Mating behaviour influences extinction risk: insights from demographic modelling and comparative analysis of avian extinction risk

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Mating behaviour has long been proposed as a potential cause of inverse density dependence that can affect the viability of small populations through the reduction of female mating rates. However, under the general designation of mating behaviour we may find a diversity of traits that are likely to influence the mating rate. In the present study, we have analysed the influence of the social mating system, mate choice and mating opportunities on population dynamics given a demographic model that explicitly takes mating behaviour into account. The effect of mate choice on extinction risk depends on aspects such as the social mating system, the probability of accepting unattractive males, mating opportunities and variation in reproductive success. Thus, mate choice *per se* only leads to a significant increase in extinction risk if the social mating system is monogamous. If mating opportunities are limited, however (e.g. reduced encounter rate), the extinction probability associated with mate choice increases considerably. The risk of extinction associated with mate choice further increases when differences in reproductive success due to male attractiveness are taken into account. A comparative analysis of the establishment success of introduced bird species supports our predictions concerning mate choice. Sexually dichromatic species have a significantly lower establishment success than monochromatic species. However, the establishment success of non-native species was not significantly correlated with the social mating system, so that monogamous species are not less likely to be successful than polygamous species.

Introduction

Since the emergence of the small population paradigm in the 1980s (Caughley 1994), the fate of small populations has been the focus of considerable interest (e.g. Shaffer 1981, Shaffer & Samson 1984). Underlying many studies of the viability of small populations is the definition of "small" itself, i.e. how small a population has to be, so that its size may result in a high risk of extinction. Although some rules of thumb have been proposed to support the decision making process (e.g. Lande & Barrowclough 1987, Soulé 1986), it has proven difficult to provide a quantitative answer to this question because the extinction risk associated with a given population size largely depends on species biology, namely its life history, ecology and behaviour.

The definition of "smallness" relies essentially on the susceptibility of the focal population to stochastic factors, e.g. demographic and environmental stochasticity, genetic drift, and catastrophes. However, another factor that is likely to play a dominant role is the existence of inverse density dependence, i.e. the reduction of the population growth rate when population size decreases (Courchamp *et al.* 1999a, Stephens & Sutherland 1999). This phenomenon, usually termed the "Allee effect", was first described by W. C. Allee in 1931 (Allee *et al.* 1949 in Courchamp *et al.* 1999a), and is associated with the need of conspecifics to assure one's own survival or reproduction (Courchamp *et al.* 1999b, 2002). Consequently, mating behaviour is one of the mechanisms likely to cause an Allee effect due to the reduction in mating efficiency at low densities (Courchamp *et al.* 1999a, Stephens & Sutherland 1999, Stephens *et al.* 1999). Under the general designation of mating behaviour we find a diversity of traits that are likely to be responsible for this phenomenon and whose interactions are still unclear.

One of the sources of reduction in mating efficiency is the inability of finding a suitable mate. This inability may be due simply to the random variation in the population sex ratio, which may result in a scarcity of males and, consequently, in some females being unable to breed (Courchamp *et al.* 1999a, Stephens & Sutherland 1999, Stephens *et al.* 1999). This hypothesis has received theoretical support, in particular in monogamous mating systems (Legendre *et al.* 1999, Møller & Legendre 2001).

Another source of reduction in mating efficiency at low population density is the eventual reduction of encounter rates. At low densities, individuals may have difficulty encountering conspecifics, resulting in a reduction of mating opportunities (McCarthy 1997, Wells 1998). The potential for reduction in encounter rate depends on breeding dispersion and mate searching strategies. Thus, when at least one of the sexes is able to actively locate potential partners, populations are less susceptible to the Allee effect than populations that rely solely on a random search process (Berec *et al.* 2001).

An additional hypothesis that has attracted recent attention concerns mate choice (Møller 2000, Møller & Legendre 2001, *see* also Kokko & Brooks 2003, Møller 2003). Given mate choice, simply finding a conspecific of the opposite sex is insufficient to assure reproduction because the prospective mate may not be acceptable. In other words, the existence of mate choice may lead to the refusal of less attractive partners and, consequently, delay or prevent some individuals from breeding. African elephants, *Loxodonta africana*, provide an emblematic example of reduced female mating rate due to mate choice. In this species, females preferentially mate with males with large tusks. Unfortunately, such males are also preferred by poachers, and in populations submitted to heavy poaching the proportion of females showing signs of pregnancy or accompanied by offspring is relatively small (Dobson & Poole 1998).

Mate choice can also result in an Allee effect even when mating does occur. In fact, when choice is constrained, mate choice can result in reduced reproductive success due to reduced fertilization rate, lower offspring viability or reduced parental investment among others (Møller & Legendre 2001). Such phenomena are widely illustrated by captive animals that cannot chose their mates, being a major concern in studies of conservation *ex-situ* for several threatened species (reviewed in Møller & Legendre 2001).

The potential effect of sexual selection on extinction risk has also been tested using the establishment success of introduced bird species

as a surrogate of local extinction of small populations. This is based on the observation that introduction failure results from an immediate extinction of introduced populations rather than a long-term decline. Such introductions could also mimic the situation when the environment changes rapidly causing a dramatic decline in local (or global) population size. It is likely that features that may predispose species to a greater influence of demographic stochasticity or Allee effect, such as the mating system or female mate preferences in sexually dichromatic species, should have a greater risk of introduction failure. In this context, McLain *et al.* (1995, 1999) have demonstrated that sexually dichromatic birds introduced to Oahu, Hawaii and Tahiti were less successful than monochromatic birds. A subsequent analysis of establishment success of birds introduced to New Zealand, controlling for the effect of propagule size and release effort, revealed a similar effect of sexual dichromatism on introduction success (Sorci *et al.* 1998). Finally, one of us analysed a very large database (at least 416 species from 45 families) and also found a significant negative relationship between sexual dichromatism and introduction success (Cassey 2002).

In the first part of the paper, we analyse the effect of several features of mating behaviour on population extinction risk through demographic modelling. In order to do so, we include a mating function that explicitly takes mating system, mate choice and mating opportunities into account (Bessa-Gomes *et al.* 2003) on the generic two sex-model proposed by Legendre *et al.* (1999). Consequently, we estimate the local probability of extinction as a function of mating system (monogamy, bigamy, polygyny), and mate choice. We explore several features of mate choice, namely the probability of accepting less attractive partners and variation in reproductive success as a function of the breeding partner. Moreover, we also examine how the number of mating opportunities affects extinction risk.

In the second part of the paper, we test our predictions by investigating whether mating behaviour is likely to influence successful establishment of introduced bird species. We compare the introduction success of species with repeated independent introduction attempts as a func-
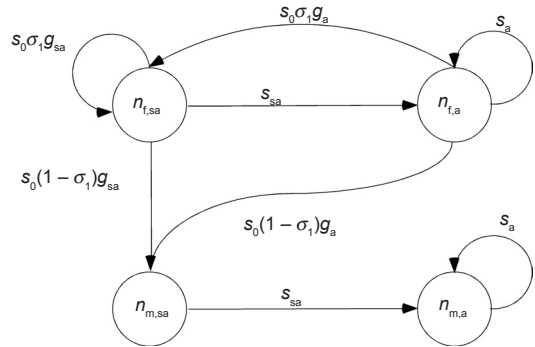

Fig. 1. Generic passerine life cycle (after Legendre *et al.* 1999), where $n_{f,sa}$ and $n_{f,a}$ are sub-adult and adult females, and $n_{m,sa}$ and $n_{m,a}$ are sub-adult and adult males. Following Legendre *et al.* (1999), offspring survival, s_0, was 0.2, sub-adult survival, s_{sa}, 0.35, and adult survival, s_a, 0.5. Mating behaviour can be accounted for by the number of pairs involving a female from class *i* and a male from class *j*, that are formed per female from class *i,* hereafter termed the female mating rate r_{ij}. Hence, g_{sa} and g_a represent respectively the sub-adult and adult female reproductive rate, where $g_{sa} = (r_{sa,sa} f_{sa,sa} + r_{sa,a} f_{sa,a})$ and $g_a = (r_{a,sa} f_{a,sa} + r_{a,a} f_{a,a})$. The average fecundity of both sub-adult ($f_{sa,sa}$ and $f_{sa,a}$) and adult females ($f_{a,sa}$ and $f_{a,a}$) was 7, and the primary sex ratio, σ_1, (i.e. sex ratio at birth) was 1:1.

tion of mating behaviour, namely mate choice, mating system, and parental care, while explicitly controlling for phylogenetic effects due to similarity among taxa as a result of common ancestry. In the final section, we evaluate the results of both the demographic model and comparative analysis of establishment success.

Methods

Modelling framework

We assume that mating behaviour affects population dynamics by changing the number and type of pairs that are formed. Consequently, when we consider a generic, stage structured, passerine life cycle, mating behaviour can be taken into account by explicitly modelling female mating probability and by allowing female fecundity to depend on their own class, as well as on their partner class (Fig. 1). In this analysis, passerine life history was modelled by a life cycle graph with two sexes and two stage classes, assuming
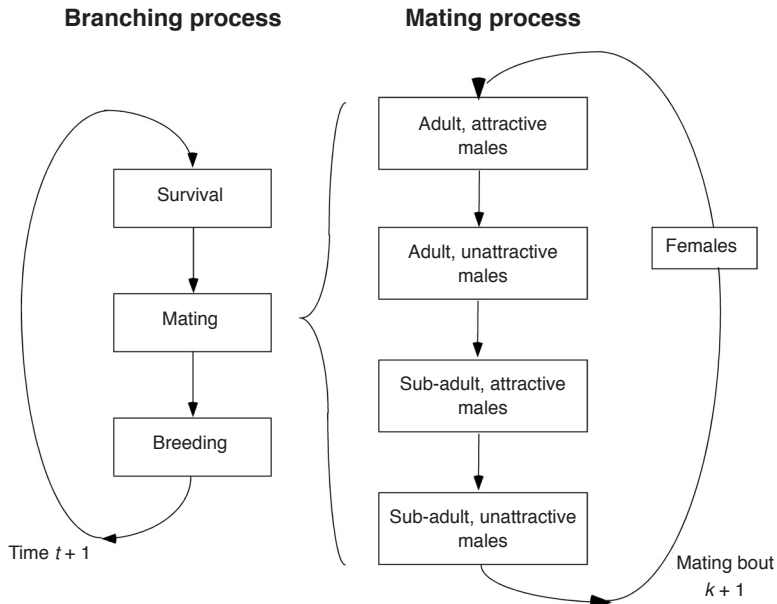
Branching process   **Mating process**

Fig. 2. Schematic representation of the branching process and mating process. The following operations were realized at each time step: computing the number of survivors as the realization of a binomial distribution whose probability is the stage dependent survival rates; computing the number and type of pairs according to the mating process; and computing the number of descendants as the sum of trials of a Poisson distribution whose mean is the pair dependent fecundity. Offspring sex and male attractiveness were computed as the realization of a binomial distribution of probability 0.5. The mating process is also stochastic, and the following operations were realized at each mating bout: the number of females mated with an adult, attractive male is the realization of a binomial distribution whose probability is the female rank 1 dependent probability of mating; the number of females that remain unmated and subsequently mated with an adult, unattractive male is the realization of a binomial distribution whose probability is the female rank 2 dependent probability of mating; the same operations are subsequently realized for the sub-adult, attractive and unattractive males.

a pre-breeding census (Fig. 1). The first class consisted of sub-adults (first year individuals) and the second class of adults (second year or older). Juveniles reproduce before their first birth. Fecundity was defined as clutch size per mated female, multiplied by the number of broods. Legendre *et al.* (1999) derived a matrix population from the life cycle graph in Fig. 1, and estimated a rather favourable population growth rate $\lambda = 1.105$.

We have adapted this generic passerine life cycle so that in addition to sex and stage, individuals can also be characterized according to two additional state variables, namely their attractiveness (attractive or unattractive), and their availability to mate (committed or still available to establish (additional) pair bonds).

Demographic stochasticity and probability of extinction

In order to analyse the effect of mating behaviour on population extinction risk under demographic stochasticity, we use a multitype branching processes (Asmussen 1983, Ferriére *et al.* 1996, Gosselin & Lebreton 2000). In contrast to continuous population dynamics models, population sizes are restricted to integer values because cycle transitions are modelled as the realization of a given probability distribution. Therefore, when we consider *n* individuals subjected to a probability of survival *s*, the number of survivors is the realization of a binomial distribution with probability *s* and sample size *n*. For the fecundity transition, the number of

descendents is the sum of trials according to a Poisson distribution (Fig. 2: branching process). The number of females that reproduced at each time step, as well as the type of males they mated with, depends on the relative number of females and males still ready to mate, on their respective classes, on the maximal number of pair bonds each individual may establish, and on female mating preferences.

Mating system and mate choice

We assume that mate choice implies the relative ranking of potential partners according to their attractiveness and that females mate in priority with attractive partners (Fig. 2: mating process). As a consequence, no unattractive male is considered while attractive males are still available. In the impossibility of mating with attractive males, which are always accepted, females accept unattractive mates with a probability β_j (Gibson & Langen 1996, Johnstone *et al.* 1996), which depends only on male class, j. Hence, the probability of acceptance is innate, not being affected by the context (e.g. available mates) or experience (Bessa-Gomes *et al.* 2003). Accordingly, we denote the female mating preference by $\{\beta_j, \alpha_j(r)\}$, where $\alpha_j(r)$ is the probability of a male in class j being classified in the relative attractiveness rank r (in this analysis, $\alpha_j(r) = 0$ or $\alpha_j(r) = 1$).

The relative attractiveness ranking affects pair formation. When we rank the potential partners, we assume that, at each mating bout, pair formation proceeds according to the attractiveness hierarchy, so that females acquire the most attractive male possible. Therefore, as long as potential partners of higher ranks are still available, individuals of lower ranks will be unacceptable. This hierarchical view of pair formation can be modelled through an iterative algorithm whose iterations, r, correspond to the mating preference ranks.

Let $f_i(r)$ be the number of females from mating class i ($i = 1, \ldots, n_f$), and $m_j(r)$ be the number of males from mating class j ($j = 1, \ldots, n_m$) at iteration r. The probability of a female from class i mating with a male from class j at iteration r is given by

$$p_{ij}(r) = \min\left(\frac{1}{\sum_k \alpha_k(r)m_k(r)}, \frac{1}{\alpha_j(r)\sum_k f_k(r)} \right) \times \alpha_j(r)\beta_j m_j(r) \quad (1)$$

At each iteration, the number of individuals available for mating depends on the number $c_{ij}(r)$ of ij pairs formed on the previous iteration, so that

$$\begin{aligned} c_{ij}(r) &= \min\{\mathrm{Binom}[f_i(r), p_{ij}(r)], m_j(r)\} \\ f_i(r+1) &= f_i(r) - \sum_j c_{ij}(r) \\ m_j(r+1) &= m_j(r) - \sum_i c_{ij}(r) \end{aligned} \quad (2)$$

The mating function and mate choice algorithm are explained in detail in Bessa-Gomes *et al.* (2003).

At each mating bout, individuals cannot establish more than one pair bound. However, the mating process may proceed through several mating bouts, allowing individuals to establish more than one pair bound (polygamy). The maximal number of pair bonds an individual may establish depends of the social mating system. We have chosen to centre our analysis on the consequences of female choice when females cannot establish more than one pair bond, meaning that, once they accept a given partner, they are committed and cannot profit from further mating bouts to change their choice of partner. In contrast, when male potential mating rate is higher than one, mated males are allowed to participate in further mating bouts. As males cannot establish more than one pair bond at each mating bout, this approach entails a minimal male investment in each pair bond he establishes.

Monte Carlo simulation

For each set of parameters, we have computed the probability of extinction in 100 years based on 300 Monte Carlo simulations. Parameters subjected to demographic stochasticity were

male and female survival rates, female mating probabilities, female fecundity, and primary sex ratio (the parameter values are indicated in Fig. 1). For simplicity, the initial population structure considers an equal number of males and females close to the stable age distribution of the linear model (63% subadults and 37% adults, after Legendre *et al.* 1999). The probability of being attractive is 0.5, and at each new generation males are randomly allocated to an attractiveness class.

In a first approach, we have centred our analysis on the consequences of female choice when females cannot establish more than one pair bond. The maximal number of pair bonds a male may establish depends on the social mating system, being set either equal to one (monogamy), two (bigamy), or five (polygyny) and only one pair bond can be established at each mating bout.

The acceptance probability of each male class is linearly proportional to its attractiveness, always being equal to one for the most attractive class, and minimal for the most unattractive class. In order to explore different degrees of "choosiness", the minimum value, denoted β_{min}, varies between 0 and 1 ($\beta_{min} = 0, 0.25, 0.5, 0.75,$ and 1).

Moreover, we explored the consequences of limiting the number of mating bouts, because they are likely to be reduced at low population density due to reduced encounter rates (McCarthy 1997, Wells 1998) or eventual perturbations (environmental or human-related). Thus, the number of mating bouts varies between 1 and 10.

Finally, we also explore the consequences of variation in female reproductive success due to male attractiveness, i.e. females that mate with less attractive males will have a lower reproductive success than females mated with attractive males (Møller & Legendre 2001). This reduction may be due to several mechanisms, such as lower offspring viability or reduced parental investment (Møller & Thornhill 1998).

We consider that the highest and lowest fecundity differed by a parameter Δ, but that the expected population reproductive success was independent of the magnitude of Δ. Therefore, in the absence of demographic stochasticity, variation in fecundity does not change the average population reproductive success. In order to do

so, the reproductive success per type of mating is set based on the expected frequency of each type of mating. In this way, we ensure that any difference in extinction risk due to variation in reproductive success is not due to a change in the expected reproductive success, but to the stochasticity associated with mate choice.

Comparative analysis of establishment success

We tested the model predictions by investigating whether mating behaviour is likely to influence successful establishment of introduced bird species because this success will depend, among others, on their capacity to persist given a small initial population size (Duncan *et al.* 2001, Green 1997, Sorci *et al.* 1998, Veltman *et al.* 1996). Here we have analysed the effect of mating behaviour on extinction risk using an extensive database collated by Cassey (2002), that includes information on 416 species and 1900 independent introduction attempts.

Data sources, life history, ecological and behavioural traits

Following Cassey (2002), we have defined an introduced land bird species as one that is recorded to have been transported and introduced free-living outside its naturally occurring geographic range. By land birds we mean avian species that are considered to have long-term terrestrial populations and that are not dependent on the ocean for feeding. The outcome of each 'introduction attempt' was defined by the success or failure of an introduction of a single species to a single mainland state/territory or oceanic island regardless of the number of events or their outcome. For comparability we have included the life history and ecological variables that we have previously found to significantly affect avian introduction success in the present analyses (Cassey 2002). Estimates of avian traits were obtained from as many studies as found in the primary literature and supplemented with taxon-specific publications, as well as references therein and unpublished data.

Body mass is likely to be the most useful univariate measure of avian body size (Freeman & Jackson 1990, Rising & Somers 1989, although *see* Piersma & Davidson 1991). Subsequently, our index of body size was average female body mass (measured in grams). Dietary generalism was based on the number of major food types that are recorded as being included in the diet of a species. The seven different food types that we considered were (in no particular order): grasses and herbs; seeds and grains; fruits and berries; pollen and nectar; vegetable material; invertebrate prey; and vertebrate prey and carrion. Migratory tendency was characterized as a species index of year-round occupancy of a site: 0, sedentary (population does not move away from breeding grounds at any time of the year); 1, nomadic (moves sporadically to find suitable breeding and feeding grounds); 2, local movement (moves short distances including altitudinal migration); 3, partial migrant (part of population is migratory, part is sedentary); and 4, migrant (the entire population is migratory).

In terms of breeding behaviour, we collated data on three variables, namely on sexual dichromatism, social mating system and parental care. Sexual dichromatism, which is an index of the intensity of sexual selection (Andersson 1994, Gontard-Danek & Møller 1999), was defined as a visible difference (however small this difference appeared to be) between plumage coloration of males and females of a given species. Hence, sexual dichromatism was defined as present or absent based on colour plates and on information given in handbooks.

Species were classified as being monogamous if there was no record of polygamy or if reliable data existed ensuring that the frequency of polygamy was less than 5%. If alternative mating systems were mentioned, but their frequency was not quantified, we did not consider the species as monogamous because it was likely that such species had a flexible mating system. Biparental care was defined as the involvement of both parents in offspring rearing, all categories of care combined (incubation, food provisioning, etc.). Therefore, even if parental investment was asymmetrical, we still considered it to be biparental care.

Data analysis

We used the GLIMMIX macro in SAS ver. 8.2 (Littell *et al.* 1996) to fit a generalised linear mixed model (GLMM) specifying a binomial error distribution and logit link function, with introduction outcome (0 = failure, or 1 = success) modelled as the response variable. The GLMM provides a statistical framework to model the likely statistical non-independence of introductions within the taxonomic hierarchy (Harvey & Pagel 1991). Following the methods established by Blackburn and Duncan (2001) we assumed a common positive correlation between introduction outcomes involving the same taxa, but a zero correlation between introduction outcomes involving different taxa (a variance components model).

Results

The importance of mating behaviour with regard to extinction probability

Overall, our estimates of the extinction probability indicate that mating behaviour is likely to have an important impact on small passerine populations, thus influencing their extinction threshold (e.g. Figs. 3 and 4). Consequently, taking mating behaviour into account increases the probability of extinction so that larger population sizes may be necessary to assure their viability. The magnitude of the mate choice effect on extinction risk depends on the mating system, the probability of accepting less attractive partners, the variation in reproductive success, and the number of mating bouts considered.

"Choosiness" alone does not have a strong effect on probability of extinction of polygamous populations…

When mating bouts are not limited, the refusal of less attractive partners entails a reduction in mating efficiency, but for polygamous species this effect is only noticeable at very small population sizes (Fig. 3). In fact, although the probability of accepting unattractive males is
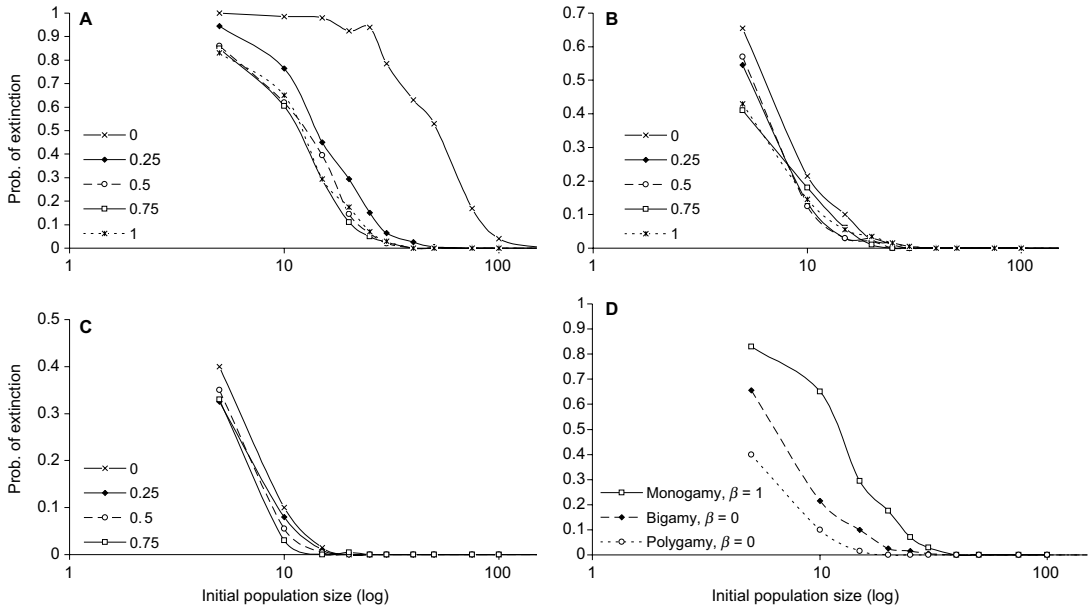
Fig. 3. Variation in extinction risk as a function of population size and probability of accepting a less attractive partner. When the probability of acceptance equals 1, mate choice is passive, i.e. results only from the relative ranking of potential partners. The mating process occurs in 10 mating bouts. — **A**: Monogamy ($h = 1$); — **B**: Bigamy ($h = 2$); — **C**: Polygamy ($h = 5$); — **D**: Comparison between monogamy given passive mate choice ($\beta_{min} = 1$) and both bigamy and polygamy when less attractive males are refused ($\beta_{min} = 1$).

negatively correlated with the probability of extinction, its effect is minor and tends to disappear as population size increases.

…but may have a strong impact when mating bouts are limited…

However, previous studies have indicated that, at low population size, individuals may have difficulty in finding a partner (Berec *et al.* 2001, McCarthy 1997, Wells 1998), which may result in a severe limitation of mating bouts. When we consider that mating bouts are limited, the extinction probability tends to increase (Fig. 4). In particular, the limitation of mating bouts magnifies the effect of mate choice and acceptance probabilities, so that when the number of mating bouts is relatively small, breeding strategies involving a lower probability of accepting less attractive partners result in a higher extinction risk.

In summary, our results indicate that mate choice reduces mating efficiency at each single bout. However, if females dispose of sufficient mating bouts, they are likely to find a mate, especially if males are polygamous. In other words, if in a given mating bout females are unable to gain access to an attractive male and subsequently refuse to mate with unattractive males, in the next bout the same polygamous attractive males may be ready to mate, and females may now gain access to them because the eventual female competitors are already committed. Therefore, mate choice entails a high extinction risk only if mating opportunities are limited either by the social mating system (monogamy), or by a reduced encounter rate (i.e. limited mating bouts).

…and when there is variation in reproductive success

The existence of differential reproductive success as a function of male attractiveness also increases the estimated probability of extinction when population sizes are small. In fact,
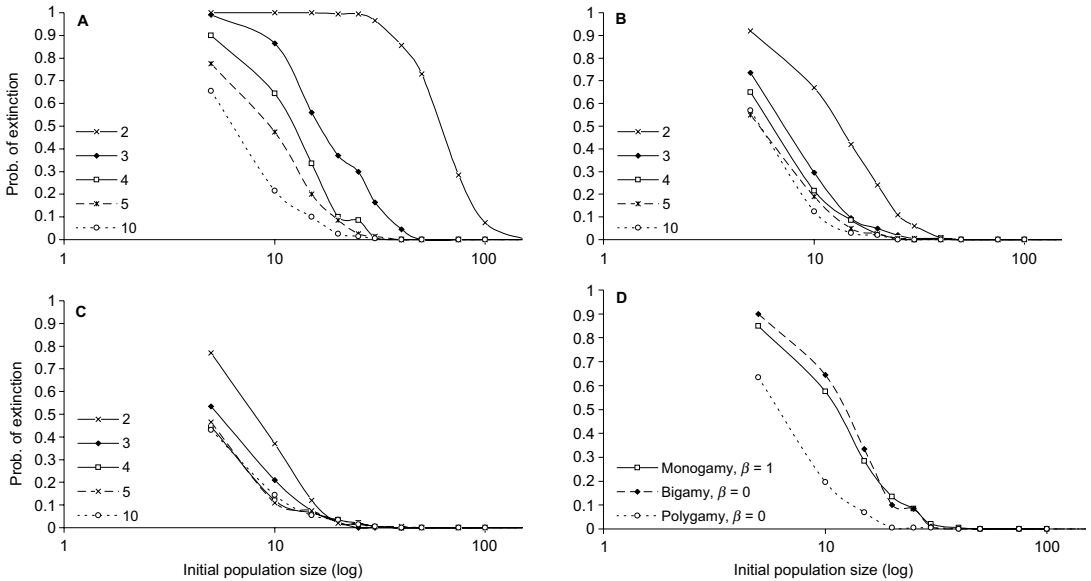
Fig. 4. Variation in extinction risk as a function of population size and number of mating bouts. The probability of accepting a less attractive partner is: — **A**: low, $\beta = 0$; — **B**: intermediate, $\beta_{min} = 0.5$; or — **C**: passive choice, $\beta_{min} = 1$. — **D**: Comparison between monogamy given passive mate choice ($\beta_{min} = 1$) and both bigamy and polygamy when less attractive males are refused.

variation in reproductive success as a function of male attractiveness amplifies the effect of both probability of acceptance and limited mating opportunities (Fig. 5).

Differential reproductive success results in an increased probability of extinction because besides reducing the mating efficiency, demographic stochasticity may also result in a scarcity of suitable partners, thus increasing the proportion of females mated with less attractive partners. As a consequence, differential reproductive success may magnify the effect of mate choice and of limited mating opportunities.

The importance of social mating system

In the absence of mate choice, monogamy is likely to result in a higher extinction risk than polygamy (Legendre *et al.* 1999, Møller & Legendre 2001). According to our results, this prediction still holds true as long as all other parameters (i.e. probability of acceptance of unattractive partners, number of mating bouts, variation in reproductive success) are identical (e.g. Fig. 3).
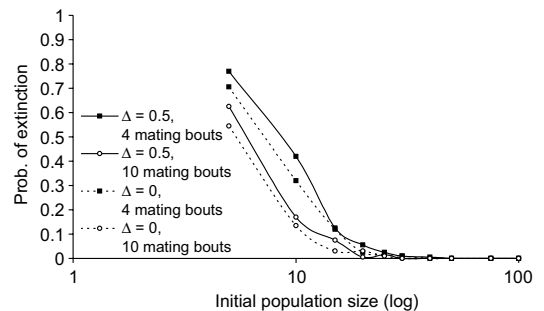

Fig. 5. Variation in extinction risk as a function of population size and probability of accepting less attractive partners when mating with less attractive partners results in half the breeding success (dashed line) or is independent of male attractiveness (full line). The mating process occurs in either 10 (■) or 4 (○) mating bouts.

However, it is unlikely that monogamous and polygamous species share the same degree of choosiness. When we compare monogamous species that accept unattractive partners and polygamous species that refuse unattractive partners, the difference between the extinction probability of monogamous and polygamous species is less important (Fig. 2D).
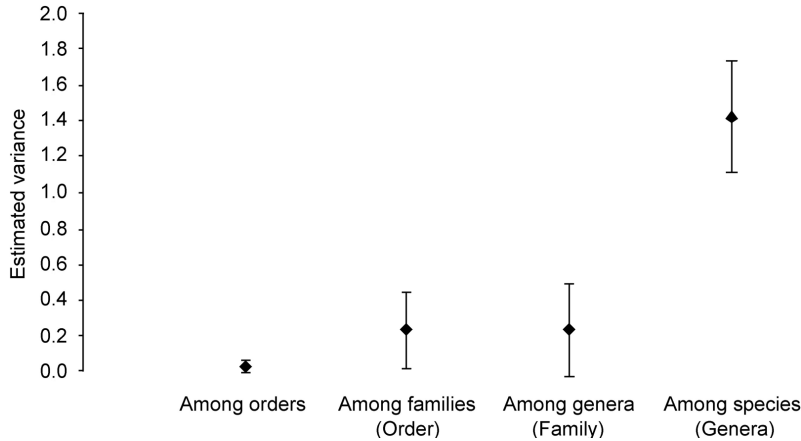
Fig. 6. Estimated variance components (± standard error) from random effects in a multivariate generalised linear mixed model (GLMM) with introduction outcome as the response variable for global land bird introductions.

Moreover, limited mating bouts are likely to surpass the importance of the social mating system. Hence, when mating bouts are limited, monogamous species that accept unattractive partners and polygamous species that refuse unattractive partners may have a similar probability of extinction (Fig. 3D). Thus, the difference between monogamous and polygamous species may no longer be noteworthy when we compare monogamous species whose mate choice is passive and polygamous species that refuse less attractive partners and have a lower encounter rate.

In summary, mate choice is likely to increase the probability of extinction when mating opportunities are limited and when mate choice is associated with variation in reproductive success. Although polygamous species are less susceptible to demographic stochasticity than monogamous species, this difference may no longer be significant or may even be reversed if we consider that monogamous and polygamous species are likely to differ in terms of mate choice strategies, as well as in terms of mate search strategies and breeding dispersion.

Breeding behaviour and avian establishment

Variation due to differences among taxa at different levels of the taxonomic hierarchy was significantly different from zero among species within genera (Fig. 6; likelihood ratio 353.6, $P < 0.001$) but not among taxonomic groups at the genus level or higher (Fig. 6). The finding that most variation in introduction success occurs among species within genera is qualitatively identical to the result of Blackburn and Duncan (2001). However, having controlled for the effects of phylogenetic independence, we found that introduction success was still significantly associated with variables that related to increasing dietary generalism, decreasing migratory tendency, sexual monochromatism, and decreased parental care (Table 1). In addition, we found a strong two-way interaction between the binary terms sexual dichromatism and social mating system.

A multivariate model confirmed that species with increasing dietary generalism and decreasing migratory tendency, and sexually monochromatic species had an increased probability of successfully establishing non-native populations. Notably, the results for increasing dietary generalism, decreasing migratory tendency, and sexual monochromatism are the same as were found for the across species model by Cassey (2002). These findings support previous studies where introduction success has also been shown to be correlated with life-history and ecological attributes such as lack of migratory tendency (Veltman *et al.* 1996), habitat generalism and behavioural flexibility (Sol & Lefebvre 2000, Sol *et al.* 2002), as well as geographical location and environmental factors (e.g. Blackburn & Duncan 2001, Duncan *et al.* 2001, Green 1997, Lockwood *et al.* 1993, Moulton *et al.* 2001) or community-level factors (e.g. Lockwood *et al.*

1993, Moulton 1985, 1993, Moulton & Pimm 1983, Moulton *et al.* 2001).

Although the univariate term for biparental care is statistically significant (Table 1), this term is not retained in the multivariate model. This is probably due to the fact that, across introduced species, biparental care is strongly correlated with sexual monochromatism ($r = 0.448$, $P < 0.001$), and weakly correlated with migratory tendency ($r = 0.107$, $P = 0.001$). Likewise, although the interactions between the binary terms sexual dichromatism and social mating system, and sexual dichromatism and biparental care are all statistically significant (Table 1), none of these terms are retained in the multivariate model. The interaction between sexual dichromatism and social mating system was significant due to the considerably lower establishment success of species that are both socially monogamous and sexually dichromatic ($t = 2.71$, $P < 0.007$). The interaction between sexual dichromatism and biparental care was significant due to the marginally greater establishment success of species that are both sexually monochromatic and have decreased parental care ($t = 1.98$, $P = 0.048$). In the multivariate model, however, neither of these interactions are able to explain any more of the variability in establishment success than is not already explained by the significant single-order terms.

Discussion

Mating behaviour, and in particular mate choice, is likely to influence the dynamics of small populations, especially when population dynamics is sensitive to variation in breeding success, as in small passerines. Overall, our estimates of extinction risk indicate that demographic stochasticity may reduce female mating rate and reproductive success, and thus increase the probability of extinction and population extinction thresholds.

According to model predictions, behavioural features such as mate choice, differential reproductive success, and social monogamy are likely to be correlated with a higher extinction risk for small populations. However, such correlation is not straightforward but depends on several factors. Hence, the extinction risk depends on the joint effect of the mating system, the probability of accepting less attractive partners, the variation in reproductive success, and the limitation of mating opportunities.

When mating bouts are unlimited, the refusal of less attractive partners entails only a minor reduction in mating efficiency, particularly for polygamous species. However, at low population size, mating bouts may be limited by the difficulty of finding a partner (Berec *et al.* 2001, McCarthy 1997, Wells 1998). When we consider

Table 1. Fixed effects estimated in univariate generalised linear mixed models (GLMM) with introduction success as the response variable for global land bird introductions. Positive parameter estimates indicate that larger values of the fixed effect are associated with a higher probability of introduction success, accounting for non-independence in the data due to taxonomic clustering of introductions as modelled by the random effects.

Fixed effects	Parameter estimate	Standard error	t	P
Continuous effects				
Log$_{10}$(body mass)	−0.120	0.283	−0.42	N.S.
Dietary generalism	0.280	0.130	2.15	0.032
Migratory tendency	−0.322	0.100	−3.24	0.012
Binary effects				
Monochromatism (Chrom)	0.678	0.261	2.60	0.018
Bi-parental care (Care)	−1.054	0.423	−2.49	0.013
Social monogamy (Monog)	−0.430	0.417	−1.03	N.S.
Binary interactions	Deviance χ^2			P
Chrom × Monog	10.79			0.013
Chrom × Care	12.37			0.006
Monog × Care	7.23			N.S.

that mating bouts are limited, we find that mate choice has a noticeably stronger effect on population extinction risk. This simple approach indicates that the interaction between mate search and mate choice is likely to be a key factor for understanding the decline in mating efficiency when population sizes are small. Hence, the magnitude of mate choice influence on the extinction probability is likely to be related with aspects such as breeding dispersion and mate search strategies.

As postulated by Møller and Legendre (2001, *see* also Møller 2003), when reproductive success depends on male attractiveness, the extinction probability of small populations increases. This is due to the fact that demographic stochasticity may result in a scarcity of suitable partners, which increases the proportion of females mated with unattractive partners. As a consequence, variation in reproductive success may augment the effect of demographic stochasticity on mating rates and reproductive success.

The comparative analysis of establishment success of introduced bird species largely supports our predictions concerning the potential effect of mate choice because sexual dichromatism, which is an indicator of sexual selection (Andersson 1994, Gontard-Danek & Møller 1999), is correlated with lower establishment success. Although this observation is not new (*see* Cassey 2002, McLain *et al*. 1995, 1999, Sol *et al*. 2002, Sorci *et al*. 1998), the previous studies had not controlled for other mating behaviour variables and were often restricted to a single introduction event or to a smaller number of species. The present analysis largely confirms the generality of previous studies because sexual dichromatism is the only mating behaviour variable that is retained even when social mating system and parental care are considered.

In particular, social monogamy was not significantly associated with establishment failure as either an univariate term or in the multivariate model, not supporting the prediction that monogamy is likely to result in a higher extinction risk than polygamy (*see* also Legendre *et al*. 1999, Møller & Legendre 2001). One possible explanation for this result is the interaction between mate choice and social mating system. If we consider that the intensity of sexual selection is significantly more intense in polygamous sexually dichromatic species than in monogamous sexually monochromatic species, then monogamy may no longer entail a significantly higher extinction risk than polygamy. This hypothesis is supported by the fact that sexual dichromatism and social polygamy are significantly associated ($\chi^2 = 7.370$, $P = 0.007$). However, only 3% of the species considered are both polygamous and monochromatic, whereas 38% of the species considered are both monogamous and monochromatic. As a consequence, we cannot analyse the effect of social mating system in the absence of active mate choice. Nevertheless, if we only consider sexually dichromatic species, social monogamous species establishment success was not significantly different from the establishment success of polygamous species. Hence, it is most likely that additional forces are operating.

Our predictions take into account only the susceptibility to demographic stochasticity but many other factors are also likely to influence extinction risk. In particular, the intensity of sexual selection may be associated with other sources of vulnerability, such as differences between sexually monochromatic and dichromatic species in stress susceptibility, parasite resistance, and predation avoidance are likely to further increase the extinction risk of dichromatic species (Møller 1997). Promislow *et al*. (1992, 1994) have indeed demonstrated that sexually selected plumage brightness in males is associated with a sex-biased mortality cost, which can be important for natural selection events during immigration and establishment in a new habitat.

An important aspect that must be considered is the fact that our modelling approach does not account for behavioural flexibility. When monogamous females accept mating with an already mated male in the absence of single males, the reduction in mating efficiency due to monogamy no longer holds true. Likewise, if females alter their acceptance strategy in the absence of attractive males, then mate choice is less likely to result in a higher extinction risk, unless there is variation in breeding success associated with male attractiveness. However, many studies in captivity show that females refuse to mate in the presence of males, even

during periods of several years (review in Møller & Legendre 2001).

Another important factor that is not taken into account in our predictions is genetic variability. It is generally accepted that mating behaviour, in particular mating systems and mate choice, can largely determine effective population size, N_e (Anthony & Blumstein 2000 and references therein). Polygamous and choosy species are likely to give rise to a large variance in male mating success, thus decreasing the population genetic variability. Hence, when genetic variability is taken into account, monogamous species may be relatively less at risk. However, it is unlikely that the reduction in genetic variability may be responsible for short-term establishment failure of polygamous species as observed for introduction attempts.

This leads to a third hypothesis related to population structure. In the present study, male and female life cycles are symmetrical, and the expected sex ratio at birth is at equilibrium. Under these assumptions, the expected adult sex ratio should equally be at equilibrium. Hence, any random variation in the population sex ratio leading to a female biased sex ratio necessarily results in a reduction in mating rate. However, many bird species experience a male biased adult sex ratio (e.g. Ewen *et al*. 2001, Willis 1974), namely due to female biased dispersal and subsequent lower female recruitment in isolated populations (Dale 2001). As a consequence, random variation in the expected sex ratio that leads to an increase in the proportion of females does not necessarily result in a female biased sex ratio, i.e. does not entail a scarcity of males and subsequent reduction of the mating rate, even when the mating system is monogamous.

Conclusions

Mating behaviour may augment the susceptibility to demographic stochasticity and, consequently, the extinction risk of small populations. Hence, mating behaviour should be taken into account in population viability analysis or when estimating minimum viable population size. However, it is difficult to make general predictions concerning the influence of specific mating behaviour

features on extinction risk because of the interaction between different features. Hence, the impact of mate choice largely depends on other aspects, such as mating opportunities (encounter rate, social mating system), and variation in reproductive success. Likewise, the influence of the social mating system also depends on mate choice so that polygamous choosy species may be as susceptible to extinction as monogamous species. Understanding how mating behaviour influences the dynamics of small population requires taking multiple features into account. In addition, to further understand the influence of mating behaviour on the persistence of small population, important questions concerning mate search, population genetics and population structure remain to be explored.

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