

# Sexual selection and the risk of extinction in mammals

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Sexual selection is commonly envisaged as a force working in opposition to natural selection, because extravagant or exaggerated traits could apparently have never evolved via natural selection alone. There is good evidence that a selection load imposed by sexual selection may be eased experimentally by restricting the opportunity for it to operate. Sexual selection could therefore potentially play an important role in influencing the risk of extinction that a population faces, thereby contributing to the apparent selectivity of extinctions. Conversely, recent theory predicts that the likelihood of extinction may decrease when sexual selection is operating because it could accelerate the rate of adaptation in concert with natural selection. So far, comparative evidence (coming mostly from birds) has generally indicated support for the former scenario, but the question remains open. The aim of this study was therefore to examine whether the level of sexual selection (measured as residual testes mass and sexual size dimorphism) was related to the risk of extinction that mammals are currently experiencing. We found no evidence for a relationship between these factors, although our analyses may have been confounded by the possible dominating effect of contemporary anthropogenic factors.

**Keywords:** selection load; extinction threshold; sperm competition; testes size; CAIC

## 1. INTRODUCTION

One important and interesting feature of Darwin's original formulation of sexual selection is that traits could evolve despite their not being favoured under natural selection (Darwin 1871). Sexual selection may therefore move a population away from some 'perfect' state favoured by natural selection (Darwin 1871). Subsequent authors agreed with this, some even going so far as to say that sexual selection has 'maladaptive tendencies' (Kirkpatrick 1982), and that there is a selection load imposed by sexual selection that could even drive a population over the edge of an extinction threshold (Lande 1980). There is evidence supporting the idea that sexual selection operates in opposition to natural selection, and that traits which evolved via sexual selection carry a selection load. For instance, Wilkinson (1987) showed that there was sexual selection for increased wing length in populations of *Drosophila melanogaster*, whereas natural selection favoured reduced wing length. Holland & Rice (1999) convincingly demonstrated that the mean fitness of a population is depressed by sexual selection, because this load can be alleviated if the opportunity for sexual selection was removed experimentally. There is also a negative relationship between how skewed the distribution of male reproductive success is and effective population size (Wright 1940). As a result, populations with intense sexual selection are more likely to suffer the negative effects of an accumulation of deleterious alleles.

A handful of models also suggest that sexual selection could promote extinction. Tanaka (1996) proposed that under changing environmental conditions, populations exhibiting sexually selected signalling behaviour were more

likely to go extinct, as a result of an increase in the selection load of possessing the signal trait. Additionally, Houle & Kondrashov (2002) showed that under some circumstances, sexually selected male display traits may become exaggerated to such an extent that the population would go extinct owing to the loss of male viability. However, as the authors point out, other features of the population not included in the model, such as density-dependent costs of mate searching by females, could limit the extent of the exaggeration. Several comparative studies support the notion that sexual selection is associated with an increased probability of extinction. Data from bird introductions onto islands indicate that sexually dichromatic species are less likely to successfully colonize than monochromatic species (McLain *et al.* 1995, 1999; Sorci *et al.* 1998). Sexual selection has also been found to be positively correlated to local extinction rates of North American birds (Doherty *et al.* 2003), and with higher turnover rates of dichromatic species in those communities. Finally, post-mating sexual selection (measured as relative testes size) was found to be positively related to the perceived risk of extinction of birds, whereas two estimates of pre-mating sexual selection (sexual size dimorphism and sexual dichromatism) did not (Morrow & Pitcher 2003).

However, theory and evidence do not all point in the same direction. In fact, sexual selection could reduce the likelihood that a population would go extinct either because sexual selection may: (i) prevent the fixation of deleterious mutations (Whitlock 2000); (ii) reduce or eliminate the cost of sex (Agrawal 2001; Siller 2001); or (iii) accelerate the rate of adaptive evolutionary change (Proulx 1999; Lorch *et al.* 2003). Legendre *et al.* (1999) found that monogamously mating birds suffered a higher risk of extinction, which the authors attributed to the larger influence of demographic stochasticity in these species.

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There was also no evidence from a comparative study of European birds that sexual selection was negatively related to population trends after phylogenetic inertia was controlled for (Prinzing *et al.* 2002). Finally, Brashares (2003) recently examined how a range of ecological, behavioural and life-history factors influence the persistence of species of mammals within six wildlife reserves in Ghana from 1969–1998, finding that mammals with monogamous mating systems, or where males monopolized only a small harem of females, were less likely to persist than species where males controlled larger harems of females.

Of the few comparative studies that have investigated the possible role of sexual selection in driving extinction, the majority of them have used birds as their study organisms. As such, there is a clear need for this question to be examined in a wider range of taxonomic groups. It is with this in mind that we conducted the present study into how sexual selection influences the risk of extinction in mammals, a taxonomic group that has had a comprehensive assessment made of their species-specific conservation status by the IUCN (2002). We examined whether two surrogate measures of the intensity of sexual selection, sexual size dimorphism and relative testes size, are related to the current threat of extinction at the level of the genus and of the species.

## 2. MATERIAL AND METHODS

### (a) *Data collection*

Data of male and female body masses of 1007 species representing 508 mammalian genera were obtained from Silva & Downing (1995), and data of testes masses were obtained from several sources (Harcourt *et al.* 1995; Rose *et al.* 1997; Breed & Taylor 2000; Hosken *et al.* 2001b; Gage *et al.* 2002). The data presented by Silva & Downing (1995) are arranged following the taxonomy of Corbet & Hill (1986); however, because the conservation status data follow the taxonomy of Wilson & Reeder (1993) (see below) we followed this latter authority. As a consequence, some data needed to be merged, split or renamed according to differences in the classification between these authorities. For each species, sexual size dimorphism was estimated as the residual mean male mass from a linear regression of log-transformed male and female body mass, and the mean sexual size dimorphism for each genus was simply the mean of the residual from all congeners. Care was taken to match body mass data for the two sexes from the same literature source. Relative testes sizes were calculated from the residuals of a regression of log male body mass versus log testes mass, where the body mass and testes mass data were obtained from the same literature source (Gage *et al.* 2002).

### (b) *Conservation status*

The 'IUCN red list of threatened species' (IUCN 2002) was used to determine the conservation status of each species for which we had body mass and/or testes mass data. This list is the result of a comprehensive assessment of all mammal species given in the taxonomy of Wilson & Reeder (1993), with very few exceptions. The list is available as a Web-based searchable database at <http://www.redlist.org> and it provides information on the category of threat (IUCN 1994) as well as information on current population trends where known (either improving, deteriorating or stable). From this, we were able to classify the conservation status of each species in three ways: according to a simple binomial system (0, not threatened; 1, threatened); on a five-point scale (0, not threatened; 1, lower risk; 2, vulnerable; 3, endangered; 4,

critically endangered or extinct); or on a three-point scale relating to the current population trends (0, not threatened; 1, improving or stable; 2, deteriorating). From the binomial classification of the current risk of extinction for each species we were also able to simply calculate the proportion of each genus that is currently threatened in relation to the total species count of each genus according to Wilson & Reeder (1993), which is also available as a Web-based searchable database at <http://www.nmnh.si.edu/msw>. These data were arcsine transformed prior to analysis because of their proportional nature (Sokal & Rohlf 1995).

In our dataset, 772 (76.6%) species were listed as not threatened, 117 (11.6%) were lower risk, 70 (6.9%) were vulnerable, 35 (3.4%) were endangered and 13 (1.3%) were critically endangered or extinct. Three species of domesticated mammals (*Sus scrofa*, *Bos taurus*, *Canis lupus familiaris*) and humans (*Homo sapiens*) were excluded from the comparative analyses because we assumed that there could not realistically be any intrinsic effects of sexual selection upon their current conservation status. However, data from these species were included in the calculations of sexual size dimorphism and residual testes size (see above).

### (c) *Phylogenetic relationships*

We compiled a composite phylogeny of mammals from several sources. The family level supertree of the Eutheria by Liu *et al.* (2001) was used as our base phylogeny, to which we added 'super-trees' or phylogenies for Primates (Purvis 1995), Bovidae (Matthee & Davis 2001), Chiroptera (Jones *et al.* 2002), Muridae (Michaux *et al.* 2001), Carnivora (Bininda-Emonds *et al.* 1999) and Marsupialia (Sánchez-Villagra 2001), including a specific phylogeny for the Dasyuridae (Krajewski *et al.* 2000). A few families were missing from Liu *et al.*'s (2001) phylogeny; we therefore placed these as polytomies according to their taxonomic position given by Wilson & Reeder (1993). These included placing the Ctenomyidae with the Octodontidae, the Petromyidae with the Hystricognathi, and the Odoberidae with the Phocidae and Otariidae.

### (d) *Comparative methods*

As in all comparative studies, species or genera data cannot be treated as statistically independent because of their shared phylogenetic history (Harvey & Pagel 1991). So, to examine how sexual selection relates to extinction risk, we needed to control for the confounding effects of phylogenetic inertia by generating phylogenetically independent contrasts following the methods developed by Pagel (1992) and Felsenstein (1985). These phylogenetically independent standardized contrasts were calculated using the computer program comparative analysis of independent contrasts (CAIC; Purvis & Rambaut 1995). We assumed equal branch lengths, representing a punctuated model of evolution (Harvey & Pagel 1991). We used the CRUNCH procedure within CAIC when the extinction risk was measured on a continuous scale and used BRUNCH when this risk was defined on a binomial scale. We examined the relationships between each of our measures of the strength of sexual selection and extinction risk using linear regressions forced through the origin as advocated by Garland *et al.* (1992). We also repeated these analyses using body size as a covariate, because it has previously been shown that body size relates positively with extinction risk in mammals (Cardillo & Bromham 2001) and birds (Gaston & Blackburn 1995), although it has also been shown to be both positively and negatively correlated with extinction risk of birds in one study (Owens & Bennett 2000).

We found that for many of the analyses, the standardized contrasts generated by CAIC failed to meet the statistical assumptions of the comparative method because of their heteroscedasticity and/or non-normal distribution. It was not possible to normalize these distributions with any of the transformations to the original data that were attempted, so we chose to employ randomization procedures described by Manly (1991) on all of the statistical tests performed. Therefore, unless specified, all  $p$ -values that we report here correspond to those obtained following the randomization procedures performed on the standardized contrasts. Randomizations of the linear and multiple regressions were carried out using POPTOOLS, a Microsoft EXCEL addin available from <http://www.cse.csiro.au/CDG/poptools> (v. 2.3). This follows a random pairing of  $x$  and  $y$  values from the dataset from which a new regression coefficient is calculated, reiterated 9999 times, to obtain a normal random distribution of regression coefficients and their associated  $t$  (the constant being excluded from the model (Garland *et al.* 1992)). A bootstrapping procedure with replacement was also employed on the  $t$ -tests, again reiterated 9999 times.

### 3. RESULTS

Data on sexual size dimorphism and body mass were obtained for 1007 species, representing 508 mammalian genera. Testes mass measurements were obtained for 325 of these species, representing 210 genera. All means are given  $\pm 1$  standard error. Absolute values of male and female body masses, testes masses, speciosity and extinction risk are given in electronic Appendices A–C.

#### (a) Genus level analyses

##### (i) Sexual size dimorphism

We found no evidence that the proportion of a genus that is currently under some threat of extinction was related to the degree of sexual dimorphism exhibited by that genus ( $n = 296$  contrasts,  $\beta = 0.500 \pm 0.320$ ,  $t = 1.565$ ,  $p = 0.164$ ; figure 1a). Including body size as a covariate in this analysis did not change this result qualitatively ( $n = 296$ ,  $F = 3.943$ ,  $p = 0.126$ ). We also found no evidence that body size itself was related to the proportion of a genus that is threatened ( $n = 296$ ,  $\beta = 0.083 \pm 0.052$ ,  $t = 1.609$ ,  $p = 0.844$ ; figure 1b).

##### (ii) Residual testes size

Again, we found no evidence that the proportion of a genus threatened was related to the mean residual testes size of that genus when either excluding ( $n = 126$ ,  $\beta = 0.285 \pm 0.155$ ,  $t = 1.841$ ,  $p = 0.109$ ; figure 1c) or including body size as a covariate ( $n = 126$ ,  $F = 1.640$ ,  $p = 0.485$ ).

#### (b) Species level analyses

##### (i) Sexual size dimorphism

After controlling for the effects of shared phylogenetic ancestry, we found no evidence that sexual size dimorphism exhibited by a species was related to the current risk of extinction. This was true for whether this perceived risk was classified using the binomial system (mean =  $0.0068 \pm 0.0048$ ,  $n = 136$ ,  $t = 1.423$ ,  $p = 0.493$ ), the five-point scale ( $n = 519$ ,  $\beta = 0.288 \pm 0.338$ ,  $t = 0.850$ ,  $p = 0.080$ ; figure 2a) or using the population trend data ( $n = 453$ ,  $\beta = 0.077 \pm 0.239$ ,  $t = 0.320$ ,  $p = 0.126$ ). These results remained unchanged after controlling for

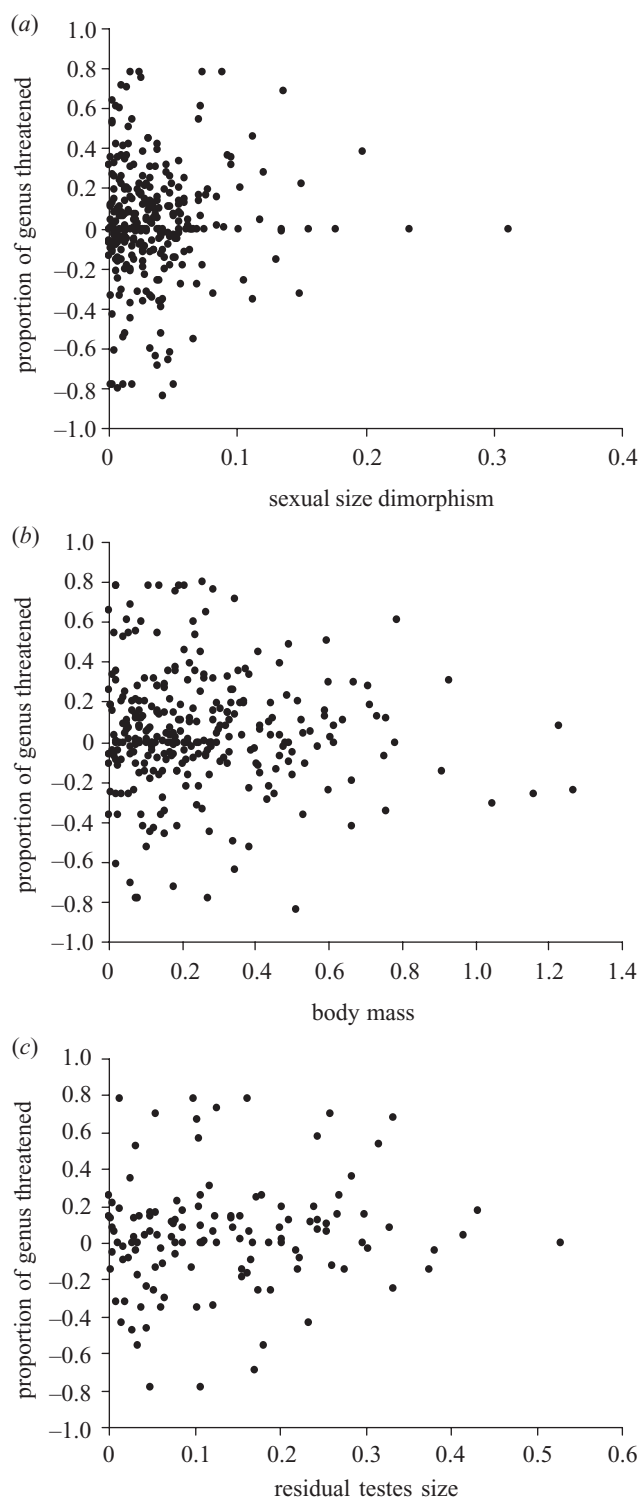


Figure 1. After controlling for phylogenetic inertia, the proportion of species within each genus that is currently threatened with extinction was not related to (a) sexual size dimorphism, (b) body size or (c) residual testes size.

the possible confounding effect of body size (five-point scale,  $n = 519$ ,  $F = 3.051$ ,  $p = 0.146$ ; population trend,  $n = 453$ ,  $F = 4.967$ ,  $p = 0.050$ ). Body mass was also found to be unrelated to extinction risk using the binomial system (mean =  $0.0459 \pm 0.0187$ ,  $n = 136$ ,  $t = 2.453$ ,  $p = 0.502$ ), the five-point scale ( $n = 519$ ,  $\beta = 0.115 \pm 0.078$ ,  $t = 1.475$ ,  $p = 0.410$ ; figure 2b) or the population

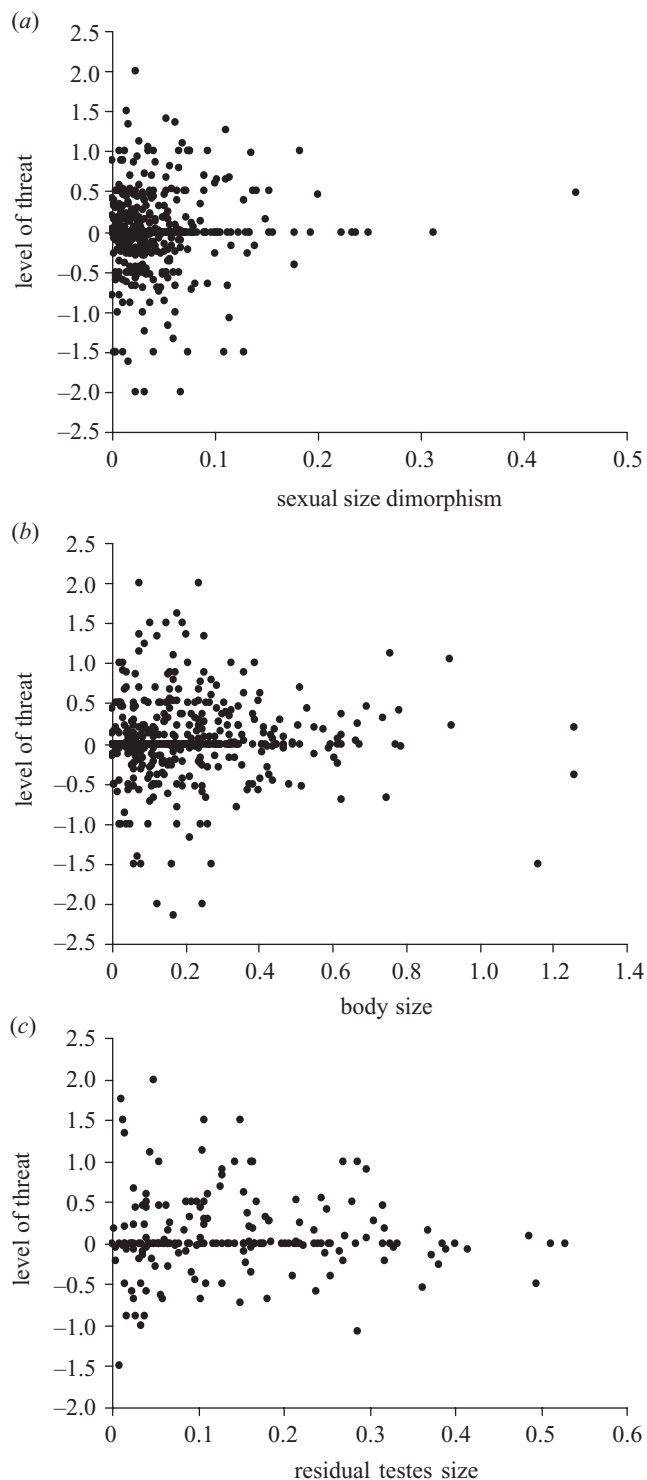


Figure 2. After controlling for phylogenetic inertia, the level of threat that each species currently experiences was also not related to (a) sexual size dimorphism, (b) body size or (c) residual testes size.

trend data ( $n = 453$ ,  $\beta = 0.100 \pm 0.051$ ,  $t = 1.952$ ,  $p = 0.347$ ).

Three mammalian orders within the dataset were large enough in themselves to generate a reasonable number of phylogenetically independent contrasts for body size and sexual dimorphism data when the risk of extinction was coded on a binary scale. These were the Carnivora ( $n = 103$  species), Rodentia ( $n = 302$ ) and Chiroptera ( $n = 250$ ).

The contrasts generated from these data did meet the statistical assumptions of the comparative method and so the results and  $p$ -values in this part are from non-randomized tests. Sexual size dimorphism was again found to be unrelated to risk of extinction in all three orders (Carnivora: mean =  $0.0199 \pm 0.019$ ,  $n = 15$ ,  $t = 1.061$ ,  $p = 0.307$ ; Rodentia: mean =  $0.0060 \pm 0.009$ ,  $n = 24$ ,  $t = 0.637$ ,  $p = 0.530$ ; Chiroptera: mean =  $-0.0031 \pm 0.007$ ,  $n = 45$ ,  $t = 0.437$ ,  $p = 0.664$ ). Body size was also found to be unrelated to extinction risk in the Rodentia (mean =  $0.0871 \pm 0.0469$ ,  $n = 24$ ,  $t = 1.855$ ,  $p = 0.076$ ) and the Chiroptera (mean =  $-0.0204 \pm 0.0215$ ,  $n = 45$ ,  $t = 0.950$ ,  $p = 0.348$ ), but members of the Carnivora that are currently at risk of extinction were found to have significantly larger body sizes than those not listed as threatened (mean threatened =  $0.0929 \pm 0.040$ ,  $n = 15$ ,  $t = 2.342$ ,  $p = 0.0345$ ).

#### (ii) Residual testes size

There was no evidence that residual testes size related to extinction risk when estimated using the binomial classification (mean =  $0.0384 \pm 0.0212$ ,  $n = 49$ ,  $t = 1.814$ ,  $p = 0.532$ ), the five-point scale ( $n = 186$ ,  $\beta = 0.323 \pm 0.200$ ,  $t = 1.614$ ,  $p = 0.664$ ; figure 2c), or the population trend data ( $n = 76$ ,  $\beta = 0.145 \pm 0.324$ ,  $t = 0.448$ ,  $p = 0.408$ ). However, a multiple regression of extinction risk measured on the five-point scale, using body size and testes size as covariates, was significant after randomization ( $n = 186$ ,  $F = 8.002$ ,  $p = 0.025$ ), with body size being significantly positively related to this measure of extinction risk ( $\beta = 0.280 \pm 0.114$ ,  $t = 2.451$ ,  $p = 0.009$ ), whereas testes size was not ( $\beta = 0.369 \pm 0.199$ ,  $t = 1.859$ ,  $p = 0.516$ ). Controlling for body size did not change the result for the population trend data ( $n = 76$ ,  $F = 0.973$ ,  $p = 0.475$ ). There were insufficient data available on testes sizes from individual orders and so it was not possible to examine these relationships at a more restricted taxonomic level as was done for the size dimorphism data.

## 4. DISCUSSION

We found no evidence that either of our two measures of the sexual-selection intensity in mammals is related to their current risk of extinction. These results were independent of the way in which the conservation status was measured, i.e. at the level of the genus, species or as a function of current population trends. We therefore failed to find any evidence in support of the theoretical predictions that sexual selection can either reduce (Proulx 1999; Whitlock 2000; Agrawal 2001; Siller 2001) or increase the likelihood of extinction (Tanaka 1996; Kondrashov & Kondrashov 1999). These results are also in disagreement with current evidence from other comparative studies that did find significant relationships between sexual selection and extinction risk (McLain *et al.* 1995, 1999; Sorci *et al.* 1998; Legendre *et al.* 1999; Brashares 2003; Doherty *et al.* 2003; Morrow & Pitcher 2003). Explaining why some taxa are more vulnerable to extinction than others is one of the most important goals of conservation biology. Furthermore, the ability to predict which groups are likely to be at highest risk would be extremely useful. However, these results suggest at present that the level of sexual selection experienced by a taxon is unlikely to contribute much to a



predictive model, at least for mammals (Purvis *et al.* 2000a).

The comparative approach we employed here, to examine how the intrinsic level of sexual selection of a species influences their vulnerability to extinction, is potentially a powerful one, because the conservation status of every mammal has been assessed and because extinction probabilities are seen to be dependent upon the characteristics that each species has, and therefore it is important to control for shared phylogenetic history (Purvis *et al.* 2000b). An important question to resolve, then, is why the results from this study are not in line with either theory or with previous evidence. There may of course, be no functional relationship between sexual selection and extinction risk. Unfortunately, there is currently no consensus within the theoretical literature as to what, if any, effect sexual selection may have upon populations near an extinction threshold (Kokko & Brooks 2003). However, so far, relatively little attention has been paid by theoreticians to this question and given that several other comparative studies have detected significant trends, it would be premature to claim that there is no causal link on the basis of this single study. Further development of the theoretical base of this question should clearly be encouraged.

Another possible answer as to why we failed to see any correlation between extinction risk and sexual selection is that the signal-to-noise ratio in our dataset is too low. There are a number of ways in which this may have arisen. First, the surrogate measures of sexual-selection intensity may be unreliable estimates of the true level of sexual selection experienced by a species. We believe this to be unlikely because there is a great deal of evidence in support of the theory that sexual selection is driving the evolution of testes size and sexual dimorphism (see, for example, Fairburn 1997; Gomendio *et al.* 1998; Lindenfors & Tullberg 1998; Taggart *et al.* 1998; Dunn *et al.* 2001; Hosken *et al.* 2001a; Lindenfors *et al.* 2002; Preston *et al.* 2003).

A second reason could be that the ecological breadth of the species included in this dataset may be so large as to confound any attempt to uncover any correlations between sexual selection and extinction risk. Because our dataset covers an enormous taxonomic range representing a large proportion of the entire mammalian fauna (*ca.* 21% of all extant species are included, representing 25 out of 26 mammalian orders), the diversity in ecology displayed by these species is also immense. This may be especially important because Purvis *et al.* (2000a) have shown that the particular attributes that contribute significantly to a species's vulnerability may differ among taxonomic groups. However, in the more restricted analyses of data from carnivores, rodents and bats in isolation we still found no indication that sexual size dimorphism was related to extinction risk (small sample sizes prevented us from conducting meaningful analyses using testes size data for these groups). Moreover, although the ecological diversity represented in our dataset is high we also captured a large portion of the standing variation in sexual-selection intensity and extinction risk. It is difficult to determine just how important the variation in ecology could be in confounding our analyses, and although we found little evidence of a relationship between body size and extinction risk (something that other authors have previously found), except when the data for carnivores were analysed separ-

ately, the exact nature of the threat may be important in determining whether it is the larger- or smaller-bodied animals that are most at risk of extinction (Owens & Bennett 2000).

Finally, and perhaps most importantly, the suite of contemporary extrinsic and/or anthropogenic factors experienced by members of the Mammalia could be the source of a considerable amount of noise, reducing the likelihood of detecting possible relationships caused by the intrinsic factors examined here. This is not a new idea and has already been suggested by other authors as a likely explanation as to why they failed to find significant associations between a variety of intrinsic factors and extinction risk (Duncan & Lockwood 2001; Fisher *et al.* 2003), although other studies have been very successful in explaining large amounts of the variation in extinction risk (Bennett & Owens 1997; Purvis *et al.* 2000a; Jones *et al.* 2003). From an evolutionary biologist's viewpoint, it would be doubly tragic if the negative impact that humans are currently having upon many taxa is so extensive that not only are we currently seeing one of the largest extinction crises in geological history (Diamond 1989), but this is hindering our ability to examine the more subtle underlying mechanisms of extinction. Controlling for the effect of anthropogenic extrinsic factors would be difficult because information about the extent to which human activities have influenced the conservation status of each species would have to be estimated, and if the effect size were large enough, this would make any attempt to control for its effect somewhat futile. This situation is further complicated because not only do different taxa apparently respond to the same threat in different ways, but also species respond to different threats in different ways (Owens & Bennett 2000; Isaac & Cowlshaw 2004). Nonetheless, comparative studies that have included both intrinsic and extrinsic factors have been successful in explaining significant portions of the variation in extinction risk seen across taxa (e.g. Purvis *et al.* 2000a; Fisher *et al.* 2003). Thus, if estimates of sexual-selection intensity could be included in these models then we may achieve a clearer picture of how sexual selection relates to extinction risk.

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