

# Sexual selection and extinction: why sex matters and why asexual models are insufficient

Anders Pape Møller

*Laboratoire de Parasitologie Evolutive, CNRS UMR 7103, Université Pierre et Marie Curie, Bât. A, 7ème étage, 7 quai St. Bernard, Case 237, F-75252 Paris Cedex 05, France (e-mail: amoller@snv.jussieu.fr)*

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Most studies of extinction risk and modelling of population viability do not take into account that higher organisms generally have two sexes, and that sex-specific demographic and other variables may play an important role in determining risks of extinction. I briefly review recent analyses of the importance of sex in demographic stochasticity and assessment of minimum populations required for maintenance of viable populations. Secondly, I review sex-specific factors that may influence such sex-specific demographic parameters. Thirdly, I review sex-specific extrinsic and intrinsic mortality factors that may contribute to increased risks of extinction. Finally, I review sex-specific genetic factors that may influence risks of extinction. Future empirical and theoretical approaches to assess extinction thresholds should consider the importance of sex.

## Introduction

The biodiversity crisis has prompted a strong theoretical development in conservation biology. In particular population viability analysis (PVA) (Soulé 1987, Boyce 1992, Burgman *et al.* 1993) has been used as a tool to predict the minimum size of a population needed for maintaining a viable population for a given period of time with a given probability. Initial modelling often did not consider demographic stochasticity effects, although such effects are important (Gabriel & Bürger 1992, Mode 1995, Kokko & Ebenhard 1996). Demographic stochasticity arises from the tyranny of small numbers because demographic parameters have mean values at the population level that are realised at the level of

individuals due to random effects. For example, survival may be 30% in a population, but 5 of 10 individuals in a small population may die for random reasons, exceeding the mean expected mortality. Demographic stochasticity effects are now being incorporated as standard into these predictive models.

Current models of extinction risk and meta-populations are excellent for asexual organisms, but hardly any such organisms are on the list of species at risk of extinction. These more advanced PVA models are not appropriate for sexually reproducing organisms because they typically are based on variation in survival and reproductive success (number of recruits contributed to the reproducing population) of adult females. Sex is hardly ever even considered

even though males may contribute considerably to variance components affecting survival and reproduction of the population. Interactions between individuals of the two sexes may be equally important. One reason for this neglect of sex in PVA models is that females are actually the sex producing the offspring, and they should therefore be more important when considering the stability of populations (Ginsberg & Milner-Gulland 1994). This oversimplification may have some merit by keeping models simple while still grasping the essential factors. However, simplification assumes that the factors that are being eliminated are unimportant. The general lack of tests of this assumption is the main problem with current models.

Does it matter that sex is included? If the effects of sex are small, we might consider this problem to be of an academic nature. How large are the effects of sex on the risk of extinction? Several studies have indicated that effects of sex can increase the risk of extinction several-fold (Caswell & Weeks 1986, Daley *et al.* 1986, Legendre *et al.* 1999, Møller & Legendre 2001). With sex included in models there are many more ways in which a population can go extinct because density- and frequency-dependent processes can now operate in an additional dimension. These processes may influence population dynamics in two ways: one relates to the acquisition of mates and the other relates to the sex ratio. There have been few attempts to answer questions concerning the importance of sex for extinction risk, but this will be reviewed below. The population dynamics may differ between one-sex and two-sex models, and the stability of the dynamics may be of general importance (Lindström & Kokko 1998).

Which are the factors contributing to sex-specific demographic stochasticity? All demographic parameters can potentially have sex-specific mean and variance expectations and thereby contribute to sex differences that can affect demographic stochasticity. The exact mechanisms resulting in such effects are extrinsic and intrinsic factors affecting mortality and reproduction. In addition, sex-specific genetic factors such as sex-specific mutation rates and their consequences may also contribute to increased

demographic stochasticity. While the importance of these factors through their effects on mate acquisition and sex ratios has not been evaluated, I emphasise that a list of such factors will allow future studies to systematically address their importance for extinction risk.

The aims of this paper are to review (1) the relationship between demographic stochasticity and sex; (2) extinction and sex-specific effects of extrinsic and intrinsic factors; and (3) extinction and sex-specific genetic effects. By doing so I hope to put the emphasis on these problems that they deserve.

## Demographic stochasticity and sexual selection

Demographic stochasticity depends on the chance realisation of demographic parameters at the individual level. Variance in demographic parameters that is specific to or predominant in one sex may have important consequences for the risk of extinction. I briefly review a demographic stochasticity analysis, using birds introduced to New Zealand as an example. In the section 'Allee effects and sexual selection', I briefly discuss how sexual selection may act as an Allee effect that caused population growth to be negative in small populations. In the section 'Sex-specific variance components', I summarise how sex-specific demographic components can contribute to demographic stochasticity.

## Bird introductions to New Zealand and demographic stochasticity

Human introductions of alien species to novel environments have provided a very useful source of information on the determinants of introduction success and risk of extinction. Early studies by McLain (1993) suggested that sexual selection was a neglected factor contributing to extinction (*see also* Møller 1997, 2000). Subsequent analyses of birds introduced to Oahu and Tahiti revealed that sexually dichromatic species had a lower probability of introduction success than sexually monochromatic species (McLain

*et al.* 1995). For species introduced to New Zealand, Sorci *et al.* (1998) were able to control the number of introductions and the size of inoculates, but still found that sexual dichromatism was a significant predictor of extinction risk. Sol *et al.* (2001) extended this analysis by suggesting that behavioural flexibility and relative brain size may have contributed to this effect. This effect could still be reconciled with a role of sexual selection, because evolution of brain size and sexual dimorphism in brain size have been linked to sexual selection (Miller 2000). Likewise, a comparative study of evolution of brain size and sexual dimorphism in brain size in birds suggested a link to sex roles (L. Garamszegi, J. Erritzøe & A. P. Møller unpubl. data). Several mechanisms giving rise to an increased risk of extinction for dichromatic species include greater male susceptibility to stress, mismatch between female preferences and male phenotypes available, and differential parental investment by females being related to the attractiveness of their mates (Møller 1997, McLain *et al.* 1998, Møller & Legendre 2001).

Legendre *et al.* (1999) explicitly modelled the effects of demographic stochasticity for the New Zealand introduction data, while taking sexual selection into account. Initial population size explained 90% of the variance in probability of extinction. How this effect came about was the subject of the following analyses.

Legendre *et al.* (1999) modelled demographic stochasticity in sex ratios among introduced individuals, although it is just as likely that other demographic variables could have contributed additional effects to overall demographic stochasticity. The difference in probability of extinction between a simple one-sex model and a two-sex model was large for small initial population sizes in the range up to 40 individuals, with asexual species having a low risk of extinction, as expected (Lynch *et al.* 1995). Social mating system also contributed significantly to the risk of extinction. When the mating system changed from polygyny to monogamy, the range of initial population sizes needed to have less than a 10% risk of extinction increased from 30 to 50 individuals. However, the most dramatic effect arose from differential parental investment by females

(Burley 1986), which is a maternal effect directly related to the attractiveness of a partner. This phenomenon has been described for a wide range of species from insects through fish to birds and mammals, and females in this situation typically withhold parental effort when mated to an unattractive partner (review in Møller & Thornhill 1998). Females mated randomly may completely cease reproduction for years, and mean reductions in reproductive output are typically in the order of 50% (review in Møller & Legendre 2001). With just a mean 10% reduction in reproduction in a monogamous mating system, the initial population size needed to have less than a 10% risk of extinction increased from 50 to 230 individuals. With larger reductions in success, demographic stochasticity could increase minimum population sizes necessary to maintain viable populations at a risk of extinction less than 10% to many hundreds.

These effects clearly demonstrate that sexual selection can dramatically alter predictions derived from models of demographic stochasticity.

### Allee effects and sexual selection

The negative frequency-dependent effect of reproductive success on population growth is commonly termed the Allee effect (Allee 1931). Recently, this effect has been implicated in conservation biology because the mechanisms leading to decreasing reproduction in small populations may provide a key to solve problems of extinction (Courchamp *et al.* 1999, Stephens & Sutherland 1999).

Sexual selection may play a direct role in creating Allee effects. Møller and Legendre (2001) developed a demographic model that incorporated the effects of lack of female choice on rates of reproduction in small populations, using graph theory as a framework. Chance realisations of even sex ratios were compared with two scenarios where genetic compatibility or a directional mate preference governed the probability of successful mating. The sex ratio effect was significant, both for a simple model of directional mate preference and a model of compatibility as seen for MHC haplotypes in many higher animals

and for compatibility systems in plants. Thus, in models where sexual selection was required for successful reproduction chance realisations of sex ratios can result in an extinction vortex giving rise to phenomena commonly described as Allee effects (Møller & Legendre 2001).

### Sex-dependent variance components

Sex-dependent variance in sex ratios, survival, fecundity and senescence can all contribute to increased demographic stochasticity.

#### Sex ratios

Most vertebrate populations have an excess of males that are not reproducing, although large populations of non-reproducing females are also common in certain species (e.g. Freed 1987, Robertson 1990). A long-term population study of the barn swallow *Hirundo rustica* in Denmark revealed that the frequency of unmated males ranged from 1.67% to 18.60% of all males during the years 1977–2002, with a mean value of 9.40% (SE = 0.98) (A. P. Møller unpubl. data). This factor will contribute to the variance in population parameters such as survival rate (if reproducing and non-reproducing individuals differ in survival due to the costs of reproduction) and reproductive success.

#### Survival

Survival rates often differ among the sexes, particularly in highly polygynous species with large sexual size dimorphism (Clutton-Brock 1990). However, sex-specific variance in survival rate can be considerable even in species with little or no sexual size dimorphism. For example, Møller and Szép (2002) found for the barn swallow that the variance in female survival rate among years was significantly larger than the variance in male survival rate ( $F = 2.82$ , d.f. = 11,11,  $P < 0.05$ ). Thus, considering only one sex in a population viability analysis will bias estimates of time till extinction if based on survival of individuals of a single sex.

#### Fecundity

Variance in male lifetime fecundity is considerably greater than variance in female fecundity (Clutton-Brock 1990), although the magnitude of this effect increases in species with greater intensity of sexual selection such as highly polygynous species or socially monogamous species with a high frequency of extra-pair paternity. For example, Møller (1998) calculated that extra-pair paternity increased the standardised variance in male reproductive success by on average a factor of 5.19 across a sample of 8 species of birds, with a maximum value of 15.20. Such dramatic differences in reproductive success among males in socially monogamous species may have genetic consequences, but potentially also demographic consequences when population size is small. The mating system is important for the stability of population dynamics across a rather large range of population sizes (*see* references in Introduction).

#### Senescence

Senescence is the decrease in age-dependent residual reproductive value (Fisher 1930), usually giving rise to a deteriorating phenotype and an increase in mortality. Such effects have been demonstrated in many different organisms. Several studies have emphasised that effects of senescence may occur very early in life. For example, a study of the barn swallow revealed that offspring body size, feather development and T-cell mediated immunity declined with paternal and/or maternal age already after the first breeding season in this short-lived species with an annual survival rate of ca. 35% (Saino *et al.* 2002a). In particular, female barn swallows suffered an age-dependent decline in offspring quality, and apparently traded quality of current offspring against that of offspring in subsequent reproductive events (Saino *et al.* 2002a). Such senescence effects can vary depending on environmental conditions, with adverse weather causing stronger effects because of difficult conditions for rearing of offspring. Hence, variance in female reproductive success may have a weaker or stronger senescence component,

while male effects may be less variable because of their less important role in rearing of offspring.

## Extinction and sex-specific extrinsic and intrinsic factors

### Extrinsic factors

Sex differences in mortality are often caused by sex-specific susceptibility to the causes of mortality, and these are briefly reviewed in this and the following section on intrinsic factors (Table 1).

#### Sex-dependent predation

A review of the literature shows that sex-specific effects are common. For example, increased movements by males increase their risk of mortality due to predation (Pitelka 1957). Predation is often strongly sex-biased with males comprising a disproportionate share of prey captured by raptors such as peregrine falcons *Falco peregrinus* (Cade 1960). Likewise, numerous studies have suggested that male secondary sexual characters increase the risk of predation (review in Zuk & Kolluru 1998).

#### Infanticide

Sexually selected infanticide is a means for individuals excluded from reproduction to increase their reproductive success by causing reproductive failure of conspecifics (Bertram 1975). Infanticide is a very important factor in many primates including humans, being a major cause of mortality (Hrdy 1979, van Schaik 2000). In addition, sex-specific hunting policies can increase the frequency of infanticide because replacement males habitually kill any dependent offspring in their home range as described for bears *Ursus arctos* (Swenson *et al.* 1998). In many birds, such as the barn swallow, infanticide is mainly due to unmated males killing dependent offspring, thereby causing females to re-mate and relay (Møller 1988). In other species, females can also be important contributors to infanticide

(Hrdy 1979, Robertson 1990). Infanticide can obviously increase the variance in reproductive success, and the factors determining the number of individuals who are potential infanticidal perpetrators may have important consequences for demographic stochasticity.

### Sex-dependent parasitism

Males are generally more susceptible to parasitism than females (Zuk 1990). That is the case in vertebrates, but not among invertebrates, although there is significant heterogeneity in the sex difference among taxa of hosts and parasites (Poulin 1996, Schalk & Forbes 1997, Sheridan *et al.* 2000). The mechanisms giving rise to such sex differences are discussed in the following section on intrinsic factors.

### Sex-dependent mortality

Mortality rates appear to be more variable in males than in females. Although predation often disproportionately affects males, females are sometimes killed in excess because of their parental behaviour, as in waterfowl (Promislow *et al.* 1992). Females are also commonly killed on their nest in many other species of birds (Promislow *et al.* 1994), and these selection pressures are supposed to have resulted in the evolution of cryptic coloration in females of many species.

**Table 1.** Relative importance of extrinsic and intrinsic factors potentially contributing to sex differences in demographic stochasticity.

Factor	Importance	Intensity of previous studies
<b>Extrinsic factors</b>		
Parasitism	Very important	High
Predation	Very important	High
Infanticide	Important?	Low
<b>Intrinsic factors</b>		
Physiology	Very important?	Low
Endocrinology	Very important?	Intermediate
Immunology	Very important	Intermediate–High

## Intrinsic factors

The extrinsic factors associated with sex-specific differences in mortality are often underpinned by sex-specific intrinsic differences in physiology, endocrinology and immunology (Table 1).

### Physiology

Males are often more active than females during the breeding season, resulting in a higher metabolic rate. This difference is directly related to sexual selection and is underpinned by endocrinology, as discussed in the following section on endocrinology. High metabolic rates imply increased rates of ingestion of food. This can have two consequences that can increase mortality rates. First, increased ingestion results in increased probability of being infected with parasites, leading to the commonly observed greater prevalence of parasites in males than in females (*see above*). Second, elevated rates of ingestion result in greater exposure to predators and parasites due to higher locomotory activity. Again, this can reduce survival rates in males compared to females.

### Endocrinology

Males are subject to a strong seasonal surge in androgens and this increase can have dramatic effects on their behaviour and the associated risks of mortality. For example, increased locomotory activity is directly associated with androgens (Wada 1986, Ketterson & Nolan 1992). Such increases in androgens may increase the risk of parasitism and disease (Alexander & Stimson 1989). Females also experience a seasonal increase in androgen levels, and females deposit androgens in their eggs, thereby affecting the physiology and the behaviour of their offspring (Schwabl 1993, Gil *et al.* 1999). Differential allocation of maternal testosterone to eggs containing sons and daughters may also have long-lasting effects on their performance when juveniles (Petrie *et al.* 2001), and potentially later when adults. Elevated levels of androgens in females may also have consequences for

female health. We can expect that positive effects of androgens in males can be selected against in females due to antagonistic effects arising from genetic correlations between the sexes (A. P. Møller, M. Eens, D. Gil & S. Hurtrez-Boussès unpubl. data). Across bird species with information on peak levels of circulating testosterone we found a strong positive correlation, implying that in species where males have very high levels, females have also evolved high levels.

### Immunology

Females invest more in maintenance and usually survive better than males because their lifetime reproductive success is more strongly influenced by long-term ability to invest in offspring. Male success may depend more on the ability to sustain a short period of intense mating competition, as epitomised in lekking species. This sex difference implies that females generally invest more in immune defence which is often more efficient in females than in males. For example, a comparative study of birds revealed a highly significant difference in the size of the spleen (an immune defence organ that is a major storage of lymphocytes) and the bursa of Fabricius (the organ where B-cells of the immune system originate). Males in general had smaller immune defence organs than females (Møller *et al.* 1998). This sex difference in spleen size was not present among juveniles, but only appeared at sexual maturity, suggesting a direct link between reproduction and sexual size dimorphism in immunity. The sex difference in spleen size across species was negatively related to the degree of extra-pair paternity (a measure of the intensity of sexual selection). In addition to these effects, males may also suffer from androgen-specific immunosuppression (Grossman 1985, Folstad & Karter 1992, Casto *et al.* 2001). Sexual selection is generally believed to have caused an evolutionary increase in levels of androgens to support the development of secondary sexual characters or the aggressive behaviour associated with such characters. However, androgens also have antagonistic effects on immune function and this effect may be responsible for increased susceptibility of males to parasitism. However, females

may suffer similar albeit less severe immunosuppressive effects due to oestrogens (Grossman 1985).

Recently, experiments on captive house sparrows *Passer domesticus* have shown that the presence of a predator reduced the level of T-cell mediated immune response by up to 35% (F. de Lope, A. Marzal, A. P. Møller & C. Navarro unpubl. data). As a consequence, malarial infection with *Haemoproteus* blood parasites increased dramatically in sparrows exposed to a predator relative to sparrows exposed to a benign control. Such effects of predator presence on immuno-suppression may subsequently increase risk of predation, in particular in the sex more susceptible to predation.

## Extinction and sex-specific effects of genetic factors

Genetic factors may also contribute significantly to sex differences in survival rate and general performance. Genetic variation is maintained by a balance between mutation and selection. While mutation for a long time has been considered to occur at a very low rate, recent studies have started to investigate variation in mutation rates, in particular in relation to sex. The mechanisms giving rise to such differences in mutation rates between species and sexes are obviously of great scientific interest. Here I will concentrate on sex differences in mutation rates, although other genetic effects such as sex-specific expression of genes, sex-specific effects of inbreeding and sex differences in recombination may also be important.

### Sex-biased mutations

Mutation rates are not necessarily similar in the two sexes. Increased sperm production, for example due to intense sperm competition, is preceded by an increase in the number of mitotic germline cell divisions in the testes, likely resulting in a higher number of replication-dependent mutations per generation. This may result in a difference in mutation rate between the sexes (Ellegren & Fridolfsson 1997). A. P. Møller and J. J. Cuervo (unpubl. data) assembled a large

data base on minisatellite mutation rates in birds, based on the extensive literature on extra-pair paternity. They hypothesised that sex-biased mutation should result in a positive relationship between minisatellite mutation rates and a measure of the intensity of sexual selection. This was the pattern observed with the frequency of extra-pair paternity explaining more than 10% of the variance among species in minisatellite mutation rates. However, this increased mutation rate associated with a component of sexual selection was not related to sperm production, since relative testes mass (which reflects sperm production ability) was unrelated to mutation rates. Reconstruction of ancestral states and estimates of rates of evolutionary change for the two characters along the branches of the phylogeny, using the continuous comparative analyses developed by Prof. M. Pagel (Pagel 1997; see also <http://www.ams.rdg.ac.uk/zoology/pagel/mppubs.html>), indicated that sexual selection was driving the evolution of mutation rates, and not vice versa, contrary to common beliefs. A possible mechanism is that female choice can maintain a greater mutation rate than the minimum possible, if mutation rate is revealed in phenotypic characters that allow females to distinguish between potential mates differing in their susceptibility to mutations (A. P. Møller & J. J. Cuervo unpubl. data).

This phenomenon was further investigated in a study of the barn swallow from Chernobyl and a control region in the Ukraine. A. P. Møller and T. A. Mousseau (unpubl. data) studied the relationship between sexual selection and mutation for a total of 41 different phenotypic characters. Microsatellite mutation rates in barn swallows have been shown to have increased by a factor 2–10 in the Chernobyl region compared to control areas (Ellegren *et al.* 1997). Similar findings have been reported for other organisms (review in Møller & Mousseau 2001). We estimated the effect of mutations on the phenotype by calculating the difference in phenotype between males from the control area and males from Chernobyl, and expressed this difference in units of standard deviations. Likewise, we estimated the difference in phenotype for the 41 different characters between mated and unmated male barn swallows from Denmark, likewise expressed in units of

standard deviations. If traits preferred by females reflect mutations, we should expect a strong positive correlation between the two estimates for the 41 characters. The correlation accounted for an astonishing 58% of the variance, suggesting that mutations indeed were reflected in the phenotype and were used by females in sexual selection (A. P. Møller & T. A. Mousseau unpubl. data).

### Antioxidants and mutations

Antioxidants play an important role as quenchers of free radicals that are the reactive products of any metabolic process (Leffler 1993, von Schantz *et al.* 1999, Møller *et al.* 2001). Hence, a deficit of antioxidants can cause permanent damage to DNA and other molecules. A study of antioxidants, radiation and phenotype of barn swallows at Chernobyl has attempted to link antioxidants to mutations (Møller & Mousseau 2001). Antioxidants like carotenoids, which are often displayed in sexual signals as in the barn swallow, are used at high rates when radiation levels are elevated. Analysis of antioxidants (carotenoids and vitamins A and E) in the liver (where most antioxidants are stored) and blood in a sample of adult barn swallows from the radioactively contaminated Chernobyl region was compared with a sample from a control region in Ukraine with background levels of radiation (A. P. Møller, T. A. Mousseau & P. Surai unpubl. data). While male barn swallows had dramatically reduced levels of antioxidants in the Chernobyl region compared to the control region, females had low levels in both regions (A. P. Møller, T. A. Mousseau & P. Surai unpubl. data). Since females deposit more than 60 times the amount of carotenoids in a single clutch of eggs than at any time circulating in the plasma (Saino *et al.* 2002b), we can predict that female barn swallows and other birds have very low levels of antioxidants during the breeding season. While non-breeding females are very rare in all populations studied so far, studies at Chernobyl, where antioxidant levels are low, have revealed that the fraction of non-breeders among females sometimes reach more than 50% in radioactively highly contaminated areas

(A. P. Møller & T. A. Mousseau unpubl. data). We have hypothesised that females may simply be unable to reproduce because of lack of antioxidants. Such side effects of maternal effects may have important implications for the occurrence of sex-biased mutations.

Partial albinism occurs as white spots of epidermis that in birds is reflected as white feathers in a feather tract that normally has a different colour (Dyck 1985). Partial albinism is a phenotypic marker of mutations, partly of germline origin (Ellegren *et al.* 1997, Møller & Mousseau 2001). The occurrence of partial albinism in the barn swallow in Denmark was quantified among adults during the years 1990–2002. Annual variance in partial albinism was significantly greater for males than for females with the variance in percentage partial albinos among years being 0.0140 for males, but only 0.0041 for females, a significant difference ( $F = 3.379$ , d.f. = 12,12,  $P < 0.01$ ; A. P. Møller unpubl. data). This finding suggests that males of at least this species are more susceptible to mutations than females.

### “Good genes” or “bad genes”

Beneficial genetic effects on offspring performance associated with sexual selection are commonly termed “good genes” (review in Andersson 1994). Although the existence of such effects has been disputed for a long time, a review of the literature revealed that “good genes” effects accounted for on average 1.5% of the variance in offspring survival across studies; a highly significant effect size (Møller & Alatalo 1999). While several potential biases were investigated in this review, their inclusion in the analyses did not change the general conclusions. Genetic paternal effects on offspring survival and other components of fitness are not necessarily due to “good genes”. As emphasised earlier in the section on sex-biased mutations, sex-biases in mutation rates may be sufficient to maintain costly mate preferences for particular male traits, if these traits reliably reveal the presence of mutations. Rather than choosing “good genes”, females may in actual fact avoid “bad genes” based on information gleaned from the expression of sexual signals.

## Conclusions

I have attempted to make a broad scale review of the effects of sex on demographic variables, demographic stochasticity and the underlying extrinsic and intrinsic mechanisms giving rise to such effects (Table 1). I found evidence of a diverse array of such effects, suggesting that sex can play an important role in determining demographic stochasticity and risk of extinction well beyond the small population sizes normally considered to be subject to such effects. Clearly we need more sex-specific models that take these effects into account. In particular, we need general assessments of the importance for risk of extinction of incorporating sex into these models.

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