



Original article

Discrete two-sex models of population dynamics: On modelling the mating function

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ABSTRACT

Although sexual reproduction has long been a central subject of theoretical ecology, until recently its consequences for population dynamics were largely overlooked. This is now changing, and many studies have addressed this issue, showing that when the mating system is taken into account, the population dynamics depends on the relative abundance of males and females, and is non-linear. Moreover, sexual reproduction increases the extinction risk, namely due to the Allee effect. Nevertheless, different studies have identified diverse potential consequences, depending on the choice of mating function. In this study, we investigate the consequences of three alternative mating functions that are frequently used in discrete population models: the minimum; the harmonic mean; and the modified harmonic mean. We consider their consequences at three levels: on the probability that females will breed; on the presence and intensity of the Allee effect; and on the extinction risk. When we consider the harmonic mean, the number of times the individuals of the least abundant sex mate exceeds their mating potential, which implies that with variable sex-ratios the potential reproductive rate is no longer under the modeller's control. Consequently, the female breeding probability exceeds 1 whenever the sex-ratio is male-biased, which constitutes an obvious problem. The use of the harmonic mean is thus only justified if we think that this parameter should be re-defined in order to represent the females' breeding rate and the fact that females may reproduce more than once per breeding season. This phenomenon buffers the Allee effect, and reduces the extinction risk. However, when we consider birth-pulse populations, such a phenomenon is implausible because the number of times females can reproduce per birth season is limited. In general, the minimum or modified harmonic mean mating functions seem to be more suitable for assessing the impact of mating systems on population dynamics.

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1. Introduction

Models of population dynamics are often based solely on the female sub-population, implicitly assuming there are always enough males to ensure female fertilization. However, this is not always the case. Sperm production is less costly than egg production, but sperm per male is not unlimited, and male participation in reproduction can take other forms. Males may contribute to reproduction after fertilization, for instance by taking care of the nest (Lindström and Kangas, 1996; Östlund-Nilsson, 2002),

by defending the breeding/feeding territory (Muller et al., 1997), by nest provisioning (Sandell et al., 1996), and by sharing incubation (Komdeur et al., 2002). In such situations, males become a critical resource for female reproduction. Even when fertilization is the males only contribution to reproduction, breeding dispersion may constrain mating systems and render males a limited resource (Krebs and Davies, 1987). This phenomenon is well exemplified by many territorial carnivores, where males make no contribution to parental care, but mating is still largely constrained by territorial tenure (Ferreras et al., 1997). Regardless of the proximate mechanisms at the root of the structure of the mating system, the probability that females will breed will depend on the mating system, which reflects the constraints imposed on reproduction by both sexes.

When the mating system is taken into account, population dynamics depends on the relative abundances of both males and

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females, and is non-linear (Caswell, 2001; Heino et al., 1998; Legendre, 2004; Rankin and Kokko, 2007). However, there is no single general prediction as to how this non-linearity affects population dynamics, and different studies have indicated diverse potential consequences, depending on model assumptions. They have variously predicted that sexual reproduction may have no effect on population dynamics (Castillo-Chavez and Wenzhang, 1995), have a stabilizing effect (Doebeli and Koella, 1994), or have either a stabilizing or a destabilizing effect, depending on other factors such as the degree of polygyny (Lindström and Kokko, 1998), sexual dimorphism (Lindström and Kokko, 1998), dispersal (Ranta et al., 1999), and density-dependence (Lindström and Kokko, 1998). Density dependence has been found to play a major role in small populations through an Allee effect on mating efficiency, i.e. the scarcity of males induced by stochastic fluctuations of the sex-ratio limits female access to a partner (Berec and Boukal, 2004; Bessa-Gomes et al., 2004; Stephens et al., 1999).

Among the assumptions that are likely to underlie the diversity of predictions regarding the impact of sex on population dynamics is the choice of mating function. Most of the studies mentioned above rely on one of two frequently-used mating functions, the harmonic mean and minimum function (Caswell, 2001). Nevertheless, they may impact population dynamics differently, and the possible consequences of this choice have not been studied.

In this study, we investigate the consequences for population dynamics of choosing one of three alternative mating functions: (1) the minimum; (2) the harmonic mean; and (3) the modified harmonic mean. This third mating function was proposed by Legendre (2004), and it imposes an extra condition on the harmonic mean, so that the probability that the females will breed cannot exceed a value of one. Firstly, we investigate how these functions influence the number of pairs and birth rates for different sex-ratios and degrees of polygyny. This analysis reviews some of the important properties of the minimum and the harmonic mean mating functions, and summarizes the assumptions underlying the choice of a given function.

Secondly, we illustrate the consequences of choosing a given mating function by comparing the influence of the different functions on two aspects: (i) the Allee effect due to stochastic sex-ratio fluctuations; (ii) the extinction risk. In particular, we investigate whether the reduction in the female mating rate in small populations is influenced by the mating function, and compare how these functions influence the time to extinction. Finally, we discuss the biological implications of choosing either the minimum or the harmonic mean mating function, and in which situations they are likely to be more suitable.

2. Mating functions

The mating function influences the population growth rate because it influences the degree of access to partners, which in turn determines the probability of breeding. Two-sex models can account for the mating systems by explicitly modelling female access to reproduction (i.e. the probability that females will breed) as a function of male availability (Caswell, 2001; Legendre, 2004). This probability should not be confused with the fecundity, which reflects the number of offspring actually produced (e.g. average litter/clutch size). As females can only breed if they mate, the probability that they will breed is given by the ratio between the number c of mated females over the number f of the total number of potentially reproductive females,

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

The number of pairs formed is computed using a mating function that reflects the social mating system, namely the degree of polygyny (Caswell, 2001; Legendre, 2004).

2.1. The minimum mating function

When we consider the minimum function, the number of pairs is set by the less abundant sex. In the context of monogamy, females and males mate one-to-one, and the number of pairs is given by

$$c = \min(f, m) \quad (1)$$

where m is the number of reproductive males. This mating function can be re-written as a function of the sex-ratio among reproductive individuals, σ ,

$$\sigma = f/n,$$

$$c = \min(\sigma n, (1 - \sigma)n) = \min(\sigma, 1 - \sigma)n.$$

where $n = f + m$ is the size of the breeding population. This mating function is frequency-dependent (Legendre, 2004).

When males and females do not mate one-to-one, the relative abundance of each sex in the mating population is biased in favor of the sex which is able to establish more pair bonds. Therefore, when males can acquire several partners, the maximum number, h , of pair bonds that males can establish is greater than one. This maximum value sets an upper limit on the number of breeding pairs, and concurrently, of breeding events, per male. This is termed their potential reproductive rate (Clutton-Brock and Parker, 1992; Clutton-Brock and Vincent, 1991). The number of mating pairs is computed as

$$c = \min(f, hm). \quad (2)$$

2.2. The harmonic mean mating function

The harmonic mean of the number of males and females can be used to model a mating system in which males and females mate one-to-one when the sex-ratio is balanced (Caswell, 2001; Lindström and Kokko, 1998; Ranta and Kaitala, 1999).

$$c = \frac{2fm}{f + m}. \quad (3)$$

Like the minimum function (eq. (2)), the harmonic mean has been adapted to model polygynous mating systems by taking into account the male potential reproductive rates (Lindström and Kokko, 1998; Ranta and Kaitala, 1999)

$$c = \frac{2f \cdot hm}{f + hm} \quad (4)$$

2.3. The modified harmonic mean mating function

Most discrete time models assume that breeding is seasonal, and that no more than one breeding event can occur during each time interval. The harmonic mean mating function can be modified, so that females cannot breed more than once, by requiring that the number of pairs cannot exceed the number of females (Legendre, 2004),

$$c = \min\left(f, \frac{2 \cdot f \cdot hm}{f + hm}\right) = \min\left(1, \frac{2hm}{f + hm}\right)f$$

3. Mating function influences the number of mating pairs and the probability that the females will breed

The relation between the number of pairs formed and the sex-ratio follows the same general pattern for the three mating functions under investigation (Fig. 1: A, B, C). In particular, all three functions share two important properties, their maximum value and the direction of the competition for partners, as explained below.

Firstly, the maximum possible number of pairs is formed when both sexes have achieved their reproductive potential, regardless of the mating function (Fig. 1: A, B, C). This condition indicates that the reproductive success of one sex is not limited by the number of possible partners (i.e. $\sigma = h(1 - \sigma)$) (Legendre, 2004). Moreover, at this optimum sex-ratio, the values of the maximum number of pairs formed, the probability that females will breed and the male mating rate (measured as c/m) are the same for all approaches (Minimum, Harmonic Mean, Modified Harmonic Mean).

Secondly, when females are relatively scarce (i.e. $\sigma < h(1 - \sigma)$), the mating rate of males is always less than their maximum potential mating rate (Fig. 1: G, H, I). This allows for variation among individual mating success rates and, consequently, males are likely to compete for mating opportunities. This property has important biological consequences, particularly in the context of

sexual selection, as it predicts that the variance in reproductive success among the individuals of the most abundant sex is likely to be greater, thus allowing sexual selection to operate. Similarly, when females are more abundant than males (i.e. $\sigma > h(1 - \sigma)$), the probability that they will breed is less than 1, meaning that not all females reproduce (Fig. 1: D, E, F).

Despite these important similarities, there are also some important differences between the different mating functions, and in particular between the two most often used: the minimum and the harmonic mean. Whenever the sex-ratio is non-optimal (i.e. $\sigma \neq h(1 - \sigma)$), the harmonic mean consistently estimates that a higher number of pairs will be formed than the minimum function (Fig. 1). In fact, when we use the harmonic mean, both the probability that females will breed and the male reproductive rate are positively correlated with their rarity (Fig. 1: E, H). The consequences are of the utmost importance. It is no longer possible to estimate the probability that females will mate, when sex-ratios are male-biased, because it would lead to values superior to one. This means that we can only use the harmonic mean as a mating function if we redefine the female breeding probability in terms of a female breeding rate. This rate could then be superior to one, but one must be fully aware of this: whenever males are operationally more abundant than females, females may breed more than once, leading to a probably artificial increase in

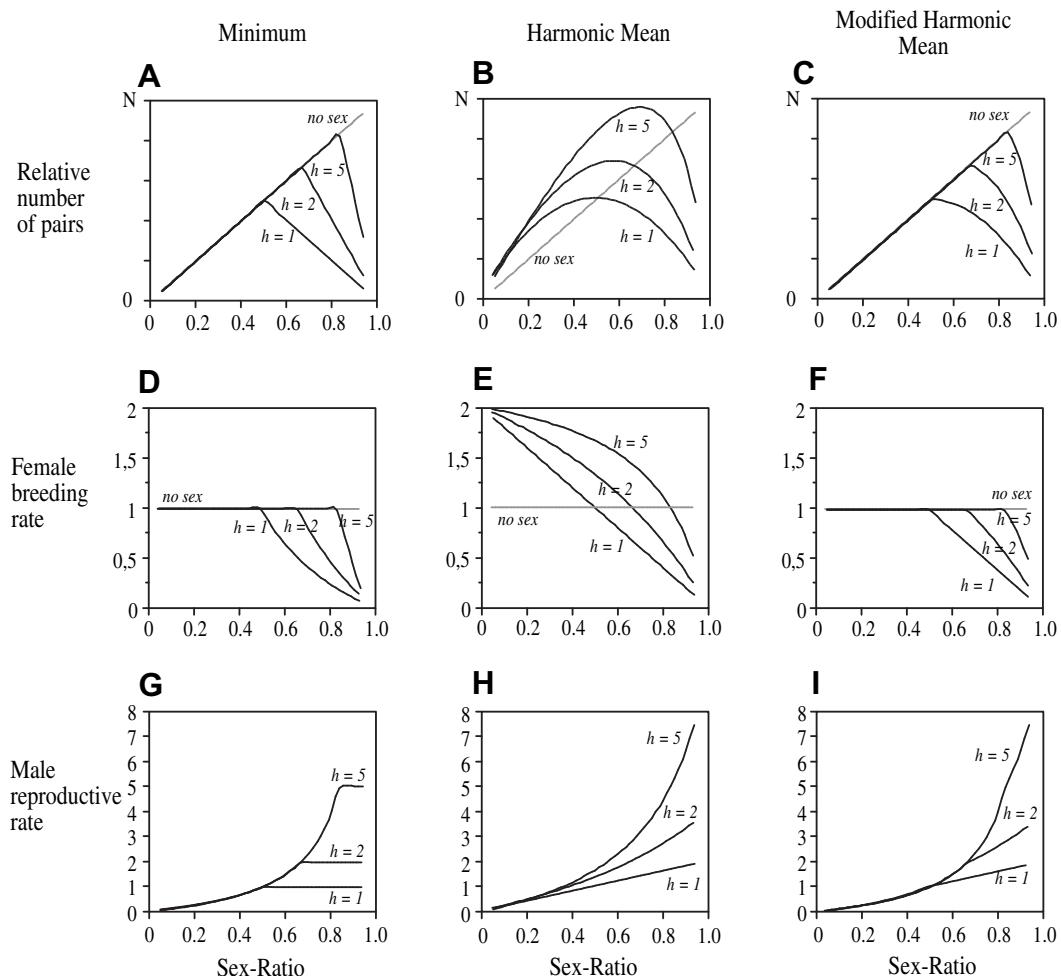


Fig. 1. Relative number of breeding pairs established in a population of size N , female breeding probability and male reproductive rate as a function of the sex-ratio (hereafter defined as the proportion of females, $\sigma = f/N$) and the mating system (where h stands for the male potential mating rate). The left column shows the results for the minimum mating function, the central column is based on the harmonic mean mating function and the right column on the modified harmonic mean mating function.

reproductive success (Fig. 1: E). This phenomenon limits the power of comparison across mating systems: if, for example, we assume that the sex-ratio is balanced and proceed to compare monogamy to bigamy, everything else being the same, we are in fact comparing birth rates that differ by almost 40%. As a consequence, population dynamics will differ due to the differences in birth rates, regardless of the impact of the mating system. The same phenomenon affects the male reproductive rate, and when males are the scarcer sex, they surpass their reproductive potential (e.g. we may have bigamy when $h = 1$).

The behavior of the modified harmonic mean proposed by Legendre (2004) depends on which sex limits reproduction, and it is the same as the minimum mating function when females are scarcer ($\sigma < h(1 - \sigma)$), but equal to the harmonic mean mating function otherwise. As a result, the risk of over-estimating birth rates is controlled, as females can only breed once during each breeding season. Nevertheless, when males are scarcer than females ($\sigma > h(1 - \sigma)$), this function still results in a reproductive rate per male that is higher than their maximum potential reproductive rate.

In summary, the harmonic mean and the minimum mating functions correspond to quite different assumptions about the mating system, specifically about the constraint imposed by the reproductive potential of each sex. When we consider the minimum mating function, we implicitly assume that the social mating system reflects the constraints affecting the reproductive potential of individuals, regardless of whether such limits are physiological, ecological, or behavioral. The monogamous minimum mating function has also been referred to as the perfect fidelity function, because it excludes the possibility of establishing multiple pair bonds. In contrast, the harmonic mean mating function describes a mating system that is plastic, allowing the least abundant sex to monopolise mating opportunities and thus increase its mating rate. As a consequence, the reproductive potential of both sexes only reflects the modeller's assumptions when the reproductive success of neither sex is limited by that of the other. Therefore, if we wish to model monogamy as a social mating system where (1) females are only able to reproduce if they have an unshared partner, and (2) the presence of additional males does not allow females to breed multiply, we can only use the harmonic mean if the sex-ratio is balanced. Likewise, when we consider bigamy, the harmonic mean overestimates the female mating rate as long as the sex-ratio is less than optimal (i.e. $\sigma < h(1 - \sigma) \Leftrightarrow \sigma < 0.667$, when $h = 2$). Therefore, if we compare monogamy and bigamy in the context of a balanced sex-ratio, bigamy necessarily results in a higher growth rate because the birth rate per female is markedly greater. Thus, the difference observed in population dynamics of monogamous and bigamous mating is not necessarily due to poorer performance by monogamous pairs, as previously predicted (Ranta and Kaitala, 1999). The danger of using the harmonic mean as a mating function is well illustrated by vertebrates. Among them, the sex-ratio among sexually mature individuals seems to vary across degrees of polygyny, so that males tend to be operationally more abundant, even under monogamy (Bessa-Gomes et al., 2004). Hence, for species such as the Ruffed Grouse, the balanced sex-ratio among sexually mature individuals (Dobson and Poole, 1998) is rendered operationally male-biased by the high degree of polygyny. The use of the harmonic mean to model the mating system will result in a high reproductive rate, as if females were able to rear multiple clutches in the same breeding season, which does not correspond to the biology of the species. Likewise, for monogamous species such as the Cliff Swallows, where females make up only about 43% of the adult population (Dobson and Poole, 1998), models using the harmonic mean will result in bigamous females.

When we consider the modified harmonic mean, we implicitly assume that the constraints imposed on reproduction differ between the sexes, being more plastic for males. This hypothesis seems to hold true in many systems. Nevertheless, if one wants to take male participation in reproduction into consideration, the function will share the limitations mentioned above for the harmonic mean.

4. Female access to reproduction under demographic stochasticity

Although all mating functions result in identical mating rates when the sex-ratios are optimal, the impact of demographic stochasticity on the female mating probability may depend on the mating function. Indeed, demographic stochasticity entails random fluctuations of sex-ratio that, at low densities, may result in a scarcity of males, limiting female access to a partner (Bessa-Gomes et al., 2004; Stephens et al., 1999). This can be considered to be an Allee effect, because there is a measurable component of individual fitness (the probability that females will breed) that can be negatively affected by low population size. This phenomenon is particularly important when sex-ratios are optimal, and the reproductive success of neither sex is limited by that of the other (Bessa-Gomes et al., 2004).

In order to take demographic stochasticity into account, we assumed that the number f of females in a population of size n and expected sex-ratio σ , is the outcome of a binomial process with probability σ , $f = \text{Bin}(n, \sigma)$ (Bessa-Gomes et al., 2004; Møller and Legendre, 2001). The remaining population is constituted of males (i.e. the number m of males is $n - f$).

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

$$\hat{r}(n) = \sum_{x=1}^n P(f = x) \frac{g(x, h \cdot (n - x))}{x} \quad (5)$$

where g is the mating function (harmonic mean, modified harmonic mean or minimum function).

4.1. The Allee effect is induced by demographic stochasticity

The female probability of mating $\hat{r}(n)$ (eq. (5)) is a function of the population size, n . When this estimator decreases at low population density, we detect a component Allee effect induced by the mating system. That is in fact what we observe when we take this form of stochasticity into account (Fig. 2), independently of the mating function.

Nevertheless, when we consider the harmonic mean mating function, the expected female probability of mating is reached with smaller populations. In contrast, both the minimum mating function and the modified harmonic mean use larger populations in order to avoid the Allee effect, regardless of the degree of polygyny. In other words, even if all functions are affected by population size, the minimum and the modified harmonic mean mating functions both result in a stronger Allee effect than the harmonic mean.

In conclusion, whether a mating systems results in a strong Allee effect depends on model assumptions, namely on whether we consider that individuals (of both sexes in the case of the minimum mating function, or females for the modified harmonic mean mating function) can only establish a limited number of pair bonds. As we have seen in Section 2, the harmonic mean provides a better description of promiscuous, plastic, mating systems. Hence, if mating systems are relatively plastic, the impact of the Allee effect

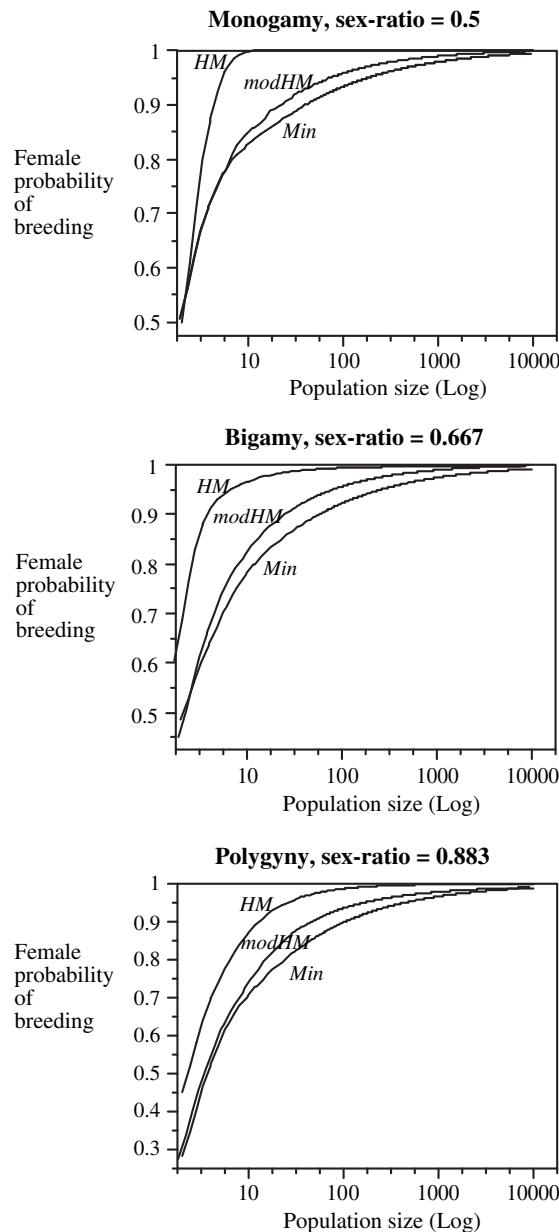


Fig. 2. Variation of the female breeding probability with population size (n) and mating function (minimum – min; modified harmonic mean – modHM; and the harmonic mean – HM), when demographic stochasticity is considered and the reproductive success of neither sex is limited by that of the other (i.e. $\sigma = h(1 - \sigma)$). The social mating systems considered are monogamy ($h = 1$), bigamy ($h = 2$) and polygyny ($h = 5$).

induced by mating systems is unlikely to be meaningful. In contrast, if the mating system constitutes a limitation for the mating potential of individuals (and particularly of females), mating systems are likely to induce a strong Allee effect.

Previous research on the Allee effect induced by mating systems has often picked out monogamy as being a particularly vulnerable mating system (Bessa-Gomes et al., 2004; Legendre et al., 1999; Møller and Legendre, 2001). However, this observation may be due not to monogamy in itself, but to the fact that monogamy is often a less plastic system. Monogamy is often associated with biparental care, meaning that even if individuals mate with multiple partners, they may be unable to raise the resulting offspring. In polygynous systems, the constraint on male availability is less likely

to impose a strong constraint. Although the Allee effects may still be present, it is more likely to be associated with other mechanisms, such as breeding dispersion (Berec et al., 2001), or sexual selection (Møller and Legendre, 2001). The impact of breeding dispersion on female access to reproduction is well illustrated by promiscuous, territorial carnivores such as polar bears (Molnar et al., 2008), where the key element underlying the Allee effect is the difficulty in finding a partner at low population density. For other species with considerable choice of mate, apart from just finding a partner, the female decision to mate and the subsequent parental investment may depend on the perceived quality of males. Hence, in low density populations of African Elephants subjected to the selective poaching of large males, female fertility is significantly reduced (Dobson and Poole, 1998).

5. Extinction risk in a context of demographic stochasticity

Demographic stochasticity can influence the risk of population extinction in two ways. The first is the random variation resulting from discrete individual birth and death events, whereas the second is the subsequent fluctuation in sex-ratios, which we discussed in Section 3. In order to illustrate how the choice of mating function influences the estimation of the extinction risk, we re-examined the model proposed by Legendre et al. (1999), and compared the probability of extinction estimated when the mating system was not taken into account (no sex) with that obtained when the mating system was taken into account using the harmonic mean, the modified harmonic mean or the minimum mating function.

Following Legendre and colleagues (Legendre et al., 1999), we consider a generic, stage-structured, monogamous passerine life cycle that was modelled by a Lefkovich matrix with two sexes and two stage classes, assuming a pre-breeding census. The first class consisted of sub-adults (first year individuals), and the second class of adults (second year or older). Sexual reproduction is taken into account by explicitly modelling the number of pairs formed. Juveniles reproduce before their first birthday. As before, fecundity was defined as clutch size per mated female, multiplied by the number of broods. Legendre et al. (1999) used a rather favourable population growth rate $\lambda = 1.105$.

In order to analyze the effect of mating function on the population extinction risk in a context of demographic stochasticity, we use a multitype branching processes (Asmussen and Hering, 1983; Ferrière et al., 1996; Gosselin and Lebreton, 2000). The parameters subjected to demographic stochasticity were the male and female survival rates, female fecundity, and primary sex-ratio. The number of pairs formed at each time step depended on the mating function. We centered our analysis on the consequences of choosing a given mating function when the social mating system is monogamous, and the sex-ratio is balanced (0.5).

For each mating function, we computed the probability of extinction in 50 years based on 500 Monte Carlo simulations. For simplicity, the initial population structure assumed an equal number of males and females close to the stable age distribution of the linear model (63% sub-adults and 37% adults).

As pointed out by Legendre et al. (1999), taking the mating system into account always leads to a higher risk of extinction than using a model where female reproduction is not affected by male scarcity. Nevertheless, the choice of mating function has a marked impact on the probability of extinction. Indeed, the extinction risk estimated using the three alternative mating functions reflects the constraints imposed by them, and the highest probability of extinction is found using the minimum mating function (Fig. 3). The modified harmonic mean mating function results in an intermediate extinction risk, and the harmonic mean mating function

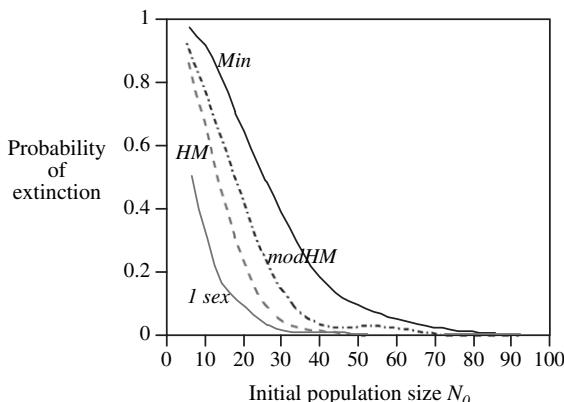


Fig. 3. Variation of the probability of extinction (over 50 years) with population size (n) and mating function (minimum – min; modified harmonic mean – modHM; and the harmonic mean – HM). The social mating systems is monogamous (the sex-ratio being balanced).

results in the lowest probability of extinction apart from the model with no mating system. Not surprisingly, a plastic, promiscuous mating system, where individuals can adjust their mating rate, is less extinction prone than a mating system where reproduction is constrained by biological, ecological or behavioral factors. Nevertheless, when females cannot reproduce more than once, the harmonic mean may underestimate the extinction risk.

The importance of the constraints acting on the social mating system for its plasticity and subsequently for the extinction risk is well illustrated by the comparative analysis of the establishment success of introduced bird species in relation to their breeding behavior (Bessa-Gomes et al., 2003). This analysis largely supports our predictions for the importance of the constraints imposed by the mating system. In particular, social monogamy *per se* was not significantly associated with establishment failure either as an univariate term or in the multivariate model, which does not support the prediction that monogamy is likely to result in a higher extinction risk than polygamy (Legendre et al., 1999; Møller and Legendre, 2001). In contrast, bi-parental care, which is associated with strict social monogamy, as both parents need to be present to ensure offspring survival, is correlated with lower establishment success.

6. Final remarks: what mating function should we use?

Although models of population dynamics often ignore the presence of males, numerous studies have highlighted the impact of males on population dynamics through various mechanisms (reviewed in Rankin and Kokko (2007)). However, the myriad of mechanisms through which males can have an impact on female fitness, may render it hard to take into account. Apart from ensuring fertilization, males may contribute positively to female fitness by conferring direct and indirect breeding advantages, but may also reduce their fitness through harassment, resource competition or sexual segregation, to cite only a few of the possible mechanisms. The extent to which such mechanisms can and should be acknowledged depends on several factors, such as how much we know about the biology of the species and the constraints acting on it, the sensitivity of population growth rate to this biology, and most of all, of the question being addressed by the model.

In this paper, we take the conservative approach of focusing on male impact solely in terms of fertilization. Previous studies have shown that we cannot always assume that every sexually mature

female can be fertilized, independently of the relative male density. Female fertilization is positively related to population density, resulting in an Allee effect (Bessa-Gomes et al., 2004; Møller and Legendre, 2001), and this can ultimately even bring about population extinction (Berec et al., 2001; Bessa-Gomes et al., 2003; Møller, 2003; Wells, 1998). But how does our choice of mating function influence our ability to estimate the degree to which males can be considered a limiting resource?

The mating function has important consequences for predicting the dynamics of birth-pulse populations, particularly due to the differences in female participation in reproduction. Therefore, when choosing a mating function, it is very important to bear in mind what question we are addressing, as well as the species biology and the constraints imposed by sexual reproduction, namely how we define the birth rate per female, whether we want to compare different degrees of polygyny, variable sex-ratios, and whether we need to take demographic stochasticity into account. The choice of mating function is likely to be of particular importance in the context of conservation.

Mating systems are often defined by the constraint they impose on reproduction through a myriad of factors, ranging from biological constraints (gestation time, egg/sperm production), to ecological factors (foraging/breeding resources), and behavioral factors (parental care, mate guarding). The minimum mating function seems to be more appropriate when the aim is to assess how these constraints affect population dynamics. In particular, assuming that females have limited fecundity makes it difficult to use the harmonic mean because any deviation in the sex-ratio that makes females the limiting sex will apparently lead to multiple reproductions by females. Indeed, if we use the harmonic mean, it may be difficult to interpret the results, because the mating potential is no longer under the modellers' control.

When the sex-ratio is optimal, neither sex is a limiting resource for the other, and the harmonic mean mating function results in mating rates that correspond to the mating potential of both sexes. The harmonic mean can therefore be used in the absence of demographic stochasticity. Nevertheless, there is little evidence that populations in nature do in fact approach this optimum sex-ratio. In a previous paper (Bessa-Gomes et al., 2004), we reported data on sex-ratio variation in natural populations of primates, ungulates and birds, and we observed that overall females tended to be scarcer than males. This implies that using the harmonic mean could lead to an overestimate of the birth rate.

The alternative mating function proposed by Legendre (2004) combines the harmonic mean and the minimum mating functions so that when females are the scarcer sex, they limit the number of pairs formed, whereas when males are the scarcer sex, the number of pairs formed is the harmonic mean of the number of males and females present in the population. This function restricts female mating potential, but allows for plasticity in the male mating potential. The male mating potential should not be seen as the upper limit of male participation, but rather as the average male participation. Hence, departures from the optimal sex-ratio allow males to increase their mating potential, and thus reduce the intensity of competition for access to partners. This function should be less vulnerable to the Allee effect than the minimum mating function. It should also lead to a lower extinction risk. Nevertheless, it does not overestimate growth rate by increasing the birth rate when females are scarcer, as the harmonic mean does.

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References

- Asmussen, S., Hering, H., 1983. Branching Processes. Birkhäuser.
- Berec, L., Boukal, D.S., Berec, M., 2001. Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. *American Naturalist* 157, 217–230.
- Berec, L., Boukal, D.S., 2004. Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. *Oikos* 104, 122–132.
- Bessa-Gomes, C., Danek-Gontard, M., Cassey, P., Møller, A.P., Legendre, S., Clobert, J., 2003. Mating behaviour influences extinction risk: insights from demographic modelling and comparative analysis of avian extinction risk. *Annales Zoologici Fennici* 40, 231–245.
- Bessa-Gomes, C., Legendre, S., Clobert, J., 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters* 7, 802–812.
- Castillo-Chavez, C., Wenzhang, H., 1995. The logistic equation revisited: the two-sex case. *Mathematical Biosciences* 128, 299–316.
- Caswell, H., 2001. Matrix Population Models. Sinauer Associates Inc.
- Clutton-Brock, T.H., Parker, G.A., 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology* 67, 437–456.
- Clutton-Brock, T.H., Vincent, A.C.J., 1991. Sexual selection and the potential reproductive rates of males and females. *Nature* 351, 58–60.
- Dobson, A., Poole, J., 1998. Conspecific aggregation and conservation biology. In: Caro, T. (Ed.), *Behavioral Ecology and Conservation Biology*. Oxford University Press, pp. 193–208.
- Doebeli, M., Koella, J.C., 1994. Sex and population dynamics. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 257, 17–23.
- Ferreras, P., Beltran, J.F., Aldama, J.J., Delibes, M., 1997. Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*). *Journal of Zoology* 243, 163–189.
- Ferrière, R., Sarrazin, F., Legendre, S., Baron, J.-P., 1996. Matrix population models applied to viability analysis and conservation: theory and practice using ULM software. *Acta Oecologica* 17, 629–656.
- Gosselin, F., Lebreton, J.-D., 2000. Potential of branching processes as a modeling tool for conservation biology. In: Ferson, S., M.B. (Eds.), *Quantitative Methods for Conservation Biology*. Springer-Verlag, pp. 199–225.
- Heino, M., Metz, J.A.J., Kaitala, V., 1998. The enigma of frequency-dependent selection. *Trends in Ecology & Evolution* 13, 367–370.
- Krebs, J.R., Davies, N.B., 1987. Parental care and mating system. In: An Introduction to Behavioural Ecology. Blackwell Scientific Publications, pp. 191–220.
- Komdeur, J., Wiersma, P., Magrath, M., 2002. Paternal care and male mate-attraction effort in the European starling is adjusted to clutch size. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269, 1253–1261.
- Legendre, S., 2004. Age structure, mating system and population viability. In: Ferrière, R., Dieckmann, U., Couvet, D. (Eds.), *Evolutionary Conservation Biology*. Cambridge University Press, pp. 41–58.
- Legendre, S., Clobert, J., Møller, A.P., Sorci, G., 1999. Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *American Naturalist* 153, 449–463.
- Lindström, J., Kokko, H., 1998. Sexual reproduction and population dynamics: the role of polygyny and demographic sex differences. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 265, 483–488.
- Lindström, K., Kangas, N., 1996. Eggs presence, egg loss, and female mate preferences in the sand goby (*Pomatoschistus minutus*). *Behavioral Ecology* 7, 213–217.
- Møller, A.P., 2003. Sexual selection and extinction: why sex matters and why asexual models are insufficient. *Annales Zoologici Fennici* 40, 221–230.
- Møller, A.P., Legendre, S., 2001. Allee effect, sexual selection and demographic stochasticity. *Oikos* 92, 27–34.
- Molnar, P.K., Derocher, A.E., Lewis, M.A., Taylor, M.K., 2008. Modelling the mating system of polar bears: a mechanistic approach to the Allee effect. *Proceedings of the Royal Society B-Biological Sciences* 275, 217–226.
- Muller, K.L., Stamps, J.A., Krishnan, V.V., Willits, N.H., 1997. The effects of conspecific attraction and territorial quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist* 150, 650–661.
- Östlund-Nilsson, S., 2002. Does paternity or paternal investment determine the level of paternal care and does female choice explain egg stealing in the fifteen-spined stickleback? *Behavioral Ecology* 13, 2.
- Rankin, D.J., Kokko, H., 2007. Do males matter? The role of males in population dynamics. *Oikos* 116, 335–348.
- Ranta, E., Kaitala, V., 1999. Punishment of polygyny. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 266, 2337–2341.
- Ranta, E., Kaitala, V., Lindström, J., 1999. Sex in space: population dynamic consequences. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266, 1155–1160.
- Sandell, M.I., Smith, H.G., Bruun, M., 1996. Paternal care in the European starling, *Sturnus vulgaris*: nestling provisioning. *Behavioral Ecology & Sociobiology* 39, 301–309.
- Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect? *Oikos* 87, 185–190.
- Wells, H., 1998. Mate location, population growth, and species extinction. *Biological Conservation* 86, 317–324.