REPORT

Allee effects, mating systems and the extinction risk in populations with two sexes

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Abstract

The Allee effect is one of the population consequences of sexual reproduction that has received increased attention in recent years. Due to its impact on small population dynamics, it is commonly accepted that Allee effects should render populations more extinction prone. In particular, monogamous species are considered more susceptible to the Allee effect and hence, more extinction prone, than polygamous species. Although this hypothesis has received theoretical support, there is little empirical evidence. In this study, we investigate (1) how variation in tertiary sex ratio affects the presence and intensity of the Allee effect induced by mating system, as well as (2) how this effect contributes to extinction risk. In contrast with previous predictions, we show that all mating systems are likely to experience a strong Allee effect when the operational sex ratio (OSR) is balanced. This strong Allee effect does not imply being exceptionally extinction prone because it is associated with an OSR that result in a relatively small extinction risk. As a consequence, the impact of Allee effects on overall extinction risk is buffered. Moreover, the OSR of natural populations appears to be often male biased, thus making it unlikely that they will suffer from an Allee effect induced by mating system.

Keywords

Allee effect, demographic stochasticity, extinction risk, mating system.

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INTRODUCTION

Sex ratio variation in natural populations has important consequences for population dynamics. When both sexes and their interaction (i.e. mating system) are taken into account, the population dynamics depend on the sex ratio, introducing a source of nonlinearity (Heino 1997). As a consequence, population dynamics may either be stabilized or destabilized, depending on the impact of density-dependence (Lindstrom & Kokko 1998), the degree of polygyny (Lindstrom & Kokko 1998), or the impact of dispersal (Ranta *et al.* 1999). Another consequence that has received particular attention is the decline in growth rate when population size is small, i.e. the Allee effect (Legendre *et al.* 1999; Stephens *et al.* 1999; Engen *et al.* 2003). Indeed, the most frequently mentioned source of Allee effects is the difficulty of finding a partner (Courchamp *et al.* 1999; Stephens *et al.* 1999; Stephens & Sutherland 1999).

Until recently, the Allee effect was regarded as an intriguing but relatively unimportant aspect of population ecology. However, recent interest in the fate of small populations has led to a re-appreciation of its consequences for ecology and conservation. Indeed, small populations may face a higher extinction risk if their *per capita* growth rate is subjected to an Allee effect (Stephens & Sutherland 1999). Allee effects may thus also impact on the establishment of introduced species (Bessa-Gomes *et al.* 2003), as well as their eradication (Liebhold & Bascompte 2003). Allee effects have equally been shown to influence the interaction between species, namely by stabilizing predator–prey cycles (De Roos *et al.* 2003).

The Allee effect is likely to occur when individuals benefit from the presence of conspecifics (Courchamp *et al.* 1999; Stephens & Sutherland 1999). Hence, when population size is small, the individual fitness decreases, leading to a decline in growth rate (Stephens *et al.* 1999). Stephens and collaborators (Stephens *et al.* 1999) introduced an important distinction between component and demographic Allee effects. A component Allee effect is a positive relation between any of the components of an individuals' fitness and the abundance of conspecifics. The demographic Allee effect is the positive relation between the *per capita* growth

rate and population size. This latter phenomenon is the result of every component Allee effect but it is also affected of other forms of density-dependence (e.g. intra-specific competition). Hence, a component Allee effect may fail to result in a demographic one if the component it affects contributes little to population growth or if its impact is compensated by other forms of density-dependence.

It has been suggested that demographic stochasticity represents a type of Allee effect (Lande 1998) but whether this is the case depends on both the definition of the Allee effect used and the type of demographic stochasticity considered. According to the definition proposed by Stephens and colleagues, the Allee effect is framed in terms of the effects of population size on individual fitness and the consequences this may have for population growth. In this respect, demographic stochasticity can be classified into two categories: (1) the random variation resulting from individual birth and death events (Armbruster & Lande 1993), which is the most commonly invoked source of demographic stochasticity; (2) the random variation resulting from sex ratio fluctuations (Caughley 1994; Lande 1998). Taking these categories separately, Stephens and colleagues showed that despite the important implications of both for population dynamics and persistence, only sex ratio fluctuations may be usefully considered as a component mechanism of the Allee effect (Stephens *et al.* 1999). Indeed, the effect of demographic stochasticity through births and deaths arises in a very different way from the effects of demographic stochasticity through population sex ratios. In the former case there is no measurable component of individual fitness that is affected by population size or interactions with other population members. The fate of an individual, in terms of its probability of dying or reproducing, is unaffected by the size of the population within which it finds itself. Therefore, although the fate of the population as a whole is affected by its size when demographic stochasticity through births and deaths occurs, this is not a consequence of changing fates of the individuals within the population and cannot be considered as an example of the Allee effect.

In contrast, when demographic stochasticity results in random fluctuations in the population sex ratio, the probability of an individual being able to mate is affected by population size. In fact, at low densities, these fluctuations may result in a scarcity of males, limiting female access to a partner (Legendre *et al.* 1999; Stephens *et al.* 1999). This can thus be considered as an example of the Allee effect because there is a measurable component of individual fitness, specifically the female mating rate, which can be related to the size of the population.

Different modelling approaches have investigated whether demographic stochasticity could lead to a component Allee effect on female mating rate, and have consistently predicted that monogamy entails a higher extinction risk than polygyny (Legendre *et al.* 1999). However, there is little empirical evidence indicating that monogamy results in a higher extinction risk. We have recently investigated whether introduced monogamous bird species had a lower probability of establishment than polygamous species, but data of over 400 release events failed to support this prediction (Bessa-Gomes *et al.* 2003). Similarly, monogamous bird species were not proven to be more likely to be classed as threatened by the IUCN-The World Conservation Union than polygamous species (Morrow & Pitcher 2003).

The two sex models predicting that monogamy is more susceptible to the Allee effect than polygyny share an important assumption: they assume that the proportion of sexually mature male and female individuals is identical. In other words, the sex ratio among sexually mature individuals (i.e. tertiary sex ratio) equals 0.5. However, often male and female life histories are different and the tertiary sex ratios are not balanced (e.g. Clutton-Brock & Lonergan 1994; Ewen *et al.* 2001). Such departures from a 0.5 tertiary sex ratio will modify the relative availability of partners and the intensity of competition for access to reproduction (Clutton-Brock & Parker 1992), and may influence mating efficiency accordingly. Moreover, unbalanced sex ratios are also likely to affect extinction risk because they are known to change the population growth rate (Legendre 2004). In fact, the maximum growth rate occurs when both sexes are equally limiting, i.e. when the number of females sought by males equals the number of available females (Legendre 2004). As a consequence, polygynous species will attain their maximum growth rate when the tertiary sex ratio is female biased.

In this paper, we investigate (1) how variation in tertiary sex ratio affects the presence and intensity of the Allee effect induced by the mating system, as well as (2) how this effect contributes to extinction risk. We relate our results to data on sex ratio variation in natural populations, and discuss implications for a more general theory relating extinction risk to social mating system.

The analysis of the component Allee effect is centered on female mating rate not only because this component of fitness is influenced by the random fluctuations of sex ratio (see above), but also because it can easily be taken into account in population models aiming to investigate the resulting demographic Allee effect. We start by examining how variation in tertiary sex ratio and mating system affect the female mating rate in the absence of demographic stochasticity. In this analysis we have assumed that (1) male and female life histories can differ, resulting in unbalanced tertiary sex ratios; (2) the mating system limits the maximum number of partners that an individual may acquire; and (3) the female mating rate characteristic of a given population in the absence of demographic stochasticity is determined by both tertiary sex ratio and mating system.

Secondly, we investigated how demographic stochasticity impacts the female mating rate. Demographic stochasticity causes random fluctuations of the tertiary sex ratio of a population of size n around its characteristic value for a given population. If such fluctuations reduce the average female mating rate when populations are small, this difference from the characteristic female mating rate indicates a component Allee effect.

Thirdly, we investigated whether this component Allee effect results in an increased extinction risk. We considered that population size, n, is itself the result of stochastic birth and death processes and we contrasted the time to extinction when demographic stochasticity influences population dynamics only through the random variation resulting from discrete individual birth and death events (the null model which does not result in an Allee effect), or when it influences the female mating rate through the random fluctuations of the tertiary sex ratio (Allee effect model).

Finally, we collected data on sex ratio variation in natural populations from the literature. This data illustrates our results and our discussion of their implications for a more general theory relating extinction risk to social mating system.

MODELLING APPROACH

Social mating system and female mating rate

The mating system influences population growth rate because it determines the degree of access to partners, which in turn influences individual reproductive rates. Two sex models can account for the mating system by modelling the expected female mating rate r as a function of male availability. This mating rate is given by the ratio between the number c of breeding pairs and the number f of females,

$$r = \frac{c}{f}$$

The number of pairs formed is computed using a mating function reflecting the mating system (Caswell 1989; Legendre 2004). A common option is to consider that the number of pairs formed is set by the less abundant sex. In the case of monogamy, females and males mate in a one-to-one way, and the number of pairs is

$$c = \min(f, m) \tag{1}$$

where m is the number of males.

According to this formula, the number of pairs is a function of the ratio among sexually mature females and males (the tertiary sex ratio σ_3) and eqn 1 can be re-written as a function of σ_3, so that

$$\sigma_3 = \frac{f}{f + m} = \frac{f}{n} \quad \text{and} \quad c = \min(\sigma_3, 1 - \sigma_3)n \tag{2}$$

where n is the population size. This mating function is frequency dependent (Legendre 2004).

When males and females do not mate in a one-to-one way, the relative abundance of each sex in the mating population is biased in favour of the sex able to establish more pair bonds. Therefore, when males can acquire several partners, the maximum number h of pair bonds males may establish exceeds one. This maximum value sets an upper bound on male mating rate which we call their mating potential. The number of mating pairs and the female mating rate are computed as

$$c = \min(f, hm) = \min[\sigma_3, h(1 - \sigma_3)]n \quad \text{and}$$
$$r = \frac{\min(f, hm)}{f} = \frac{\min[\sigma_3, h(1 - \sigma_3)]}{\sigma_3}. \tag{3}$$

Female mating rate and the OSR theory

When the number of pairs formed depends on the relative number of males and females available to mate, each sex may constitute a limiting resource that constraints the reproductive success of the other. As a consequence, the members of the more frequent sex will compete for the access to partners. The operational sex ratio (OSR) is commonly defined as being the average sex ratio among individuals that are ready to mate at any given time (Emlen & Orring 1977), and can be estimated by accounting for the 'potential reproductive rate' of both sexes (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992). We assume here that the 'potential reproductive rate' is correlated with the maximum number of partners an individual may acquire. Hence, the OSR, denoted by σ_{oper}, may be computed correcting the population sex ratio by the male mating potential h (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992),

$$\sigma_{oper} = \frac{f}{f + hm}. \tag{4}$$

When males and females mate monogamously, the tertiary sex ratio is identical to the OSR (Fig. 1, $h = 1$). However, when the male mating potential increases, the relationship between tertiary sex ratio and OSR reflects the difference in mating opportunities between the two sexes (Fig. 1, $h = 2$ and 5). Therefore, when the tertiary sex ratio is balanced, the OSR is biased towards males (Owens & Thompson 1994). On the other hand, when the OSR is balanced the tertiary sex ratio is $\sigma_3 = h/(1 + h)$ (Legendre 2004).
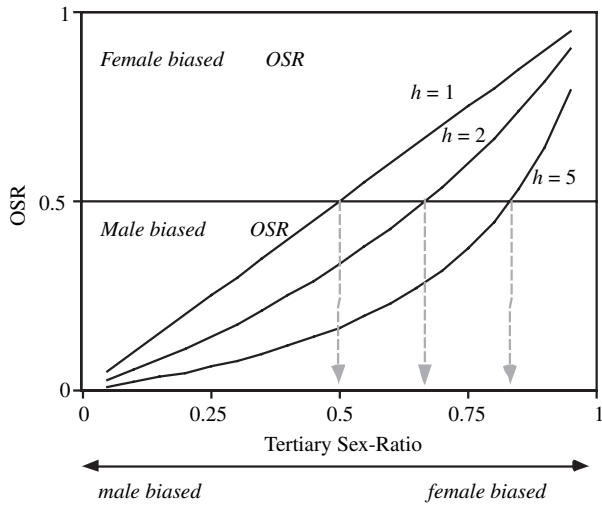
Figure 1 Variation in operational sex ratio (OSR) with the tertiary sex ratio and maximum number of pair bonds males may establish (h). The mating systems considered are monogamy ($h = 1$), bigamy ($h = 2$), and polygyny ($h = 5$). Arrows indicate the balanced OSR.

The mating function can be re-written as a function of the OSR. If we consider n_{oper} as the population size corrected by the male mating potential ($n_{oper} = f + hm$), the number of mating pairs is

$$c = \min(\sigma_{oper}, 1 - \sigma_{oper})n_{oper}. \tag{5}$$

Female mating rate under demographic stochasticity

Demographic stochasticity results in random fluctuations in the tertiary sex ratio σ_3, influencing the female mating rate. Following Møller & Legendre (2001), we assumed that the number f of females in a population of size n and expected tertiary sex ratio σ_3, is the realization of a binomial process with probability σ_3,

$$f = Bin(n, \sigma_3).$$

The realized number m of males is then

$$m = n - f.$$

When we consider that the probability of having x females, $P(f = x)$ is given by the binomial probability distribution function, the average female mating rate $\hat{r}(n)$ when population size is n can be estimated as being,

$$\hat{r}(n) = \sum_{x=1}^{n} P(f = x) \frac{\min[x, h(n - x)]}{x}. \tag{6}$$

This estimator is a function of population size, n. Thus, unlike r (eqn 3), which depends only of the relative frequency of females, the average female mating rate $\hat{r}(n)$

also depends on population size. If this estimator decreases at low density, we thus detect a component Allee effect induced by mating system.

Expected time to extinction under demographic stochasticity

Demographic stochasticity can influence population dynamics in one of two ways. The first of these (random variation resulting from discrete individual birth and death events) does not result in an Allee effect, whereas the second (fluctuation in sex ratios), results in the component Allee effect of interest here. Therefore, in order to investigate whether the component Allee effect induced by mating system affects the extinction risk, we need to assess the contribution of each form of demographic stochasticity to the overall extinction risk. We have compared the expected time to extinction estimated by two alternative models, the first one only considering the first category of demographic stochasticity (null model), whereas the second takes into account both forms (Allee model).

Following Richter-Dyn & Goel (1972) in Goodman (1987), when demographic stochasticity is the random variation resulting from individual birth and death events, the population dynamics can be described by its density dependent birth and death rates. The expected time to extinction, $E[T]$, can be estimated by a stochastic birth–death process as

$$E[T] = \sum_{x=1}^{n} \sum_{y=x}^{k} \frac{1}{y\,d(y)} \prod_{z=x}^{y-1} \frac{b(z)}{d(z)} \tag{7}$$

where $b(z)$ and $d(z)$ are the density dependent birth and death rates, n is the initial population size, and k is the carrying capacity ($n \le k$).

We have modified this stochastic birth–death process to model a population with two sexes. In the null model, although we take into account the tertiary sex ratio, the female mating rate is not affected by the random fluctuation of this sex ratio. Therefore, the female mating rate r depends only on the average tertiary sex ratio σ_3 (eqn 3) and demographic stochasticity affects the expected birth rate $b(\sigma_3)$ by influencing the number f of females in the population. This birth rate $b(\sigma_3)$ can be estimated as being

$$b(\sigma_3) = \left[\sum_{x=0}^{n} P(f = x) \frac{x}{n} \right] rb. \tag{8}$$

where b is the birth rate *per* female.

In contrast, in the Allee model, female mating rate is also affected by the tertiary sex ratio fluctuations. Hence, the average birth rate of a population of size n depends on the number of pairs formed and is estimated by

$$b(n) = \left\{ \sum_{x=0}^{n} P(f = x) \frac{\min[x, h(n - x)]}{n} \right\} b. \qquad (9)$$

RESULTS

Mating system and female mating rate

In the absence of stochasticity, the number of pairs is maximum when there are as many females as males looking for (additional) partners (i.e. $\sigma_3 = h(1-\sigma_3)$, Fig. 2a,b). Under such condition, the reproductive success of neither sex is limited by the other. The above property can be rephrased in terms of the OSR. The number of pairs is maximum

(a)

(b)

Figure 2 Number of pairs formed (a), and female mating rate (b) as a function of tertiary sex ratio and mating system (where h stands for male mating potential; eqn 3). The mating systems considered are monogamy ($h = 1$, solid line), bigamy ($h = 2$, short-dashed line), and polygyny ($h = 5$, long-dashed line). Arrows indicate the balanced operational sex ratio.

when the OSR is balanced $[\sigma_3 = h(1 - \sigma_3) \Leftrightarrow \sigma_3 = h/(1 + h) \Rightarrow \sigma_{oper} = 0.5]$. When the OSR is biased, only the relatively scarce sex fully achieves its mating rate (Fig. 2b). Hence, when the OSR is male biased (i.e. $\sigma_3 < h/(1 + h) \Leftrightarrow \sigma_{oper} < 0.5$), all females have access to a partner.

Allee effect: impact of demographic stochasticity on female mating rate

Demographic stochasticity may result in random fluctuations in the population tertiary sex ratio. If such fluctuations are to originate an Allee effect, the average female mating rate $\hat{r}(n)$ should be significantly smaller than expected when populations are small. That is in fact what we observe when we take this form of stochasticity into account (Fig. 3), independently of the mating system. Moreover, the average female mating rate tends to approach the expected female mating rate in the absence of stochasticity as population size increases.

Under balanced population sex ratio ($\sigma_3 = 0.5$) it takes larger populations for monogamous than polygynous species to reach the expected female mating rate. In other words, under a balanced tertiary sex ratio ($\sigma_3 = 0.5$), monogamy results in a stronger Allee effect because the average female mating rate is significantly reduced for small populations and the expected female mating rate is only reached for relatively large populations.

However, when the tertiary sex ratio is unbalanced, the reduction in female mating rate in relation to population size may not necessarily follow the above pattern. To analyze the relation between tertiary sex ratio and Allee effect on female mating rate, we focus on the minimal population size that
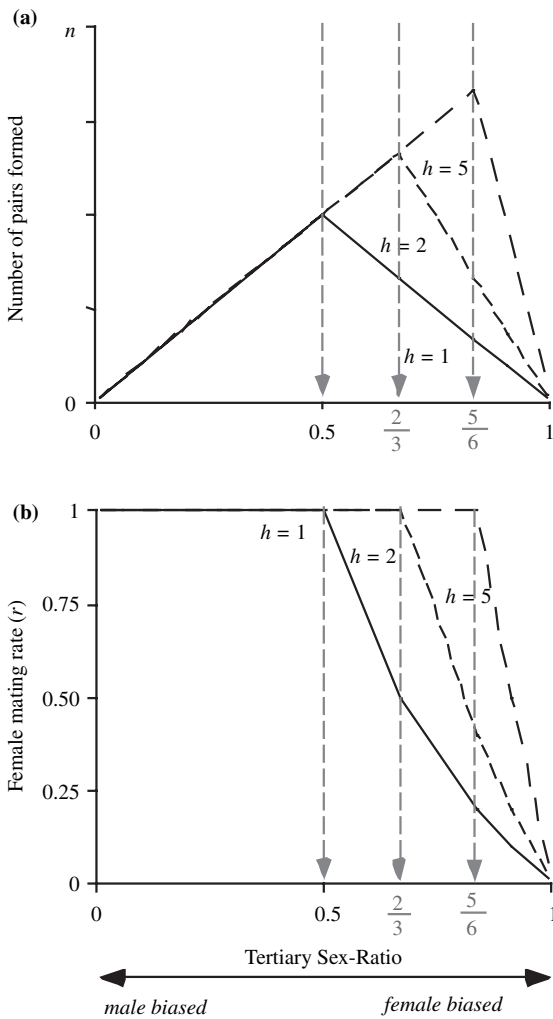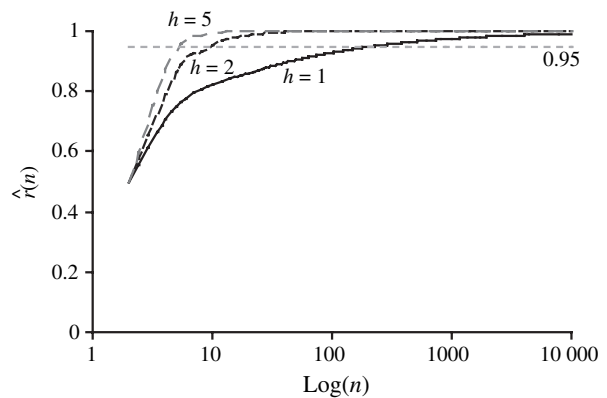

Figure 3 Variation in average female mating rate with population size $\hat{r}(n)$, in the presence of demographic stochasticity (eqn 6). The tertiary sex ratio is balanced ($\sigma_3 = 0.5$), corresponding to balanced OSR when mating system is monogamy ($h = 1$). The mating systems considered are monogamy ($h = 1$), bigamy ($h = 2$), and polygyny ($h = 5$). Grey dashed line indicates the average female mating rate of 0.95.

results in a mating rate close to the expected female mating rate (i.e. the mating rate in the absence of stochasticity). For simplicity reasons, we have chosen to centre our analysis on the minimal population size that results in an average female mating rate of at least 95% of the expected female mating rate, $n_{0.95}$. This value is a relative measure of the strength of the Allee effect because when this effect is strong, the expected female mating rate will only be approached for large populations (e.g. Fig. 3).

When we consider monogamy, we observe that the Allee effect is very strong when the tertiary sex ratio is balanced (Fig. 4). However, if the tertiary sex ratio is unbalanced, the Allee effect becomes much weaker. This result is not due to a higher expected mating rate when the sex ratio is balanced, because when the sex ratio is male biased, the expected mating rate is equally high and still no Allee effect is observed. Likewise, when we consider polygynous mating systems, we observe that there exists a characteristic tertiary sex ratio that results in a strong Allee effect. Although this tertiary sex ratio differs between mating systems, it always corresponds to the balanced OSR (i.e. $h = 1 \Rightarrow \sigma_3 = 0.5$; $h = 2 \Rightarrow \sigma_3 = 2/3$; $h = 5 \Rightarrow \sigma_3 = 5/6$). Moreover, the intensity of the Allee effect at balanced OSR increases with h (Fig. 4).

In addition, the effect of demographic stochasticity on female mating rate is also noticeable when the population tertiary sex ratio is strongly male biased, independently of the social mating system (Fig. 4). This effect is due to the fact that the random realization of such extreme sex - ratios may sometimes result in the absence of females, rendering reproduction impossible.

In conclusion, social mating systems are likely to promote an Allee effect whenever the OSR is balanced. Hence, even polygynous mating systems can experience an Allee effect if the population tertiary sex ratio is strongly female biased. Moreover, the Allee effect is likely to be more important when h is large because for each male lacking, h females will not reproduce.

In contrast, when the OSR is biased, the mating system is no longer likely to be a cause of reduced mating efficiency, independently of the direction of the skew. In particular, when the OSR is male biased, the social mating system no longer significantly reduces the female mating rate because the impact of random fluctuations in the tertiary sex ratio is buffered by the relative male excess. Indeed, when the population tertiary sex ratio is male biased (e.g. $0.2 < \sigma_3 < 0.4$), monogamy no longer significantly reduces the female mating rate at small population size.

Tertiary sex ratio variation and expected time to extinction

In order to investigate the extinction risk in a population with two sexes, we use a birth–death process to estimate the
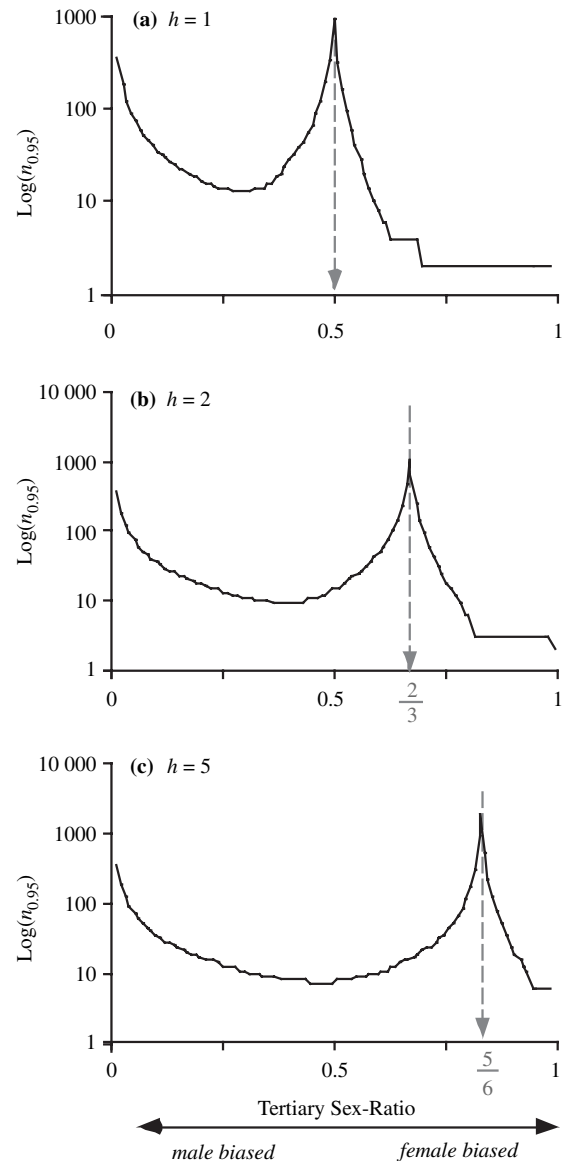

Figure 4 Variation in minimal population size resulting in an average mating rate of 95% of the expected mating rate in the absence of demographic stochasticity ($N_{0.95}$). The social mating systems considered are (a) monogamy ($h = 1$), (b) bigamy ($h = 2$), and (c) polygyny ($h = 5$). Arrows indicate the balanced operational sex ratio.

expected time to extinction when the birth rate is influenced by random fluctuations in the tertiary sex ratio (eqn 9 – 'Allee model'). When we consider a constant initial population size n, the expected time to extinction (Fig. 5) reflects the number of pairs formed (see also Fig. 2a). Since the number of pairs formed differs among mating systems, the expected time to extinction also varies accordingly. Whether monogamy faces a higher extinction risk than polygyny depends on the tertiary sex ratio. When the tertiary
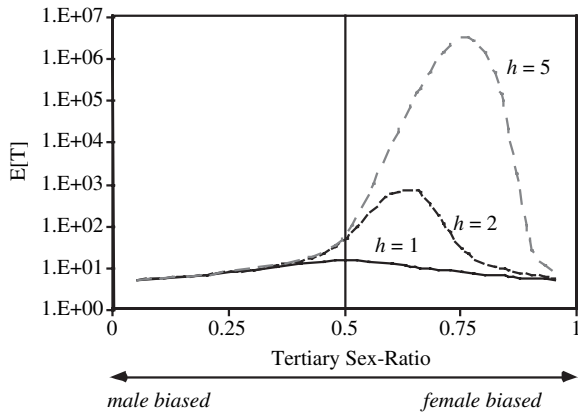
Figure 5 Time to extinction $E[T]$ across mating systems as a function of tertiary sex ratio when both classes of demographic stochasticity are taken into account (eqn 9: Allee model). The social mating systems considered are monogamy ($b = 1$, black, solid line), bigamy ($b = 2$, grey short-dashed line), and polygyny ($b = 5$, grey long-dashed line). Population size N equals 20. Time to extinction is estimated by a birth–death process ($b = 1.85$, $d = 0.9$), and initial populations are saturated, i.e. $n = k$. For simplicity reasons, we have assumed a constant mortality rate d.

sex ratio is male biased, the extinction risk tends to be similar for both monogamous and the polygamous mating systems (Fig. 5). However, when the tertiary sex ratio is balanced or female biased, this risk is higher for monogamous species (Fig. 5). Indeed, the expected time to extinction tends to increase as the number of breeding females increases until a point where male scarcity limits reproduction. After this point, the time to extinction decreases with the increased proportion of females. Polygynous mating systems will thus face a smaller extinction risk because male scarcity is felt when the proportion of females that actually breed is higher.

Contribution of the component Allee effect to the extinction risk

In order to investigate the impact of a component Allee effect in female mating rate on population extinction risk, we assessed the contribution of stochastic fluctuations of the tertiary sex ratio to the population extinction risk. Therefore, we compared our previous estimates of expected time to extinction to the equivalent estimates when the birth rate is unaffected by random fluctuations in tertiary sex ratio (eqn 8 – 'null model').

The expected time to extinction in the presence of a component Allee effect tends to be shorter than for the null model (Fig. 6). The difference between models is maximum when OSR is balanced. This observation is consistent with a strong Allee effect close to balanced OSR. However, the
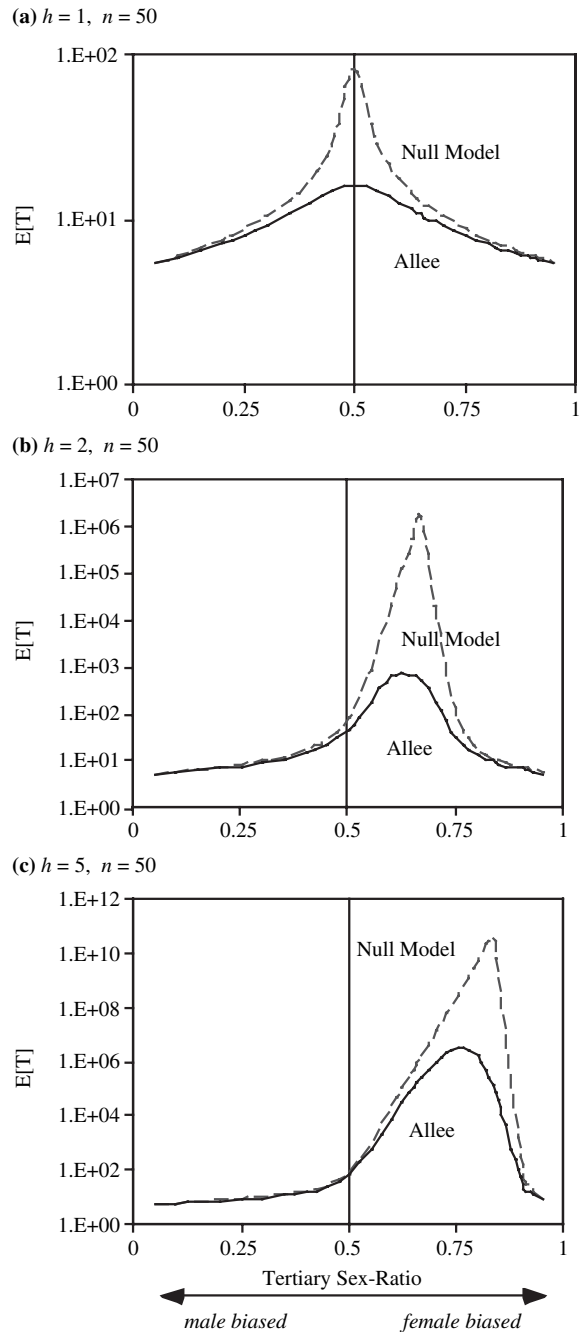

Figure 6 Time to extinction $E[T]$ as a function of tertiary sex ratio when demographic stochasticity results only in the random variation resulting from discrete individual birth and death events (eqn 8: null model, in grey, dashed line) and when demographic stochasticity results also in fluctuation in sex ratios (eqn 9: Allee model, in black, solid line). The social mating systems considered are (a) monogamy ($b = 1$), (b) bigamy ($b = 2$), (c) polygyny ($b = 5$). Population size N equals 50. Time to extinction is estimated by a birth–death process ($b = 1.85$, $d = 0.9$), and populations are saturated, i.e. $n = k$. For simplicity reasons, we have assumed a constant mortality rate d.

maximal difference occurs when the absolute extinction risk is smallest. Therefore, tertiary sex ratios leading to a strong Allee effect do not correspond to a higher absolute extinction risk.

DISCUSSION

Monogamy is not necessarily more susceptible to the Allee effect

Demographic stochasticity is likely to generate an Allee effect on mating efficiency by reducing the female mating rate when population size is small (Stephens *et al.* 1999). However, the susceptibility to such an Allee effect is not a general property of a given mating system, but depends strongly on sex ratio. When the mating system constitutes a limit to individuals' mating rates, all mating systems are likely to experience an Allee effect if the OSR is balanced. Therefore, and unlike previous predictions (Legendre *et al.* 1999; Bessa-Gomes *et al.* 2003), monogamy is neither always susceptible to the Allee effect nor generally more susceptible than other mating systems. Such predictions were based on the assumption that the tertiary sex ratio was balanced (Legendre *et al.* 1999; Bessa-Gomes *et al.* 2003), and, consequently, that the OSR of monogamous populations was balanced, whereas the OSR of polygynous populations was male biased. Indeed, this resulted in an Allee effect only for the monogamous populations. Nevertheless, if such analysis had considered a male biased sex ratio instead, no significant difference would have been found.

From Allee effects to population extinction risk

In our study, we show that the component Allee effect on female mating rate influences the extinction risk of both monogamous and polygamous populations close to balanced OSR. Nevertheless, such negative impact does not mean that populations are particularly extinction prone close to balanced OSR. Indeed, we observe the opposite, i.e. the extinction risk is minimal at this point (Fig. 6). The extinction risk depends on the demographic Allee effect (Stephens *et al.* 1999), and the impact of the component Allee effect may be compensated by other demographic mechanisms. In the case of mating systems, the component Allee effect is strongest when the number of breeding females is maximum. Therefore, the high number of breeding females compensates its negative impact, and the overall population extinction risk is lower.

Although all mating systems are likely to experience an Allee effect, they are not equally extinction prone. This difference is due to the fact that the maximum number of females that may have access to reproduction in a population depends of the mating system. This number

tends to be higher in polygynous systems (Fig. 2). As a consequence, when the OSR is balanced, small monogamous populations may be more susceptible to extinction than equally small polygynous populations because fewer females participate to the reproduction.

When we consider populations with an equivalent number of females, polygynous species are still less vulnerable because it takes fewer males to ensure that all females breed. Nevertheless, this advantage is partially buffered by the fact that overall population size is smaller, increasing the impact of demographic stochasticity and specifically, the impact of sex ratio fluctuations.

Sex ratios in natural populations

According to our analysis, the vulnerability to extinction of small populations largely depends on their tertiary sex ratio. Therefore, the relevance of our results to the current understanding of extinction risk depends on the tertiary sex ratios prevalent in natural populations with various mating systems. The tertiary sex ratio is often unbalanced due to several phenomena, such as variation in sex ratio at birth, delayed maturation, differential survival, or senescence. We have collected data on tertiary sex ratios of natural populations of birds, primates and ungulates (Table 1). This data indicates that the sex ratio is female biased in polygynous species, whereas it is male biased in monogamous species. Polygynous species often have a male biased OSR due to the high male mating potential (Clutton-Brock & Parker 1992; Mitani *et al.* 1996). Although these examples are still scarce, they support the hypothesis that in many natural monogamous populations, the average tertiary sex ratios are male biased, leading also to a male biased OSR.

Some monogamous passerines apparently have male-biased tertiary sex ratios (Table 1). These values must be interpreted with care, as non-breeding female birds are often less detectable than males, leading to biased estimations. Nevertheless, if monogamous birds have a male biased tertiary sex ratio, we no longer expect them to be more susceptible to an Allee effect than polygynous birds. Unbalanced sex ratios could thus explain why neither the establishment success nor the extinction risk of monogamous birds significantly differ from those of polygynous birds (Bessa-Gomes *et al.* 2003; Morrow & Pitcher 2003).

In contrast, polygynous mammals such as ungulates and primates provide well-documented examples of female-biased tertiary sex ratios (Table 1). In red deer, for example, males have a very high mating potential. Therefore, although some breeding populations may have up to 20 females per male, there are very few examples of natural populations where male scarcity affects birth rate (Ginsberg & Milner-Gulland 1994). Nevertheless, selective harvesting may alter

Table 1 Tertiary sex ratio variation in natural populations of birds, ungulates and primates (after (a) Arnold *et al.* 2001; (b) Dobson & Poole 1998; (c) Clarke *et al.* 2002; (d) Ewen *et al.* 2001; (e) Willis 1974; (f) Ginsberg & Milner-Gulland 1994; (g) Mitani *et al.* 1996). Both birds and mammals (ungulates and primates) are sorted by relative female abundance

Species	σ_3	Mating system
Birds		
Noisy miner (*Manorina melanocephala*)	0.30	Cooperative breeder (a)
Saltmarsh Sharp-tailed sparrow (*Ammodramus caudacutus*)	0.34	Polygyny (b)
Bell miner (*Manorina melanophrys*)	0.36	Cooperative breeder (c)
Black-eared miner (*Manorina melanotis*)	0.36	Cooperative breeder (d)
Lincoln's sparrow (*Melospiza lincolnii*)	0.36	Monogamy (b)
Pygmy nuthatch (*Sitta pygmaea*)	0.36	Cooperative breeder (b)
Brown-headed nuthatch (*Sitta pusilla*)	0.40	Cooperative breeder (b)
Cliff swallow (*Hirundo pyrrhonota*)	0.43	Monogamy (b)
Northern beardless tyrannulet (*Campstoma imberbe*)	0.44	Monogamy (b)
Bicolored antbird (*Gymnopithys bicolor*)	0.45	Monogamy (e)
Spotted antbird (*Hylophylax naevioides*)	0.45	Monogamy (e)
Ocellated antbird (*Phaenostictus mcleannani*)	0.47	Monogamy (e)
Least flycatcher (*Empidonax minimus*)	0.48	Monogamy (b)
Blue grouse (*Dendragapus obscurus*)	0.50	Lek/Promiscuity (b)
Bobolink (*Dolichonyx oryzivorus*)	0.50	Polygyny (b)
Sharp-tailed grouse (*Tympanachus phasianellus*)	0.50	Lek/Promiscuity (b)
Ruffed grouse (*Bonasa umbellus*)	0.50	Lek/Promiscuity (b)
Brewer's blackbirds (*Euphagus cyanocephalus*)	0.52	Polygyny (b)
Great-tailed grackle (*Quiscalus mexicanus*)	0.56	Polygyny (b)
Marsh wren (*Cistothorus palustris*)	0.61	Polygyny (b)
Mammals (ungulates and primates)		
Borneo orangutan (*Pongo pygmaeus*)	0.52	Polygyny/Promiscuity (g)
Red howler (*Alouatta seniculus*)	0.54	Polygyny/Promiscuity (g)
Gorilla (*Gorilla gorilla gorilla*)	0.55	Polygyny/Promiscuity (g)
Chacma baboon (*Papio hamadryas ursinus*)	0.57	Polygyny (g)
Soay sheep (*Ovis aries*)	0.60	Polygyny (f)
Black-and-gold howler (*Alouatta caraya*)	0.61	Promiscuity (g)
White-throat capuchin (*Cebus capucinus*)	0.67	Polygyny/Promiscuity (g)
Western red Colobus (*Procolobus badius*)	0.72	Promiscuity (g)
Blue monkey (*Cercupithecus mitis*)	0.72	Promiscuity (g)
Gelada baboon (*Theropithecus gelada*)	0.72	Polygyny/Promiscuity (g)
Impala (*Aepyceros melampus*)	0.75	Polygyny (f)
Bighorn sheep (*Ovis canadensis*)	0.75	Polygyny (f)
Mantled howler (*Alouatta palliata*)	0.76	Polygyny/Promiscuity (g)
Chimpazee (*Pan troglodytes*)	0.78	Polygyny/Promiscuity (g)
Red deer (*Cervus elaphus*)	0.80	Polygyny (f)
Fallow deer (*Dama dama*)	0.80	Polygyny (f)
Hanuman langur (*Semnopithecus entellus*)	0.83	Polygyny/Promiscuity (g)
Red-backed squirrel monkey (*Saimiri oerstedii*)	0.84	Polygyny (g)
Kudu (*Tragelaphus strepsiceros*)	0.92	Polygyny (f)

this scenario. Harvesting is often influenced by secondary sexual traits, such as (larger) body size or ornaments, affecting mainly males. This has led to a perception of a reduced cost of harvesting, as breeding females are spared. Nevertheless, if harvesting increases bias towards females up to a point where the OSR is no longer male biased, the extinction risk is likely to increase. Indeed, in exploited populations of ungulates, selective harvesting of males has been shown to reduce the birth rate (Ginsberg & Milner-Gulland 1994; Milner-Gulland *et al.* 2003), probably due to the scarcity of males.

FINAL REMARKS

In summary, our study indicates that all mating systems are likely to induce a strong component Allee effect.

Nevertheless, this does not render populations more extinction prone because this Allee effect is associated with the balanced OSR, a sex ratio where the extinction risk is minimum. Hence, although the component Allee effect increases the extinction risk of populations with balanced OSR, these populations are still less threatened than if their OSR were unbalanced.

These results have implications both for the current understanding of Allee effects, and for the impact of mating systems on population viability. In the context of Allee effects, our study supports the need of distinguishing between component and demographic Allee effects. This distinction may help us to understand why previous studies failed to identify an Allee effect in nature. Indeed, if the component Allee effect induced by mating systems is buffered by the frequency dependence due to sex ratios, then it will be difficult to observe it in nature.

Although the risk of extinction associated to a balanced OSR is in general weak, the Allee effect induced by the mating system may still have implications for conservation because this Allee effect reduces the overall advantage of a balanced sex ratio. Moreover, mating systems may be a conservation issue for reasons other than the Allee effect. This is illustrated by the case of selective harvesting of male ungulates, where there is evidence of a reduction in birth rate due to scarcity of males. In contrast with most predictions, this example comes from polygynous species, supposedly less susceptible to variation in sex ratio. Thus, in the absence of data on population structure and breeding biology, absolute population size or number of females may often be poor indicators of the extinction risk. To further understand the extinction risk faced by small populations we need to further understand sex ratio variation and its association with population dynamics.

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