

Allee effect, sexual selection and demographic stochasticity

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The negative frequency-dependent effect of reproductive success in animals on population growth refers to a category of phenomena termed the Allee effect. The mechanistic basis for this effect and hence an understanding of its consequences has been obscure. We suggest that sexual selection, in particular female mate preferences, is a previously neglected component giving rise to the Allee effect. Lack of breeding and reduced reproductive success of females at low population densities are commonly described in situations where females have little or no opportunity to choose a mate, consistent with this suggestion. We developed a demographic model that incorporated the effects of lack of female choice on rates of reproduction. Using either a mating system with incompatibility or a system with a directional mate preference, we show that commonly encountered levels of reproductive suppression in the absence of suitable mates in a population, where sexual selection still operates, may increase the effects of demographic stochasticity considerably.

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The so-called Allee effect (Allee 1931, 1951, 1958) is a common term for a group of phenomena associated with negative density-dependent reproductive success affecting the rate of population growth. Initial findings demonstrated for the flour beetle *Tribolium confusum* that small population densities were associated with low population growth rates (Allee et al. 1949). This type of negative frequency-dependence has recently attracted considerable attention in the context of conservation biology because of the obvious consequences for persistence time of small populations (Lande 1987, Dennis 1989, Dobson and Poole 1998). Several recent reviews have discussed the various factors contributing to the Allee effects (Courchamp et al. 1999, Stephens and Sutherland 1999, Stephens et al. 1999), but none of these even mentioned sexual selection as an important force generating such effects. The zoological literature is replete with case studies of lack of reproduction even among presumably fully reproductive, healthy adults that are relieved from negative effects of parasitism,

predation and lack of food. For example, giant pandas, *Ailuropoda melanoleuca*, often refrain from reproduction in captivity resulting in costly airline transport of pandas across the world to ensure fertilization (Kleiman 1994). For this species, even artificial insemination does not work well. Similarly, mated female hamadryas baboons, *Papio cynocephalus hamadryas*, may spend years as non-reproducers even when having the opportunity to copulate with other males (Biquand et al. 1994). Examples of Allee-like effects have been described for most animal taxa (Fowler and Baker 1991), although demonstrations based on population data are rare (Fowler and Baker 1991, Myer et al. 1995, Sæther et al. 1996). However, the lack of demonstration of Allee effects with population data is not necessarily of great significance because estimates of demographic parameters are often relatively unreliable.

The mechanisms underlying Allee effects are much less clear than the mere description of the phenomenon. Examples of potential mechanisms include (1) increased

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risk of predation at low population densities (Andrewartha and Birch 1954, Birkhead 1977, Clark 1974), (2) reduced mating efficiency (Andrewartha and Birch 1954, Dennis 1989), and (3) reduced foraging efficiency (Ward and Zahavi 1973, Bertram 1978). Each of these potential mechanisms again provide a multitude of possible mechanisms.

Sexual selection is a generally neglected aspect of conservation (Grahn et al. 1998), and the often large effects of sexual selection on population growth and hence persistence are generally not appreciated. Legendre et al. (1999) have emphasized that the mating system may dramatically increase effects of demographic stochasticity if a number of individuals refrain from reproduction because mates are unavailable in a monogamous mating system. However, the social mating system is far from the only component of sexual selection that can influence effects of demographic stochasticity. In particular, females often refrain from reproduction or reproduce at a low rate if only males of an incompatible or non-preferred phenotype are available. Female mate preferences generally have a quantitative genetic basis, with heritabilities in 20 species ranging from 0.10 to 0.65 (Bakker and Pomiankowski 1995). The mechanisms involved in reduced reproductive success of females mated to males with non-preferred phenotypes can either be caused by differential access by females to preferred males, or to differential parental investment in reproduction in relation to male phenotype (Burley 1986). Both these mechanisms have received empirical support from observational and experimental studies, and we assess the magnitude of these effects below.

Here, we provide an extensive review of the Allee effect as caused by sexual selection by focusing on two possible mechanisms: (1) poor reproductive success due to differential parental investment by females not encountering suitable or preferred mates, and (2) an inability to find a suitable mate, which reduces the frequency of reproduction. The mechanisms of reproductive suppression discussed in the first part of the review obviously may influence many or all of the reproductive mechanisms discussed in the second part of the review. We use a model to test the predictions that females regularly do not reproduce when preferred males are unavailable, and that females reproduce at a lower rate when such males are unavailable. Finally, we estimate the consequences of such reduced reproduction on demographic stochasticity of small populations. Analyses demonstrate that purely demographically stochastic effects may appear in even relatively large populations when females invest differentially in reproduction relative to the phenotype of their mate.

Sexual selection, differential parental investment and reproductive success

Sexual selection may not only act through its effect on variance in social mating success of males, as initially emphasized by Darwin (1871), but can also influence other components of variance in male success (Andersson 1994). These include pre-fertilization, fertilization and post-fertilization mechanisms such as timing of mating, sperm competition and choice of sire, differential abortion and infanticide, and differential parental investment (Møller 1994a). Any of these mechanisms may influence the survival prospects of small populations. Here we emphasize the importance of reproductive decisions of females, but we fully acknowledge that any of these mechanisms can play an important role in the maintenance of viable populations.

Post-mating reproductive decisions by females can dramatically affect population growth, since females have been hypothesized to invest in reproduction relative to the phenotype of their social partner (Burley 1986). Burley's original study of zebra finches, *Taeniopygia guttata*, provided with more or less attractive leg bands showed an average reproductive success of 33.67 surviving offspring for males with red bands, 15.00 for males with orange bands, and 20.67 for males with green bands, i.e., an average reduction in reproductive success by 47% among males with unattractive bands (Burley 1986: Table 4). When analysing patterns of reproduction for monogamously mated females only paired with a male with one colour type throughout the experiment, average reproductive success was 34.33 for females mated to red-banded males, 14.20 for females mated to orange-banded males and 14.25 for females mated to green-banded males, i.e., an average reduction in reproductive success by 58% (Burley 1986: Table 7). These patterns have been confirmed in subsequent experimental studies of the same species (Burley 1988), the barn swallow *Hirundo rustica* (de Lope and Møller 1993, Møller 1994a, b, Kose and Møller 1999; mean reduction in reproductive success by 35%) and the collared flycatcher *Ficedula albicollis* (Qvarnström 1997).

Many other studies based on correlational evidence also suggest that females once mated to more attractive or compatible males provide more care for the offspring than females mated to less attractive males (review in Møller and Thornhill 1998). However, differential investment and cryptic female choice at the post-fertilization level are not restricted to species with biparental care. The original hypothesis proposed by Thornhill (1983, 1984) was based on patterns of reproduction in female scorpionflies mated to males differing in attractiveness. Subsequently, additional studies have provided similar evidence for more than ten other species of animals (review in Møller and Thornhill 1998). For example, studies of invertebrates such as the white-

spotted sawyer, *Monochomus scutellatus* (Hughes and Hughes 1985), and the butterfly *Polygonus c-album* (Wedell 1996), and vertebrates such as the quail, *Coturnix coturnix* (Adkins-Regan 1995) and the peacock, *Pavo cristatus* (Petrie and Williams 1993), have shown that females reproduce at a lower rate for less preferred males even in species without male parental care. Finally, many studies of sexual selection that traditionally have been interpreted as evidence for variance in male social mating success associated with female choice can just as readily be interpreted as the outcome of cryptic female choice for preferred males (Møller and Thornhill 1998).

In conclusion, extensive observational and experimental evidence suggest that female reproductive decisions related to the phenotype of their mate can dramatically influence the reproductive rate and hence the population growth of small populations.

Effects of mate choice on reproductive success

Many studies of captive animals have provided evidence for reduced reproduction in the absence of sexual selection. The primary source of evidence for this kind of effect comes from experiments in which females are forcibly mated to a particular male rather than being allowed to mate according to their own preference. Forced mating can lead to spontaneous abortion, miscarriage, lower fertilization rates, or offspring with low viability in both birds and mammals (e.g., Klint and Enquist 1981, Thomas et al. 1985, Hedrick 1988). Unsuccessful breeding and low reproductive success as a consequence of forced mating has been reported in tigers, *Panthera tigris* (van Bemmell 1968), black rhinoceros, *Diceros bicornis* (Smith and Read 1992), and kangaroo rats, *Dipodomys merriami* (Chew 1958). Mate incompatibility and rejection of apparently reproductively healthy individuals is a major problem in zoos. For example, extensive evidence is present for gorillas, *Gorilla gorilla* (Nadler and Collins 1984, Watts 1990), cheetahs, *Acinonyx jubatus* (Brand 1980, Schuman 1991, Stearns 1991), clouded leopards, *Neofelis nebulosa* (Yamada and Durrant 1989), leopards, *Panthera pardus* (Shoemaker 1982), snow leopards, *Panthera uncia* (Marma and Yunchis 1968), giant pandas (Kleiman 1994) and kangaroo rats, *Dipodomys hermanni* (Thompson 1995).

Free choice of mates often increases the probability of reproduction and in the case of reproduction the actual reproductive success, as shown in this and the following four paragraphs. Random pairing in tree shrews, *Tupaia glis*, showed that only 20% resulted in successful pair formation (Schreiber et al. 1993). Onager, *Equus hemionus*, introduced into Israel had ini-

tially very low reproductive success since less than 30% of all females gave birth within two years of translocation. For females aged five years or less, fewer than 50% bore young (Saltz and Rubenstein 1995).

Effects of minimum size of groups on successful reproduction in captivity are often large. There are examples reported for birds (flamingos (Stevens 1991, Pickering et al. 1992)) and mammals (black lemurs, *Eulemur macaco*, and mongoose lemurs, *Eulemur mongoz* (Hearn et al. 1996)). In Przewalski's horse, *Equus przewalskii*, white rhinoceros, *Ceratotherium simum*, and vicuna, *Vicugna vicugna*, reproductive success increased in larger groups (Bareham 1973, Dolan 1977). Although the cause of reduced reproductive success is often undetermined in such studies, it is possible that the lack of free choice or the reduced opportunities for choice may have been a contributing factor.

In cockatiels, *Nymphicus hollandicus*, enforced mating reduced reproductive success since more than 90% of birds that chose their mate laid eggs, while only ca 55% of those that were randomly allocated to a mate laid eggs (Yamamoto et al. 1989). Egg fertility was ca 70% in naturally formed pairs, but only 45% in force-paired individuals (Yamamoto et al. 1989). In canvasback, *Aythya valisineria*, females of naturally formed pairs laid eggs in 89% ($n = 19$) of the cases, while none of 19 force-paired females laid eggs (Bluhm 1985). Randomly mated American kestrels, *Falco sparverius*, produced eggs with 65% fertilization, while pairs that were formed through mate choice produced 80% fertile eggs (Bird 1982). A study of domestic pigeons, *Columba livia*, showed that spontaneously formed pairs laid eggs earlier, produced larger clutches and had greater fertilization success than randomly assigned pairs (Klint and Enquist 1981).

Several studies of threatened species show similar effects. For example, Puerto Rican parrots, *Amazona vittata* (Brock and White 1992, Anonymous 1994, Wilson et al. 1994), and California condors, *Gymnogyps californianus* (Cox et al. 1993), reproduce at a higher rate when given free choice of a mate. Similarly, in the threatened Mauritius kestrel, *Falco punctatus*, eggs collected from free-breeding pairs had higher hatchability than eggs collected from pairs breeding in captivity (Jones et al. 1991). Infertility of eggs and incompatibility of members of a pair is common in whooping cranes, *Grus americana* (Lewis 1990). We are not aware of any studies of random mating showing an absence of an effect on frequency or extent of reproduction.

In conclusion, lack of mate choice may severely reduce the frequency of reproducing females, but also the rate of reproduction of these females. Such effects on means and variances of reproductive success can affect the prospects of survival of small populations, as shown below.

Demographic stochasticity and sexual selection

Methods

We modelled the consequences of the effects of demographic stochasticity in sex ratios on probability of mating and hence reproductive success. This was done by comparing the results from chance realisations of an even sex ratio with two additional scenarios; (1) genetic compatibility between potential partners is required for successful mating; and (2) a directional mate preference governs the probability of successful mating. We did this by considering a population comprising n individuals, with an average sex ratio $\sigma = 0.5$, and computed the probability of one individual being mated, assuming monogamous pair formation.

Chance realisation of the sex ratio

The number f of females followed a binomial distribution, $f \equiv \text{Binom}(n, \sigma)$, with σ the sex ratio. The number of males was $m = n - f$, and the number of monogamous matings $\min(f, m)$. The probability of one individual being mated was

$$p(n) = \frac{E(\min(f, m))}{\sigma n}$$

($E(X)$ denotes the expectation of X). This could be computed exactly as

$$p(n) = 1 - \frac{1}{2^n} \binom{n}{h} \quad \text{for } n \text{ even, } n = 2h,$$

$$p(n) = p(n-1) \quad \text{for } n \text{ odd}$$

$\binom{n}{h}$ denotes a binomial coefficient), with the approximation

$$p(n) \approx 1 - \frac{\sqrt{2}}{\sqrt{\pi n}}. \quad (1)$$

Genetic compatibilities

Males and females were assumed to be of two types A and B, in average proportion $\alpha = 0.5$. Fertile matings occurred only within identical types (A and B were not compatible). The number of females and males of each type was

$$f_A \equiv \text{Binom}(f, \alpha), \quad f_B = f - f_A,$$

$$m_A \equiv \text{Binom}(m, \alpha), \quad m_B = m - m_A.$$

The probability of one individual being mated successfully was

$$p'(n) = \frac{E(\min(f_A, m_A) + \min(f_B, m_B))}{\sigma n},$$

and could be computed as

$$p'(n) = \frac{1}{n2^{n-1}} \sum_{i=1}^n i \binom{n}{i} p(i).$$

A good approximation was given by replacing n by $n/2$ in eq. 1:

$$p'(n) \approx 1 - \frac{2}{\sqrt{\pi n}}.$$

Mating preferences

We assumed that, on average, each individual chooses its mate with probability c . More precisely, each female was willing to mate with, on average, cm of the m potential male partners, and refused to mate with the $m - cm$ remaining ones. The same applied to males towards females. Compatibility between males and females then occurred with probability $z = c^2$. Preferences were supposed to have evolved in such a way that when there are $n = 50$ individuals, the choice probability c has a value ensuring a probability of being mated very close to 1: we used $c = 0.5$. We then computed by simulation the probability $p''(n)$ of being mated when individuals select their partners with this value of c . It was convenient to use the framework of graph theory (Bollobás 1998). The network of individual compatibilities was considered as a bipartite graph comprising two sets of vertices, the set of males and the set of females, and edges joining these two sets. Edges represented compatibilities between males and females, and they were constructed randomly with probability z . We then searched for a maximum matching in this bipartite graph, i.e. the maximum set of pairs that could be formed under the compatibilities. The procedure was the following: for each population size n , we drew 10000 values of the number f of females, and for each value of f we built a random bipartite graph representing the compatibilities; we computed the maximum number C_n of pairs; the average of the C_n values over the 10000 runs divided by σn gave the probability $p''(n)$. In fact, since we searched for maximum matchings, our procedure overestimated the probability $p''(n)$.

Results

In a population of n individuals, the chance realisation of the number of males and females had a non-negligible impact on the probability of one individual being

mated under various scenarios (Fig. 1). Concerning the chance realisation of the sex ratio (intrinsic to the demographic process), eq. 1 showed that the probability $p(n)$ of being mated converged to 1 with increasing n (as expected), but that the convergence was rather slow. For $n = 50$, we had $p(n) \approx 90\%$, and for $n = 10$, $p(n) \approx 75\%$. In this first case, there was no assumption on the success of the matings.

Incompatibility between phenotypes was then considered, assuming two incompatible phenotypes in equal average proportions. For $n = 50$, the probability $p'(n)$ of one individual being mated successfully was 85%, and for $n = 10$, $p'(n)$ was 65%. Concerning directional mating preferences, individuals were assumed to choose their partners with probability 0.5. This had almost no impact on reproduction when population size n is above 50, but, importantly, these preferences reduced the probability of being mated for small n . For $n = 10$, we had $p''(n) \approx 55\%$.

We further considered that the number of males and females could be controlled for (as could be the case when animals are translocated from the wild to a zoo), with males and females in equal number (Fig. 2). The corresponding probabilities of being mated were now denoted by $q(n)$, $q'(n)$, and $q''(n)$. We had $q(n) = 1$, because there was no chance realisation of the sex ratio. For genetic compatibility, we had $q'(n) = p(n)$, because we accounted for the chance realisation of the number in each type, genetic type now playing the role of gender. For mating preferences, we computed $q''(n)$ by simulation as in the methods section, but with an equal

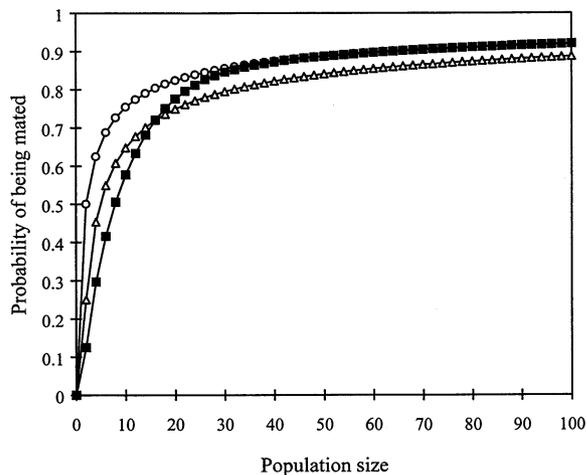


Fig. 1. The probability of one individual being mated as a function of the number n of individuals with monogamous pair formation and sex ratio 0.5, in three different scenarios. Chance realisation of the number of males and females (circles). Same as the previous scenario with two incompatible phenotypes A and B in equal proportions, fertile matings occurring only within compatible phenotypes (triangles). Same as the first scenario with mating preferences, each individual choosing its mate with probability 0.5 (filled squares).

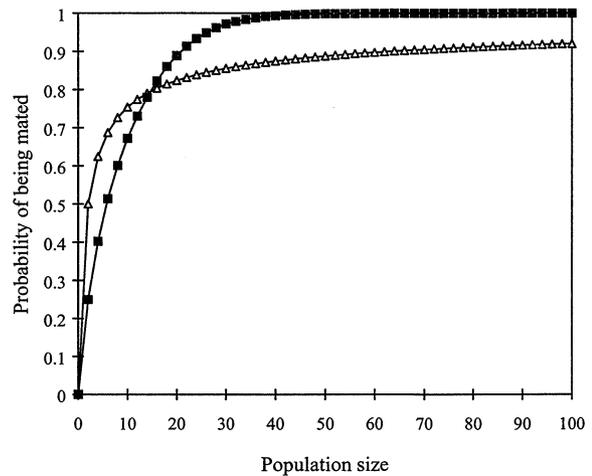


Fig. 2. The probability of one individual being mated as a function of the number n of individuals with monogamous pair formation, assuming an equal number of males and females, in two different scenarios. Two incompatible phenotypes A and B in equal proportions, fertile matings occurring only within compatible phenotypes (triangles). Mating preferences, each individual choosing its mate with probability 0.5 (filled squares).

number of males and females. We found that, even if males and females were in equal number, genetic incompatibility and mating preferences had a non-negligible impact on the probability of successful mating. In the later case, we obtained $q''(n) \approx 65\%$ for $n = 10$.

Discussion

Sexual selection often leads to an absence of or a severe reduction in reproductive success among females with a restricted choice of mates. Effects range from complete absence of reproduction in several cases (e.g., Bluhm 1985) to reduction in success by up to half or more in cases where females adjust their reproductive effort to the phenotype of their mate (e.g., Burley 1986). Our model quantified the impact of the chance realisation of the number of individuals according to gender or type (genetic compatibility, attractiveness) on the probability of being mated monogamously, when the number of individuals is small. In other words, we modelled the impact of demographic stochasticity, as reflected by random realisations of sex ratios, on monogamous pair formation in a small population. This will obviously have consequences for variation in reproductive success and hence population viability. In all cases considered, the probability of being mated was unity when the population was large. Genetic compatibilities and mating preferences did not occur simultaneously. Under realistic assumptions, we found that reproduction could drop to 80% for $n = 50$ individuals, and to 60% for $n = 10$ individuals. Such figures agree with the observa-

tions presented previously, and are likely to lead to a population decline. In this way, demographic stochasticity as determined by random realisations of sex ratios generated a form of Allee effect by reducing the individual fitness (probability of being mated and hence reproductive success) when individuals are in low numbers (see Stephens et al. 1999). In the same sense, Legendre et al. (1999) showed that demographic stochasticity on pair formation in a two-sex passerine life cycle increases the probability of extinction, as compared to a female-based life cycle.

The most striking result was perhaps the role of mating preferences. While individuals could be choosy for their mates without jeopardizing reproduction when numerous (and even enhancing reproduction if being choosy provides some advantage), a reduction in their number, with no adaptation of their preferences to the restricted choice possibilities, had a dramatic impact (Figs 1, 2).

The effects of sexual selection on the incidence and the rate of reproduction will have different consequences for demographic stochasticity. While the variance in reproductive success is considerable for the case in which females completely refrain from reproduction, variance in reproductive success is less affected by reductions in the rate of reproduction. The models were based on the assumption of complete incompatibility. While the literature review shows several cases of complete incompatibility, less extreme scenarios may be more common. Obviously, the results arising from partial incompatibility will be intermediate to those reported in Figs 1, 2. We might expect that females of long-lived species delay reproduction completely more readily than females of short-lived species. Although available data prevent a rigorous comparative analysis, the observation that short-lived zebra finch females mainly reduced reproductive rates (Burley 1986), while long-lived female canvasbacks and cockatiels completely refrained from reproduction (Bluhm 1985, Yamamoto et al. 1989), is consistent with this suggestion. However, we will need detailed information on frequency and rate of reproduction for species with different life histories to be able to fully examine the consequences of sexual selection for demographic stochasticity.

In the literature review we described many examples from captivity of absence of reproduction or severe suppression of reproduction. How realistically do these examples reflect the phenomena discussed here? Obviously, particular features of the captive environment may be absent and thus cause reproductive suppression. However, we assume that this is generally not the case because females often will reproduce in the same environment when given a proper partner. Many examples of this phenomenon have been reported in the literature (e.g. Brock and White 1992, Cox et al. 1993, Wilson et al. 1994, Kummer 1995).

Sexual selection has been hypothesized to play an important role in extinction. McLain (1993) suggested that the evolutionary trend for increased body size in mammalian lineages and the associated extinction risk may arise as a consequence of sexual selection for larger male body size. Consistent with this suggestion, McLain et al. (1995) found that sexually dichromatic species of birds introduced to Hawaii and Tahiti were less likely to be successful than monochromatic species. A separate study of birds introduced to New Zealand for which the size of the introduced population was known demonstrated that this increased risk of extinction of small populations was greater for dichromatic species even when the number of individuals introduced was controlled statistically (Sorci et al. 1998). The mechanisms behind this greater probability of extinction are unknown, although a number of possibilities have been advanced (McLain et al. 1995, Sorci et al. 1998). Models of demographic stochasticity based on the New Zealand data set suggest that most of the variation in extinction risk could be accounted for by random factors due to small population size (Legendre et al. 1999). Here we hypothesize that additional variation may be accounted for by the general observation that females provided with restricted choice often have lower reproductive success than females with free choice.

Sexual selection may be based on entirely phenotypic or genetic benefits accruing to choosy individuals, and secondary sexual characters subject to sexual selection may likewise reflect genetic and/or environmental effects (Andersson 1994). For example, maternal effects may have important implications for the performance of males, but potentially also for female choice and female reproductive decisions (Mousseau and Fox 1998). Here we briefly consider genetic effects because of the obvious close links between genetic variation, small populations and conservation status. Sexual selection has been hypothesized to be more important when there is greater genetic variability among males because females then have more to gain from their mate choice (Petrie and Lipsitch 1994). Intense directional selection due to strong female mate preferences or male-male competition is traditionally assumed to be associated with a reduction in genetic variability (e.g. Charlesworth 1987, Andersson 1994). However, recent studies suggest that species of birds with intense sexual selection arising from extra-pair paternity have more genetic variation than species with less intense sexual selection (Petrie et al. 1998). Two interpretations are possible: Sexual selection is more important when environmental conditions lead to increased genetic variation, or directional sexual selection may actually increase genetic variation (Petrie et al. 1998). For example, directional selection may give rise to increased genetic variability (Pomiankowski and Møller 1995), and recombination or mutation rates may change as a

consequence of sexual selection. The causal relationship between sexual selection and genetic variation remains to be critically addressed to fully assess the effect of sexual selection on demographic stochasticity.

Island populations are generally depauperate in genetic variability compared to mainland populations (review in Frankham 1997). Furthermore, island populations have been hypothesized to be subject to less intense sexual selection resulting in a loss of sexual dichromatism (Murphy and Chapin 1929, Amadon 1953, Grant 1965), although the generality of this observation is in need of confirmation using modern comparative analyses. This reduction of intensity of sexual selection has been supported by comparative studies of extra-pair paternity in island and mainland populations of birds (Griffith 2000, Møller 2000), suggesting that sexual selection is less intense in genetically more depauperate populations (Møller 2000). Furthermore, island species tend to be threatened and go extinct more often than mainland species (King 1978, Temple 1986, Collar et al. 1994). Threatened island endemics such as the Puerto Rican parrot and the Mauritius kestrel show important signs of reproductive depression in the absence of free mate choice (Jones et al. 1991, Brock and White 1992, Anonymous 1994, Wilson et al. 1994). This observation suggests that the intensity of sexual selection even in these cases is sufficiently large to severely affect reproductive decisions by females. The reasons for the increased threat to insular species and their high rate of extinction are not well known, although the considerations listed above may suggest that sexual selection has played a role in this process.

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