R. & Møller, A. P. 1998 *Sperm competition and sexual selection*. London: Academic Press.

Brooks, R. 2000 Negative genetic correlation between male sexual attractiveness and survival. *Nature* **406**, 67–70.

Clement, P. 2000 *Thrushes*. Princeton University Press.

Cramp, S. (ed.) 1985, 1988, 1992 *Handbook of birds of Europe, the Middle East and North Africa*. Oxford University Press.

Cramp, S. & Perrins, C. M. (eds) 1993, 1994*a*,*b* *Handbook of birds of Europe, the Middle East and North Africa*. Oxford University Press.

Cramp, S. & Simmons, K. E. L. (eds) 1977, 1980, 1983 *Handbook of birds of Europe, the Middle East and North Africa*. Oxford University Press.

Darwin, C. 1859 *The origin of species*. London: Penguin.

Darwin, C. 1871 *The descent of man*. New York: Prometheus Books.

Dawkins, R. & Krebs, J. R. 1979 Arms races between and within species. *Proc. R. Soc. Lond.* B **205**, 489–511.

Dunn, P. O., Whittingham, L. A. & Pitcher, T. E. 2001 Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**, 161–175.

Ehlrich, P. R., Dobkin, D. S. & Wheye, D. 1988 *The birder's handbook—a field guide to the natural history of North American birds*. New York: Fireside Books.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Gage, M. J. G., Parker, G. A., Nylin, S. & Wiklund, C. 2002 Sexual selection and speciation in mammals, butterflies and spiders. *Proc. R. Soc. Lond.* B **269**, 2309–2316. (DOI 10.1098/rspb.2002.2154.)

Gavrilets, S. 2000 Rapid evolution of reproductive barriers driven by sexual conflict. *Nature* **403**, 886–889.

Gavrilets, S., Arnqvist, G. & Friberg, U. 2001 The evolution of female mate choice by sexual conflict. *Proc. R. Soc. Lond.* B **268**, 531–539. (DOI 10.1098/rspb.2000.1382.)

Harrap, S. & Quinn, D. 1995 *Chickadees, tits, nuthatches, and treecreepers*. Princeton University Press.

Harrsion, C. & Castell, P. 1998 *Bird nests, eggs and nestlings of Britain and Europe*. Milan: Harper Collins.

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford Series in Ecology and Evolution. Oxford University Press.

Heilbuth, J. C. 2000 Lower species richness in dioecious clades. *Am. Nat.* **156**, 221–241.

Higashi, M., Takimoto, G. & Yamamura, N. 1999 Sympatric speciation by sexual selection. *Nature* **402**, 523–526.

Hilton-Taylor, C. 2000 (compiler) *2000 IUCN Red List of Threatened Species*. Gland, Switzerland and Cambridge: IUCN/SSC.

Holland, B. 2002 Sexual selection fails to promote adaptation to a new environment. *Evolution* **56**, 721–730.

Holland, B. & Rice, W. R. 1999 Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl Acad. Sci. USA* **96**, 5083–5088.

Houle, D. & Kondrashov, A. S. 2002 Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. R. Soc. Lond.* B **269**, 97–104. (DOI 10.1098/rspb.2001.1823.)

IUCN 1994 *1994 Categories and Criteria*, vol. 2002. Gland, Switzerland and Cambridge, UK: IUCN.

IUCN 2002 *2002 IUCN Red List of Threatened Species*, vol. 2002. Gland, Switzerland and Cambridge, UK: IUCN.

Jaramillo, A. & Burke, P. 1999 *New World blackbirds—the icterids*. Princeton University Press.

Jennions, M. D. & Petrie, M. 2000 Why do females mate multiply? A review of the genetic benefits. *Biol. Rev.* **75**, 21–64.

Katzourakis, A., Purvis, A., Azmeh, S., Rotheray, G. & Gilbert, F. 2001 Macroevolution of hoverflies (Diptera: Syrphidae): the effect of using higher-level taxa in studies of biodiversity, and correlates of species richness. *J. Evol. Biol.* **14**, 219–227.

Kaufman, K. 1996 *Lives of North American birds*. Boston, MA: Houghton Mifflin.

Keller, L. F. & Waller, D. M. 2002 Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**, 230–241.

Kirkpatrick, M. 1982 Sexual selection and the evolution of female choice. *Evolution* **36**, 1–12.

Kirkpatrick, M. & Ravigné, V. 2002 Speciation by natural and sexual selection: models and experiments. *Am. Nat.* **159**, S22–S35.

Knell, R. J. 1999 Sexually transmitted disease and parasite-mediated sexual selection. *Evolution* **53**, 957–961.

Kokko, H. & Brooks, R. 2003 Sexy to die for? Sexual selection and the risk of extinction *Ann. Zool. Fennici* **40**, 207–219.

Kotiaho, J. S. 2001 Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biol. Rev.* **76**, 365–376.

Lande, R. 1980 Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34**, 292–305.

McLain, D. K. 1993 Cope's rules, sexual selection, and the loss of ecological plasticity. *Oikos* **68**, 490–500.

McLain, D. K., Moulton, M. P. & Redfearn, T. P. 1995 Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos* **74**, 27–34.

McLain, D. K., Moulton, M. P. & Sanderson, J. G. 1999 Sexual selection and extinction: the fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. *Evol. Ecol. Res.* **1**, 549–565.

Madge, S. & Burn, H. 1994 *Crows and jays*. London: Christopher Helm.

Mayr, E. 1942 *Systematics and the origin of species*. New York: Columbia University Press.

Mitra, S., Landel, H. & Pruett-Jones, S. 1996 Species richness covaries with mating system in birds. *Auk* **113**, 544–551.

Møller, A. P. 1991 Sperm competition, sperm depletion, paternal care, and relative testis size in birds. *Am. Nat.* **137**, 882–906.

Møller, A. P. 1998 Sperm competition and sexual selection. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller), pp. 55–90. London: Academic Press.

Møller, A. P. 2000 Sexual selection and conservation. In *Behaviour and conservation* (ed. L. M. Gosling & W. J. Sutherland), pp. 161–171. Cambridge University Press.

Møller, A. P. & Briskie, J. V. 1995 Extra-pair paternity, sperm competition and the evolution of testis size in birds. *Behav. Ecol. Sociobiol.* **36**, 357–365.

Møller, A. P. & Cuervo, J. J. 1998 Speciation and feather ornamentation in birds. *Evolution* **52**, 859–869.

Møller, A. P. & Hedenström, A. 1999 Comparative evidence for costs of secondary sexual characters: adaptive vane emargination of ornamented feathers in birds. *J. Evol. Biol.* **12**, 296–305.

Moore, S. L. & Wilson, K. 2002 Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* **297**, 2015–2018.

Morrow, E. H., Pitcher, T. E. & Arnqvist, G. A. 2003 No evidence that sexual selection is an 'engine of speciation' in birds. *Ecol. Lett.* **6**, 228–234.

Murton, R. K. & Westwood, N. J. 1977 *Avian breeding cycles*. Oxford: Clarendon Press.

Nunn, C. L., Gittleman, J. L. & Antonovics, J. 2000 Promiscuity and the primate immune system. *Science* **290**, 1168–1170.

Owens, I. P. F. & Bennett, P. M. 1994 Mortality costs of parental care and sexual dimorphism in birds. *Proc. R. Soc. Lond.* B **257**, 1–8.

Owens, I. P. F. & Hartley, I. R. 1998 Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond.* B **265**, 397–407. (DOI 10.1098/rspb.1998.0308.)

Owens, I. P. F., Bennett, P. M. & Harvey, P. H. 1999 Species richness among birds: body size, life history, sexual selection or ecology? *Proc. R. Soc. Lond.* B **266**, 933–939. (DOI 10.1098/rspb.1999.0726.)

Pagel, M. D. 1992 A method for the analysis of comparative data. *J. Theor. Biol.* **156**, 431–442.

Panhuis, T. M., Butlin, R., Zuk, M. & Tregenza, T. 2001 Sexual selection and speciation. *Trends Ecol. Evol.* **16**, 364–371.

Parker, G. A. & Partridge, L. 1998 Sexual conflict and speciation. *Phil. Trans. R. Soc. Lond.* B **353**, 261–274. (DOI 10.1098/rstb.1998.0208.)

Payne, R. J. H. & Krakauer, D. C. 1997 Sexual selection, space, and speciation. *Evolution* **51**, 1–9.

Pitnick, S., Miller, G. T., Reagan, J. & Holland, B. 2001 Males' evolutionary responses to experimental removal of sexual selection. *Proc. R. Soc. Lond.* B **268**, 1071–1080. (DOI 10.1098/rspb.2001.1621.)

Price, T. 1998 Sexual selection and natural selection in bird speciation. *Phil. Trans. R. Soc. Lond.* B **353**, 251–260. (DOI 10.1098/rstb.1998.0207.)

Prinzing, A., Brändle, M., Pfeifer, R. & Brandl, R. 2002 Does sexual selection influence population trends in European birds? *Evol. Ecol. Res.* **4**, 49–60.

Promislow, D. E. L., Montgomerie, R. & Martin, T. E. 1992 Mortality costs of sexual dimorphism in birds. *Proc. R. Soc. Lond.* B **250**, 143–150.

Promislow, D. E. L., Montgomerie, R. & Martin, T. E. 1994 Sexual selection and survival in North American waterfowl. *Evolution* **48**, 2045–2050.

Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**, 247–251.

Rice, W. R. 1996 Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature* **381**, 232–234.

Rice, W. R. 1998 Intergenomic conflict, interlocus antagonistic coevolution, and the evolution of reproductive isolation. In *Endless forms: species and speciation* (ed. D. J. Howard & S. H. Berlocher), pp. 261–270. Oxford University Press.

Rice, W. R. & Holland, B. 1997 The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behav. Ecol. Sociobiol.* **41**, 1–10.

Ridgeway, R. 1901–1946 *The birds of North and Middle America*. Washington, DC: Government Printing Office.

Rising, J. D. 1996 *A guide to the identification and natural history of the sparrows of the United States and Canada*. London: Academic Press.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. 1998 Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491–494.

Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds. A study in molecular evolution*. London: Yale University Press.

Simmons, L. W. 2001 *Sperm competition and its evolutionary consequences in the insects*. Monographs in Behavior and Ecology. Princeton University Press.

Sokal, R. R. & Rohlf, F. J. 1995 *Biometry: the principles and practice of statistics in biological research*. New York: Freeman.

Sorci, G., Møller, A. P. & Clobert, J. 1998 Plumage dichromatism of birds predicts introduction success in New Zealand. *J. Anim. Ecol.* **67**, 263–269.

Stiles, F. G. & Skutch, A. F. 1989 *A guide to the birds of Costa Rica*. Ithaca, NY: Cornell University Press.

Stutchbury, B. J. & Morton, E. S. 1995 The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* **132**, 675–690.

Tanaka, Y. 1996 Sexual selection enhances population extinction in a changing environment. *J. Theor. Biol.* **180**, 197–206.

Thrall, P. H., Antonovics, J. & Dobson, A. P. 2000 Sexually transmitted diseases in polygynous mating systems: prevalence and impact on reproductive success. *Proc. R. Soc. Lond.* B **267**, 1555–1563. (DOI 10.1098/rspb.2000.1178.)

Turelli, M., Barton, N. H. & Coyne, J. A. 2001 Theory and speciation. *Trends Ecol. Evol.* **16**, 330–343.

Turner, G. F. & Burrows, M. T. 1995 A model of sympatric speciation by sexual selection. *Proc. R. Soc. Lond.* B **260**, 287–292.

Vamosi, J. C. & Otto, S. P. 2002 When looks can kill: the evolution of sexually dimorphic floral display and the extinction of dioecious plants. *Proc. R. Soc. Lond.* B **269**, 1187–1194. (DOI 10.1098/rspb.2002.2004.)

West-Eberhard, M. J. 1983 Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**, 155–183.

Whitlock, M. C. 2000 Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution* **54**, 1855–1861.

Wilkinson, G. S. 1987 Equilibrium analysis of sexual selection in *Drosophila melanogaster*. *Evolution* **41**, 11–21.

Wingfield, J. C. 1984 Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia*. *Gen. Comp. Endocrinol.* **56**, 406–416.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.