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Sexy to die for? Sexual selection and the risk of extinction

Hanna Kokko[1,2] & Robert Brooks[3]

[1)] *Department of Biological and Environmental Science, University of Jyväskylä, FIN-40014 Jyväskylä, Finland (e-mail: hanna.kokko@jyu.fi)*
[2)] *School of Botany and Zoology, Australian National University, Canberra, 0200, A.C.T., Australia*
[3)] *School of Biological, Earth and Environmental Science, The University of New South Wales, Sydney, 2052, N.S.W., Australia*

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Sexual selection is a field with a strong focus on the 'costs' of traits. However, whether such costs have an influence on the demography of the population is very rarely discussed. Here we present various processes through which sexual selection might have an impact on population viability and thus increase or decrease the risk of extinction. We argue that evolutionary 'suicide' — as sometimes suggested e.g. to have caused the extinction of the Irish elk — is unlikely in deterministic environments, except if costs are not paid by the same individual that bears the trait. Thus, intra- or inter-locus sexual conflict could in principle drive a population extinct, and we do not know why this does not frequently happen. Whether sexual selection increases or decreases extinction risks when populations face variable or unforeseen environmental conditions is likewise unknown, and we outline mechanisms that could account for either pattern. Inbreeding is another factor that could either increase or decrease population viability in sexually selected species. Inbreeding may be caused by a high mating skew, but it could also be reduced if females adaptively choose mates to avoid inbred offspring. Finally, when intraspecific competition for resources is taken into account, it is unclear how individual viabilities translate to extinction risks faced by the population. We show an example where greater mortality of males due to sexual dimorphism improves the carrying capacity of the environment, and thus presumably population viability.

Introduction

Over the past two decades, sexual selection has become an extremely popular topic of evolutionary study. One reason may be the intellectual challenge of explaining the existence of traits that at first sight appear maladaptive — the peacock's tail being a famous example (Andersson 1994). There are three main ways in which sexual selection can bring about the evolution of such 'apparently maladaptive' or, more correctly, 'costly' traits. Male–male competition favours traits that enable males to outcompete each other, even when the trait concerned reduces expected survival (e.g. Moore & Wilson 2002). Female choice may also favour male traits that lower male life expectancy (Zahavi 1975) and/or the survival or fecundity of sons and/or daughters (Brooks 2000). Last, sexual selection results in conflict between the sexes which may have costly consequences: for example, sexual harassment by males can result in lower female fecundity or even death (e.g., Chapman *et al*. 1995, Reale *et al*. 1996).

One of the triumphs of modern evolutionary biology is the ever-improving ability to explain how individuals benefit from being a successful competitor, an attractive male or a choosy female in ways that outweigh the considerable costs. Moreover, the pervasiveness of intersexual conflict as an evolutionary force is becoming ever more apparent (Rice & Holland 1997, Rice & Chippindale 2001). The demographic consequences of costs arising from sexual selection have, however, seldom been explored. Is sexual selection generally expected to lead to situations where survival of individuals is compromised? If so, is this reflected by population persistence times? Perhaps sexual selection could prove an example of an evolutionary process where the survival of an entire population, or a species, may become endangered. These questions are relevant to the broader debate in evolutionary biology about whether evolution can ever lead to deterministic 'suicide' of a population (Matsuda & Adams 1994a, 1994b, Ferrière 2000, Gyllenberg & Parvinen 2001). Even though it is well known that sexual selection can cause male and/or female phenotypes to diverge from naturally selected optima (Lande 1980, 1987), consequences such as a possible increase in extinction risk have rarely been discussed (for exceptions, *see* Tanaka 1996, Houle & Kondrashov 2002, Møller 2003 and references therein).

In contrast to the arguments outlined above regarding the costs that arise as a consequence of sexual selection, there may be good reason to expect that sexual selection may reduce the chances of population extinction. There is considerable evidence that mating success is positively correlated with 'genetic quality' within populations (Møller & Alatalo 1999, Jennions *et al*. 2001). The Fisher-Zahavi model of the evolution of mate choice (Eshel *et al*. 2000, Kokko *et al*. 2002, 2003) requires that females mating with attractive males bear offspring with 'good genes' as a consequence. Whitlock (2000) shows that if deleterious mutations reduce mating success, then sexual selection will prevent the fixation of such alleles, allowing relatively small populations to avoid extinction as a consequence of genetic decay. Other authors have demonstrated that sexual selection can facilitate the shedding of mutational load (Agrawal 2001) and accelerate adaptive evolutionary change (Proulx 1999, P. D. Lorch *et al*. unpubl.). These outcomes are likely to influence not only population persistence time but other important phenomena such as the rate of adaptation to new environments and the maintenance of sex (Proulx 1999, Agrawal 2001, P. D. Lorch *et al*. unpubl.).

The goal of this paper is not to give a definitive answer to whether sexual selection increases or decreases the vulnerability of a population to extinction. Instead, its purpose is to draw attention to some dynamics that may be important and, hopefully, to encourage research in a little studied field. We will provide several sketches of models of how sexual selection and extinction risk could be related.

Trade-offs between viability and male traits: Did the Irish elk go extinct because of its antlers?

Megaloceros giganteus, the 'Irish elk', has been extinct for about 10 000 years (Moen *et al*. 1999). Adult males grew the largest antlers — up to 40 kg — of any extinct or extant cervid (Gould 1974). A popular image is that the antlers simply grew too large for the animals to be viable: O'Rouke (1970: p. 111) speculates that extinction may have been 'the result of the excessive size of the antlers which made it difficult for the animals to feed'. To this date, such speculation remains popular: a characteristic anonymous web page (http://www.ucmp.berkeley.edu/mammal/artio/irishelk.html) states that 'the Irish elk finally went extinct when the antlers became so large that the animals could no longer hold up their heads, or got entangled in the trees.' Somewhat more scientifically, Moen *et al*. (1999) estimated the energetic requirements for antler growth in this species and suggest that an inability to evolve smaller antlers quickly enough during a climate change event 10 600 years ago contributed to the extinction of the species. Gould (1974) likewise suggests that the antlers became a too heavy burden in this climatic and habitat change.

There is little doubt that adaptations that improve a male's mating success can be detrimental to his survival (Promislow 1992, Promislow *et al.* 1992, Owens & Bennett 1994, Moore & Wilson 2002). This applies both to 'armaments' used in male-male competition, and to 'ornaments' favoured by choosy females. Note that larger traits can be more detrimental despite the fact that in comparisons between individuals ornamental traits often correlate with higher viability (de Jong & van Nordwijk 1992, Jennions *et al.* 2001). But can these detrimental effects drive a population extinct?

Consider a polygynous population, where males express a trait that improves their mating success over other males, but at a cost of reduced viability. It seems to us that evolutionary suicide — i.e. deterministic evolution towards extinction in a constant environment — is impossible in this scenario. Regardless of the details of the species' life history, extinction would require that too few males survive to maturity to fertilize a sufficient number of females to maintain a viable population. Since we are assuming that detrimental effects are evident in males only, a male which survives better than average would in this situation encounter a large number of surviving females, and virtually no competitors. The cost of being an inferior competitor must, therefore, diminish and disappear when surviving males become scarce. Selection must, therefore, favour the less extreme male genotypes, and it appears impossible to generate a scenario where males with larger antlers are still selected for when the lifetime reproductive success of males with large antlers approaches zero (as required for deterministic extinction to occur).

Formally, assume that the annual mating success of a more extremely armed male is M, and his expected lifespan is L, while the less well armed competitor mates and survives according to m and l. If lifetime reproductive success are ML and ml, respectively, selection will only favour a further increase in antler size if $ML > ml$, that is, $M/m > l/L$. Since l/L tends to infinity as L tends to zero, the equation can only remain true with ever-decreasing L if the mating success of inferior competitors is zero. Suicide, thus, only happens if a better armed male, in the rare case when he survives, is able to monopolize every single female in the population. Such extreme monopolization ability must be regarded as unlikely when females vastly outnumber the poorly surviving males, so that less heavily-armed males must have good opportunities to find unfertilized females.

While deterministic 'suicide' thus appears very difficult to envisage based on trade-offs between male mating success and viability, the situation may be radically different in variable environments. McLain (1993, McLain *et al.* 1995) suggested that sexually selected males may be adaptively compromised in other respects, such as performance with respect to environmental change or coevolutionary responses of parasites, predators or prey. While the above modelling sketch suggests that in constant environments such compromises should become balanced before extinction occurs, the matter could be different under variable or unforeseen circumstances (Tanaka 1996).

We examine this with a simple stochastic model. We assume simply that the proportion x of males with large antlers increases in 'good' years, due to their higher mating success. Large antlers, however, make males more vulnerable to adverse environmental conditions. The simplest way to picture this is that a 'bad' or catastrophic year occurs on average every T_C years. To provide a particularly simple and extreme example, we assume that a catastrophe leads to the death of all males with large antlers. At least some of the males with less developed antlers are assumed to survive the catastrophe. As a consequence, the population as a whole goes extinct if the proportion x reaches 1 before the catastrophe happens, but remains viable otherwise. A catastrophe always returns x to 0, and new large-antlered males have to arise by mutation.

Let us assume that starting from $x = 0$, a successful mutant that introduces $x > 0$ to the population arises, on average, every T_0 years, and it takes a further sequence of T_1 good (non-catastrophic) years before it becomes fixed in the population. Mutations as well as catastrophes occur as a Poisson process. The time interval

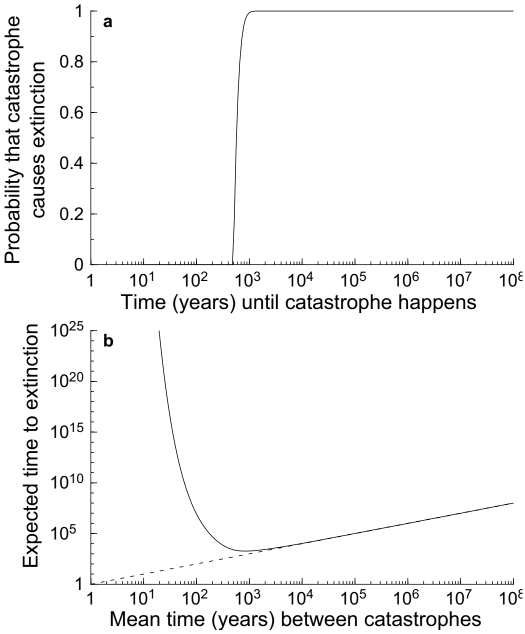

Fig. 1. Predictions of the stochastic trade-off model with T_0 = 500 years, T_1 = 100 years. — **a**: Probability that a catastrophe extirpates the population when it arrives after a given number of 'good' years. The probability equals zero for time intervals smaller than T_1 = 500. — **b**: Expected time to extinction (solid line) when catastrophes occur according to a Poisson process, with average time between catastrophes as indicated. The dotted line indicates solutions where the expected time to extinction equals the expected time to the first catastrophe.

between catastrophes is, therefore, exponentially distributed (parameter $1/T_C$). The expected time to extinction, $E[T_E]$, obeys a relatively complicated relationship to T_0, T_1 and T_C (derived in the Appendix). However, when the interval T_C between catastrophes is large compared to T_0 and T_1, the expected time to extinction simplifies to $T_C + 2T_0 + T_1 \approx T_C$. This means that when catastrophes are rare, the population will remain viable until the first catastrophe happens, but no longer after that.

Figure 1a graphs the probability ($p(t)$) that a catastrophe causes extinction of the sexually selected population if it occurs after T years, when the trait that makes males vulnerable to catastrophes successfully invades on average every 100 years, and takes 500 years after successful invasion to become established. Figure 1b depicts the expected time to extinction of the population given an average interval T_C between catastrophic years. Note that a non-sexually selected species ('small antlers') persists indefinitely under our assumptions. The expected time to extinction in the sexually selected species is non-linear: if catastrophes are very frequent, the evolution of the vulnerable type is kept at bay, and extinction is unlikely to occur. In Fig. 1b, the expected time to extinction exceeds 10^{25} years if $T_C < 20$, which is many orders of magnitude longer than the currently estimated age of the universe (approximately 10^{10} years, Freedman 2000, Cayrel *et al.* 2001). This simply means that populations evolve to 'take into account' challenges that occur frequently. If catastrophes are very infrequent, extinction of the sexually selected population will be almost certain to occur once a catastrophe happens (as there will have been time for the vulnerable mutant to spread, Fig. 1a), but it takes a long time before this happens, thus the expected time to extinction again increases with very infrequent catastrophes (Fig. 1b with large T_C).

According to this model, sexual selection may cause finite persistence times for otherwise indefinitely persisting populations, and rare unforeseen circumstances can prove fatal. Recent anthropogenic change in the environments worldwide is a clear example of unforeseen environmental change. As a special case, human introductions of species to novel environments can be interpreted as a novel environmental challenge. McLain *et al.* (1995) used a database of introduction success to investigate whether brightly dimorphic (and thus probably sexually selected) bird species fail more often when introduced to tropical islands (Oahu and Tahiti). They find support for the idea, and additionally show that the probability of extinction increased with the number of species already introduced — possibly suggesting that sexually selected species perform poorly in interspecific competition. Sorci *et al.* (1998), and McLain and Vives (1998) have found similar patterns in birds and beetles, respectively.

However, Prinzing *et al.* (2002) analyzed a dataset on recent changes in population sizes in European birds (Central European non-passeriformes), and report that plumage dimorphism is unrelated to population responses to recent anthropogenic change. Similarly, Badyaev (1997), and Badyaev & Ghalambor (1998) found mixed support for the idea that sexually selected species are less able to cope with altitudinal variation in their species ranges. Thus, the evidence that trade-offs between sexual selection and other forms of adaptation may result in increased extinction probabilities is currently equivocal. Our model simply made the assumption that there is a trade-off — the male phenotype that was inferior in intrasexual competition was *a priori* assumed to be able to survive catastrophic years. Whether this assumption should hold, requires much more empirical and theoretical study. The matter is probably complicated by the fact that sexual traits often show condition-dependence (e.g. Kotiaho *et al.* 2001), so that superior males might simply reduce trait expression in harsh conditions.

Sexual conflict

Even though every offspring in diploid species has one mother and one father, the reproductive interests of the mother and the father rarely coincide completely. First, genes that are beneficial in males can have harmful effects if they are expressed in females, or vice versa (intralocus conflict: Chippindale *et al.* 2001, Rice & Chippindale 2001). Second, one sex may behaviourally harm the interests of the other (interlocus conflict: Rice 1996, Rice & Holland 1997). For example, a gene that makes male water striders or gammarids physically guard a female can harm female feeding efficiency or fecundity (Rowe *et al.* 1994). Generally, as the importance of sexual selection increases in a population, so the likelihood increases that male adaptations will evolve that incidentally inflict harm on females (Brooks & Jennions 1999). Since reproduction in a population relies on female fecundity, if sexual selection results in widespread fecundity costs to females, it may also have important demographic consequences. A clear experimental demonstration of this effect was provided by Holland and Rice (1999) who minimised the potential for sexual conflict (by enforcing monogamy in *Drosophila melanogaster* for 47 generations), and reported an increase in net reproductive rate compared with controls in which males competed for the chance to mate with females.

We shall consider intralocus conflict to show that sexual conflict can indeed threaten the survival of a population. We consider a trade-off where an allele A that causes higher competitive ability in males (by enhancing his mating success) comes at a cost of reduced fecundity when expressed in a female. We assume that mating success of males improves by a factor of m, while fecundity of females is reduced to a factor of f, when the individual has the A allele, as compared with the mating success and fecundity of individuals with allele a. Assuming haploid inheritance and equal survival of males and females, it is easy to calculate changes in the proportion, x, of allele A in the population. First, the proportion of fathers who carry the A allele is biased upwards, due to their higher mating success: $p_A = mx/[mx + (1 - x)]$. An offspring may inherit the A allele either if both parents were A (number of such offspring $n_{A1} = fxp_A$), if the father was A but the mother not ($n_{A2} = p_A(1 - x)/2$), or if the mother was A but the father was not ($n_{A3} = fx/2(1 - p_A)$). These have to be compared with the numbers of offspring having allele a, $n_{a1} = p_A(1 - x)/2$, $n_{a2} = fx/2(1 - p_A)$, and $n_{a3} = (1-x)(1-p_A)$, for fathers, mothers or neither having allele A, respectively. The new frequency of A is $x(t + 1) = (n_{A1}(t) + n_{A2}(t) + n_{A3}(t))/(n_{A1}(t) + n_{A2}(t) + n_{A3}(t) + n_{a1}(t) + n_{a2}(t) + n_{a3}(t))$. Solving for equilibria $x(t + 1) = x(t)$, one finds three possible equilibria that can be stable or unstable: 0, 1, and $(2 - m - f)/[2(1 - m - f + mf)]$.

Figure 2a shows an example where 0 and 1 are unstable equilibria, and the intermediate equilibrium is stable. To illustrate, this example uses rather extreme values for m and f: the allele A causes five times higher mating success ($m = 5$), but reduces female fecundity by 70% ($f = 0.3$). Negative frequency dependence maintains A at a proportion of 59%; at higher frequencies, the relative competitive advantage of A diminishes, as most males now harbour the A allele. The key question regarding population stability is: if 59% of females suffer a 70% reduction in fecundity, can this result in population extinction? Clearly, the answer depends on how large their fecundity

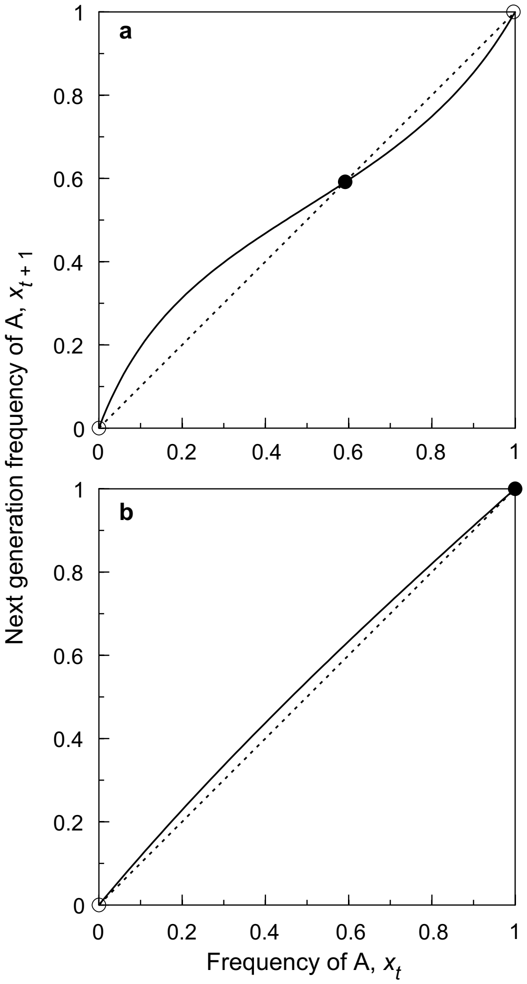

Fig. 2. Allele dynamics in the haploid sexual conflict model. The solid curve gives the frequency x_{t+1} of the allele *A* in generation $t + 1$, given its frequency x_t in generation *t*. Where the curve lies above the $x_t + 1 = x_t$ diagonal (dotted line), the frequency of *A* will increase. Open and solid dots indicate unstable and stable equilibria, respectively. — **a**: allele *A* brings about a five-fold benefit to males and a 70% reduction in female fecundity ($m = 5$, $f = 0.3$), and results in a polymorphism with 59% frequency for *A*. — **b**: both the benefit to males and the cost to females is slighter ($m = 1.5$, $f = 0.9$), and *A* evolves to fixation.

is in terms of absolute number of offspring. If fecundity (number of same-sex offspring) is 1.75 for '*a*' females, the average population growth rate is still 2.7% when *A* is at equilibrium (since $0.41 \times 1.75 + 0.59 \times 0.3 \times 1.75 = 1.027$). But if it is 1.65, the population will go deterministically extinct once the frequency of *A* reaches its equilibrium: $0.41 \times 1.65 + 0.59 \times 0.3 \times 1.65 = 0.9685$. There is nothing that selects against the 'selfish' allele *A*, even as population density reaches critically low levels (Fig. 3).

The intermediate equilibrium for *A* does not always exist (the value of $(2 - m - f)/(2(1 - m - f + mf))$ does not always fall between 0 and 1), but the problem is not diminished in these cases: in Fig. 2b, the harmful allele *A* becomes fixed regardless of population size.

We have phrased the conflict at an intralocus level, but there is no reason to expect populations would not face similar problems in interlocus conflicts. Vamosi and Otto (2002) describe a model of insect-pollinated dioecous plants, in which they show first that as pollinators become common, and females are unlikely to be pollen-limited, male investment in attractive flowers should outstrip female investment, resulting in increased sexual dimorphism in flowers. They then show that this dimorphism makes a population vulnerable to extinction if there is a stochastic decrease in pollinator numbers. This is because the few pollinators that are present are attracted to male flowers, and the resulting female pollination limitation causes marked reductions in fecundity.

If evolution can lead to extinction under sexual conflict, and sexual conflict is as widespread an evolutionary force as some suggest (Rice & Holland 1997, Rice & Chippindale 2001), why don't all species fall victim to this process and become extinguished? We currently have no answer to this question. One possibility is that females are strongly selected to develop countermeasures to antagonistic male adaptations (Arnqvist & Rowe 2002), and tend to do so quickly enough that extinction is avoided. Another is that extinctions indeed commonly occur: Vamosi and Otto (2002) speculate that dioecous plants are typically wind-pollinated because pollinator-dependent dioecous species have gone extinct. The effect of sexual selection on extinction rates within clades provides several intriguing opportunities for comparative study.

Muir and Howard (1999) consider the interesting possibility that an allele that is strongly favoured by sexual selection but has some associated large viability or fecundity disadvantage may rapidly become fixed in a population and result in its eventual extinction. They further point out that many transgenes, such as a gene for superenhanced growth in salmon, may fit these criteria. If such 'Trojan genes' find their way into natural populations (such as when transgenic individuals escape), their increase in frequency by sexual selection may bring about extinction.

Evolutionary suicide thus appears possible when the costs of a trait are not paid by the same individual who enjoys the benefits (compare the model of this section to the impossibility of suicide in the deterministic case of male trade-offs, above). Theory, thus, cannot rule out the possibility that the Irish elk went extinct because males hungry for nutrients ate all the grass that could have fed females! We will return to this scenario below when considering density dependence.

Female choice

So far, we have concentrated on processes that could make a sexually selected population more vulnerable than one where sexual selection is absent or weak. By contrast, studies on female choice have typically emphasized how it selects for high-quality males (Zahavi 1975, Andersson 1994, Jennions *et al.* 2001, Møller & Alatalo 1999, Whitlock 2000). Sexual selection due to mate choice could, thus, reinforce natural selection and lead to quicker responses to environmental changes, should they occur (Proulx 1999, P. D. Lorch *et al.* unpubl.). For example, a mutation that enhances parasite resistance will spread through the population more quickly if females choose males that signal their parasite-free state (Hamilton & Zuk 1982).

Mate choice may evolve by indirect selection when attractive males bestow genes for increased fitness on offspring (Fisher 1930, Zahavi 1975). These fitness benefits may be in increased survival or fecundity, but they may equally be for increased male attractiveness at the expense of survival and fecundity (Eshel *et al.* 2000, Kokko *et al.* 2002). Mate choice can have opposite consequences for offspring of different sexes: for example, in a declining population of barn swallows *Hirundo rustica*, an increase in a condition-dependent sex trait was associated with a temporal reduction in survival in males, but increased survival in females (Møller & Szep 2002). It is, therefore, possible that mate choice may drive sexual selection that has either positive or negative consequences for population productivity and thus probability of persistence (Tanaka 1996, Whitlock 2000).

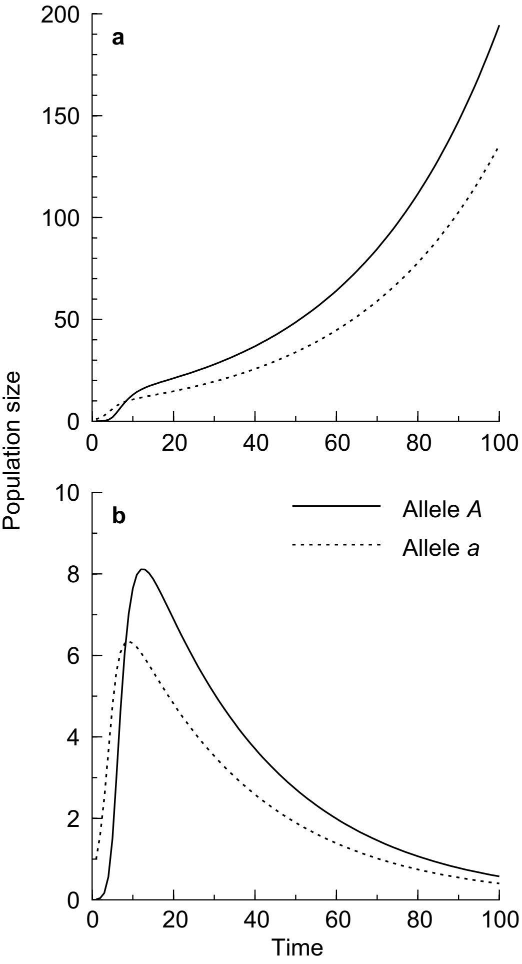

Fig. 3. Dynamics of a population that has sexual conflict as in Fig. 2a, and starts from a population size of unity, with a 1% frequency of the *A* allele, at time $t = 0$. — **a**: each female produces $F = 1.75$ female offspring (and an equal number of male offspring); — **b**: $F = 1.65$. In both cases, the frequency of *A* evolves to exceed that of a (stable equilibrium has 59% *A*, as predicted in Fig. 2a). In panel **a**, females are fecund enough that the prevalence of *A* does not limit population growth. In panel **b**, the population evolves towards extinction: the frequency of *A* does not diminish even though it causes a deterministic population decline with an asymptotic growth rate 0.9685.

Houle and Kondrashov (2002) discuss a theoretical case where evolutionary suicide appears possible under female choice for genetic benefits. This may seem paradoxical in light of the fact that meta-analysis reveals that females tend, on average, to choose males that survive longer than non-chosen males (Jennions *et al.* 2001). Thus mate choice might be expected to result in the evolution of increased mean male lifespan (*see* also Whitlock 2000). The costs of producing attractive signals, however, are often exacted in reduced viability (Folstad & Karter 1992, Promislow 1992, Promislow *et al.* 1992, Kokko 1997), such that in populations where mate choice imposes the strongest sexual selection, mean male viability might be depressed the most, irrespective of the relationship between viability and attractiveness within populations. Moreover, it is unclear how directly survival of individuals (especially males) relates to population extinction, for reasons that we will discuss in the next section.

In species where females receive direct benefits from their chosen mate (including the minimization of fecundity costs), it is conceivable that stronger sexual selection (and thus greater benefits or lower costs) may result in increased female survival and condition. This may result in increased female fecundity as well as improved offspring viability and fecudity due to nongenetic maternal benefits (Møller & Jennions 2001). Likewise, when the benefit of mating with an attractive male is high-quality parental care that results in improved offspring survival and fecundity (Hunt & Simmons 2000), strong sexual selection may intuitively be expected to enhance the probability of population persistence. Things are unlikely to be this straightforward, however. For example, the effects of competition among males to provide benefits may also impact on population dynamics. There are several questions here ripe for empirical study.

To complicate matters further, female choice that favours a subset of males leads to smaller effective population sizes. Inbreeding depression can pose significant threats to population survival (Frankham 1995, Saccheri *et al.* 1998, Daniels & Walters 2000, Keller & Waller 2002). And again, the coin has two sides: females may adaptively avoid the accumulation of inbreeding, so that female choice might increase effective population size. Avoiding mating with relatives is an obvious mechanism (Pusey & Wolf 1996, Blomqvist *et al.* 2002), but more subtle suggestions include mating strategies that select for genetically diverse mates (Amos *et al.* 2001a, 2001b). Inbreeding avoidance does not necessarily require abilities to discriminate kin: for example, in the black grouse, inbred males perform poorly on leks and are consequently avoided by females (Höglund *et al.* 2002). In guppies members of both sexes prefer to court and mate with unfamiliar individuals (Hughes *et al.* 1999, Kelley *et al.* 1999), and this is likely to result in higher levels of outbreeding. We can only conclude that the influence of mate choice on population viability needs much more study.

Intraspecific competition and density dependence

Above, we have pointed to the asymmetry of the demographic importance of males and females: reproduction of females is crucial, whereas males are to some extent replaceable (Ginsberg & Milner-Gulland 1994, Kokko *et al.* 2001, Mysterud *et al.* 2002). Since males and females usually consume, at least partially, the same resources, intraspecific competition might be an important factor to consider before we can assess how male or female survival relates to threats of extinction.

Sexual selection in males often leads to size dimorphism (Lande 1980, Andersson 1994). Larger-bodied males as a rule consume more resources, and thus, strong sexual selection may increase male competition for resources that limit female fecundity. By contrast, males often have elevated mortality rates (Promislow 1992, Promislow *et al.* 1992, Zuk & Kolluru 1998, Moore & Wilson 2002), and they thus might leave more resources to females if strongly sexually selected. We demonstrate such effects with another simple model.

Consider an island with a population of deer. Resources (‘grass’) grow at a fixed rate g. The total resource level is G. We denote the number of male deer by M, and the number of females by

F. Male and female deer eat grass with a type II functional response (Holling 1965): each female consumes grass at a rate $\ln(G + 1)$, and each male at $\gamma\ln(G+1)$. γ is a parameter that describes how much more food males consume than females ($\gamma \geq 1$).

For simplicity, fecundity is fixed: number of births (of each sex) equals rF, where r is a constant and F is the number of females. Density dependence operates through mortality. Female mortality is inversely related to resources, $\mu_F = G^{-1}$. Male mortality is greater by a factor v: $\mu_M = vG^{-1}$, where the parameter $v \geq 1$ describes male vulnerability.

The dynamics of the deer population is governed by three equations: the growth of grass, the growth of the male population, and the growth of the female population:

$$dG/dt = g - M\gamma\ln(G + 1) - F\ln(G + 1)$$

$$dM/dt = rF - \mu_M M$$

$$dF/dt = (r - \mu_F)F$$

From this one can solve the equilibrium:

$$G = r^{-1}$$

$$M = \frac{g}{(\gamma - v)\ln(1 + r^{-1})}$$

$$F = \frac{g}{(\gamma/v + 1)\ln(1 + r^{-1})}$$

Unsurprisingly, the more males consume relative to females (the higher γ is), the smaller the stable population size of both males and females. Again unsurprisingly, higher vulnerability of males (higher v) results in a smaller equilibrium number of males — but it also allows a *larger* number of females to exist. And, potentially surprisingly, the total population size becomes larger ($M + F$ increases) if males become more vulnerable (Fig. 4). Larger populations are generally thought to be safer from extinction (Gilpin & Soulé 1986, Fiedler & Jain 1992, Caughley 1994), and the number of females is clearly of particular importance. Thus, an increase in the mortality of males as a result of sexual selection — if sexual selection has this effect in the first place, *see* above — is not necessarily bad news regarding the survival of the population.

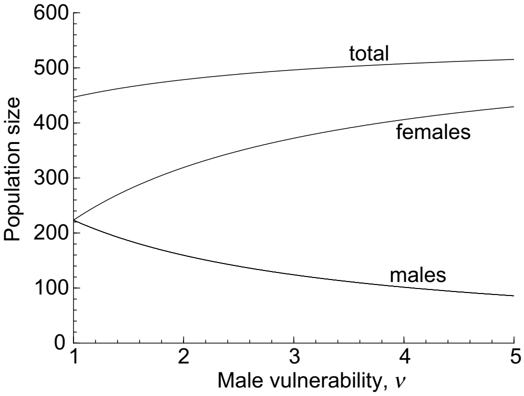

Fig. 4. Equilibrium population sizes in the density-dependent model when males are equally (v = 1) or more (v > 1) vulnerable than females. The more vulnerable the males, the larger the equilibrium populations. Other parameters: 1000 units of resources grow in the area in a time unit (g = 1000), males eat 50% more than females (γ = 1.5), and birth rate r = 0.2.

One should add, however, that if sexual selection increases male resource demands more strongly than it increases male vulnerability ($\gamma > v$), population sizes of both females and males will suffer as a consequence of sexual selection.

Discussion

It is remarkable how little is known about how ‘costs’ of sexually selected traits relate to the demography of populations. We are particularly uncertain about the direction in which sexual selection will influence extinction risks. As a general pattern from our preliminary modelling efforts, it appears that sexual selection can increase extinction risks and even result in evolutionary suicide, but this seems to be limited to cases where the costs of mating competition are not paid by the same individual who gains the benefits. If males gain an upper hand in sexual conflict, females — who are ultimately responsible for the ‘survival of the species’ — may suffer to an extent that the result is population extinction. Where males alone suffer the consequences, we do not expect sexual selection to drive a population extinct, except possibly in unforeseen environmental circumstances. Due to the nature of intraspecific competition, higher mortality of males can in fact enhance population viability. The possibility also remains that natural and sexual selection may act in the same direction, improving adaptation and enhancing the chances of population persistence (Whitlock 2000).

However, in all the sections of this paper we have noted caveats and additional factors that warrant further study: for example, the role of inbreeding remains highly unclear. It may be that individuals mate adaptively to avoid inbreeding (Blomqvist *et al.* 2002), so that sexual selection is advantageous at the population level too; or skewed mating success could instead promote inbreeding (Falconer & Mackay 1996). Moreover, our list of possible mechanisms by which sexual selection could influence population viability is by no means exhaustive. For example, sexual selection can have a profound influence on the dynamics of small populations via its effects on demographic stochasticity, including the possibility of generating Allee effects (Legendre *et al.* 1999, Møller & Legendre 2001). These mechanisms are described in greater detail elsewhere in this volume (Møller 2003).

Interspecific competition and hybridization are two other issues we have not touched on. Female choice may evolve in response to the danger of interspecific matings that produce less fit offspring (Veen *et al.* 2001). It is conceivable that the resulting sexual conflict, where males discriminate less strongly between conspecific and heterospecific mates than females, has similar ramifications for population viability as the intra- and interlocus conflicts described above. The questions regarding the importance of viabilities of individuals also become vastly more complicated when interspecific competition is included.

And, finally, sexual selection may influence biological diversity not only by altering the likelihood of extinction, but also by affecting speciation rates (Lande 1981, Turner & Burrows 1995, Payne & Krakauer 1997, Parker & Partridge 1998). For example, there is some evidence that species richness in birds is associated with the degree of dimorphism (Barraclough *et al.* 1995, 1998, Møller & Cuervo 1998, Owens *et al.* 1999, but *see* also Gage *et al.* 2002). Obviously, conservation problems will be different in a species flock of small populations than in the ancient single species.

Species with strong sexual selection are often bright, dimorphic and the details of their mating systems produce natural spectacles well known to the public. It is curious how little we know about the conservation needs of such species.

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Appendix

The expected time to extinction is given by the expression

$$E[T_{\mathrm{E}}] = \sum_{i=0}^{\infty} (1-P)^i P(iT_{\mathrm{V}} + T_{\mathrm{N}}) = T_{\mathrm{V}} \frac{1-P}{P^2} + T_{\mathrm{N}}$$

Here, T_{V} is the expected number of years between catastrophes that leave the population viable, T_{N} is the expected length of the last series of good years, ended by a catastrophe leading to extinction, and P is the probability that a population with $x = 0$ is starting its last series of good years, i.e. the series will end in a catastrophe that terminates the population.

P is calculated as

$$P = \int_{t=0}^{\infty} p(t)c(t)dt$$

where $p(t)$ gives the probability that a catastrophe that happens t years after the population has been reverted to $x = 0$ will lead to extinction, and $c(t)$ is the exponential probability distribution function of the time interval between catastrophes. $p(t)$ is given as

$$p(t) = \begin{cases} 0 & \text{if } t < T_1 \\ 1 - e^{-(t-T_1)/T_0} & \text{if } t \geq T_1 \end{cases}$$

and $c(t) = \exp(-t/T_{\mathrm{C}})/T_{\mathrm{C}}$. Therefore,

$$P = \int_{t=T_1}^{\infty} \left(1 - e^{-(t-T_1)/T_0}\right) \frac{e^{-t/T_{\mathrm{C}}}}{T_{\mathrm{C}}} dt = \frac{T_{\mathrm{C}}}{T_0 + T_{\mathrm{C}}} e^{-T_1/T_{\mathrm{C}}}$$

For T_{V} and T_{N}, we obtain the expressions

$$T_{\mathrm{V}} = (1-P)^{-1} \left[\int_{t=0}^{T_1} t \frac{e^{-t/T_{\mathrm{C}}}}{T_{\mathrm{C}}} dt + \int_{t=T_1}^{\infty} t e^{-(t-T_1)/T_0} \frac{e^{-t/T_{\mathrm{C}}}}{T_{\mathrm{C}}} dt \right]$$

$$T_{\mathrm{N}} = P^{-1} \int_{t=T_1}^{\infty} t\left(1 - e^{-(t-T_1)/T_0}\right) \frac{e^{-t/T_{\mathrm{C}}}}{T_{\mathrm{C}}} dt$$

Solving the integrals and simplifying, we find a (rather complicated) analytical expression for E[T_{E}]:

$$E[T_{\mathrm{E}}] = \frac{e^{T_1/T_{\mathrm{C}}} \left\{ \left[\left(e^{T_1/T_{\mathrm{C}}} - 1\right) T_{\mathrm{C}} - T_1 \right] (T_0 + T_{\mathrm{C}})^3 + T_1 (T_0 + T_{\mathrm{C}})^2 + T_{\mathrm{C}} T_0{}^2 + T_{\mathrm{C}}^2 T_0 \right\} + T_1 T_{\mathrm{C}}^3 + T_1 T_{\mathrm{C}}^2 T_0 + 2 T_{\mathrm{C}}^3 T_0 + T_{\mathrm{C}}^4}{T_{\mathrm{C}}^2 (T_0 + T_{\mathrm{C}})}$$

Note that the time to extinction tends to infinity when T_{C} tends to zero, and has a limit $T_{\mathrm{C}} + 2T_0 + T_1$ when T_{C} tends to infinity.