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# Male mate choice: why sequential choice can make its evolution difficult

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Male reproductive success is typically mate limited, which implies that males should rarely be choosy. On the other hand, females often vary greatly in their fecundity or other determinants of male reproductive success. There are two coexisting threads in the current literature on male mate choice: a number of studies emphasize that male mate choice has been underappreciated in the past, while another set reminds us that it nevertheless evolves less easily than female choice. Here we show that when mate choice is sequential rather than simultaneous (which is often the case for the mate-limited sex), male mate choice may fail to evolve even if there is large variation among fitness prospects offered by various females, and when mating is very costly. Our model is inspired by the mating system of the sexually cannibalistic praying mantid *Pseudomantis albofimbriata*. Males of this species do not stop approaching females that have turned to face them even though this female behaviour greatly increases the risk of being cannibalized. We show that low mate availability can override the effect of all other factors that select for male mate choice: rejecting a current mating opportunity in the hope of better future opportunities is then not easily selected for. We conclude that studies of mate choice should examine why individuals refuse to take advantage of every opportunity, instead of merely focusing on the fact that some opportunities are better than others. Our results also call for more rigorous empirical tests of mate choice.


In the majority of species, the reproductive success of males is traditionally thought to be limited by the availability of mating opportunities, which creates little scope for male mate choice: why reject opportunities that are rare and limiting? However, the study of male mate choice has experienced a certain revival in recent years, and the reminders that male choice is an underappreciated evolutionary force are by now so common (Amundsen & Forsgren 2001; Bonduriansky 2001; Saether et al. 2001; Wedell et al. 2002; Gowaty et al. 2003; Preston et al. 2005; Bateman & Fleming 2006; Byrne & Rice 2006; Chenoweth et al. 2007; Stoltz et al. 2007; Bel-Venner et al. 2008) that the topic hardly qualifies as underappreciated any longer. Intriguingly, these reminders coexist with a thread in the literature that emphasizes that male mate choice, nevertheless, does not evolve as easily as female choice (Johnstone et al. 1996; Kokko & Johnstone 2002; Schmeller et al. 2005; Parker 2006; Reading & Backwell 2007; Servedio 2007). Depending on the study, the emphasis may be on the difficulties of mate acquisition for males or on the fact that females often vary greatly in fecundity (indeed often much more than males vary in the fitness prospects they offer as mates). The latter fact supports the evolution of male mate choice, the former selects against it.

As such, conditions important for the evolution of male mate choice are well understood (e.g. Johnstone et al. 1996; Kokko & Monaghan 2001). Males typically have a steeper Bateman gradient (regression of reproductive success against mating success) than females (Arnold & Duvall 1994; Jennions & Kokko, in press), which means that being choosy, that is, rejecting a mating opportunity, tends to reduce the reproductive success of a male more than it would for a female. Still, high parental investment, limited ability to produce sperm, high variation in female quality and low effort required to find new mates can select for choice (e.g. Bateman & Fleming 2006). However, our aim in this paper is to provide a reminder that mating costs and large variation in female quality do not automatically mean that males will become choosy. Many empirical mate choice studies are conducted as simultaneous choice tests where it is relatively obvious that a male is better off if

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he mates with, say, the larger and thus more fecund female. In nature, however, mates are often encountered sequentially, and any argument for adaptive choice must explain why it is beneficial to refuse to take advantage of some mating opportunities even if an alternative (and better) option is not immediately available. Why a mate-limited sex should benefit from being choosy in sequential mate encounters will thus always require careful analysis (Reading & Backwell 2007; Candolin & Salesto 2009; Jennions & Kokko, in press).

Here our aim is to perform such an analysis for a system with frequent precopulatory sexual cannibalism that causes extreme differences in the value of different mating attempts for males (thus making male mate choice intuitively plausible, Thornhill & Alcock 1983; Maxwell 1999; Huber 2005). This exercise serves to re-emphasize the importance of analysing mate availability, not merely available variation in the benefits offered by potential mates, and also places mate choice studies in the context of population-wide sex ratios (Fromhage et al. 2005, 2008; Kokko & Jennions 2008). Our model was inspired by the mating system of the praying mantid *Pseudomantis albofimbriata*. In this species females vary in the fitness prospects they offer to males in at least three ways: they may be mature or not; they may differ in body condition; and, most importantly, they may notice the approaching male or not. The first two factors (maturity and body condition) are to some extent correlated, as is body condition and the risk of cannibalism (poor-condition/hungry females are more likely to cannibalize males; Barry et al. 2008).

To avoid delving into mantid-specific questions we focused on the last condition: cannibalism becomes considerably more likely if females notice the male and turn to face him (Barry et al. 2009; Barry et al., in press). Male mantids proceed to attempt mating if the female has turned to face them. Even though they can clearly perceive the turning, males simply freeze and then continue their approach after a while (Barry et al. 2009). Similarly, after visually locating a potential mate, they rarely reject females in poor nutritional condition (Barry et al. 2008; Barry et al., in press).

These behaviours raise the question of why male mate choice does not evolve despite obvious differences in the profitability of approaching different females. Compared with mere differences in expected fecundity, addressed in most male mate choice models, the varying chance that a mating attempt ends in death (often without any current fecundity benefits) indicates very large variation in the fitness prospects offered by different females. An unusual feature of the system is that this variation is almost synonymous with the costs of mating: although fecundity variation exists, and males can sometimes also gain paternity in matings that lead to their death (see below), the risk of mortality is so high that the risk of death clearly drives most of the variation in the profitability of each mating. Males should be able to detect clear differences in the risk of cannibalism because of the readily observable visual cue of the female turning to face them or not. Here we show why male mate choice often fails to evolve even though matings can be costly to males and there is substantial variation in the expected reproductive success from a given mating, conditions that contrast greatly with any preconception that a strong enough impact of either factor might be sufficient to facilitate choice even when acting on its own.

## THE MODEL

Although our model was inspired by *P. albofimbriata*, we aim here for some generality and thus ignore the large number of combinations of traits (e.g. female in poor body condition at borderline maturity which has turned to face the male; reject or not?) and instead focus on one major component of fitness prospects: is the male cannibalized or not? Naïvely, one might imagine that since the cue is easily detectable by the male (is the female 'front facing' or 'away facing'?) and correlates extremely well with the danger posed by the female, males should readily evolve choice.

We assume that cannibalism occurs with probability $C_0$ by away-facing females (potentially unaware of the approaching male), and $C_1$ by front-facing females. At its most extreme, the model includes cases where away-facing females are never able to cannibalize males ($C_0 = 0$) and front-facing females always cannibalize them ($C_1 = 1$), but the model will consider all possibilities where $0 \leq C_0 < C_1 \leq 1$. As explained above, we keep the model simple by assuming that males cannot detect any other cue of expected fitness offered by a female than whether she is front facing or away facing. This simplification is justified because we need to understand the absence of male sensitivity to this large-effect cue before proceeding to subtler cues such as a correlation between a female's body condition and the number of eggs.

Since multiple mating is not the focus of our study we also assume that females only mate once. This simplifying assumption is very probably violated in many cases, although in *P. albofimbriata* it is a reasonable first approximation because mated females become chemically unattractive to males (although males will still mate with them if encountered visually; Barry et al., in press). Finally, we assume that a noncannibalized male returns to the pool of searching males unaltered. This is true for *P. albofimbriata*, although it is unknown how many times males can mate before becoming sperm depleted.

It has recently been emphasized that when life histories evolve to become sex specific this can change adult sex ratios, impact mate availability, and thus play a large role in mating system evolution (Fromhage et al. 2005, 2008; Kokko & Jennions 2008; Nakahashi 2008; Beltran et al. 2009; Jennions & Kokko, in press). Cannibalism is an obvious route to female-biased adult sex ratios (see Hurd et al. 1994; Maxwell 1998 for mantid examples) and thus our model of male mate choice should take into account the following feedback: the more cautiously males behave, the fewer of them die in the mandibles of females, and the more males will be alive competing with each other for females (for the importance of such feedbacks in general see e.g. Fromhage et al. 2008; Kokko & Jennions 2008). We assume that reproduction leads to a continuous input $m_0$ and $f_0$ of newly recruited (mature) virgin males and females (respectively) into the population. This assumption requires that sex ratio biases do not become so large that females become sperm limited or, alternatively, that density dependence operates such that if some females fail to mate, the offspring of the remaining ones survive better. Note that either scenario justifies our assumption of a constant input of newly matured individuals. Mate-searching males have a mortality rate $\mu_m$ which excludes death by cannibalism (which we deal with separately, below). Females waiting to be mated have a mortality rate $\mu_f$.

We are interested in deriving the fitness of males that either reject or accept front-facing females (the latter type of male accepts all females). Consider that $\alpha mf$ is the number of all matings per unit time in the population. Here $m$ is the number of mate-searching mature males, and $f$ is the number of females available for matings. Thus the per-male encounter rate of females is $\alpha mf/m = \alpha f$, where $\alpha$ is a mate location efficiency factor that scales how easily mates find each other and corresponds to the parameter $M$ in, for example, Kokko & Monaghan (2001); also see Hutchinson & Waser (2007) for these types of mate encounter models in general. At any point in time, a male may mate (this happens at a rate $\alpha f$ per male) or die (rate $\mu_m$). It follows that a searching male encounters a female before dying with probability $\alpha f/(\alpha f + \mu_m)$, and dies before

encountering another female with probability $\mu_m/(\alpha f + \mu_m)$ (see e.g. Kokko & Monaghan 2001). Because matings are assumed to be short compared with the life span of individuals, we do not include an explicit term for handling time in our model.

We next need to consider what happens in a mate encounter. We denote by $P$ the probability that a female is front facing at the end of a male approach. This includes cases where she becomes aware of the male and turns to face him, or she faces him from the beginning of his approach. We assume that the male can always perceive whether the female faces him or not. $R$ denotes the probability that a male stops approaching (rejects) the female given that the female is in the front-facing state. In our model it is always optimal to mate with females that are in the away-facing state, as these are the safest options ever encountered. We are interested in male behaviour if the female is front facing, that is, the value of $R$ favoured by selection. If $R = 0$, males show no mate choice and never stop their approach, even for low-profit (risky) females. If $R = 1$, males always reject these low-profit front-facing females. Our model also allows for intermediate values of $R$ should these be optimal.

A mating approach ends in male death with probability $p_1 = (1 - P)C_0 + P(1 - R)C_1$. This expression combines two options: (1) the female is in the away-facing state (probability $1 - P$) and cannibalizes him nevertheless (probability $C_0$), and (2) a female is front facing (probability $P$), the male does not reject her (probability $1 - R$), and is cannibalized (probability $C_1$). Optionally, a mating approach that ends in death yields some fitness for the male ($\beta$; see below for details) because, in *P. albofimbriata*, sperm transfer can occur after the onset of cannibalism. Some males are fully cannibalized before they can mate, while for others being consumed during mating actually increases their immediate reproductive output by up to 40% compared with males that mate and are not cannibalized (Barry et al. 2008).

With probability $p_2 = (1 - P)(1 - C_0) + P(1 - R)(1 - C_1)$, the approach ends with a successful copulation without cannibalism. With probability $p_3 = PR$ the male stops his approach because the female is front facing; in this case nothing happens, that is, the male continues searching elsewhere. Note that $p_1 + p_2 + p_3 = 1$.

Before proceeding with male fitness, we should derive the quantity $m/f$ to describe how many mate-searching males there will be per available female. These numbers are influenced by male behaviour because the male is removed from the mating pool if he dies (probability $p_1$), while the female, which is assumed to mate only once, is removed in the case without cannibalism (probability $p_2$) and also a proportion $\beta$ of females are removed in the cannibalism case (successful sperm transfer despite cannibalism). The dynamics of searching males and fertilizable females are thus described by

$$\frac{dm}{dt} = m_0 - \alpha m f p_1 - \mu_m m \tag{1a}$$

$$\frac{df}{dt} = f_0 - \alpha m f(\beta p_1 + p_2) - \mu_f f \tag{1b}$$

The three terms on the right-hand sides of these equations correspond, respectively, to recruitment into the population, the removal of individuals from the mating pool as a consequence of mating (cannibalism for males, getting fertilized for females), and death through other means (while mate searching or waiting, for males and females, respectively). Equations (1a, b) can be solved for equilibria $m$ and $f$ by setting $dm/dt = 0$ and $df/dt = 0$. There is a closed form solution, although it is unwieldy:

$$m = \frac{m_0}{2\mu_m} - \frac{\mu_f}{2\alpha(\beta p_1 + p2)} - \frac{f_0 p_1}{2\mu_m(\beta p_1 + p_2)} + \frac{\sqrt{4\alpha f_0 p_1 \mu_m \mu_f + \left(\alpha(m_0(\beta p_1 + p_2) - f_0 p_1) + \mu_m \mu_f\right)^2}}{2(\mu_m(\beta p_1 + p_2))} \tag{2a}$$

$$f = \frac{f_0 - m_0(b + p_2/p_1)}{2\mu_f} - \frac{\mu_m}{2\alpha p_1} + \frac{\sqrt{4\alpha f_0 p_1 \mu_m \mu_f + \left(\alpha(m_0(\beta p_1 + p_2) - f_0 p_1) + \mu_m \mu_f\right)^2}}{2\alpha(\beta p_1 + p_2)} \tag{2b}$$

Male fitness, which we denote by $W$, can be solved recursively by noting that an encounter that leads to option $p_1$ (cannibalism) ends a male's life but may yield some fitness gains because some males manage to sire offspring during a cannibalistic copulation. We denote these gains by $\beta$ ($0 \le \beta \le 1$), expressed as a fraction of the expected success of a noncannibalized male. Option $p_2$ (mating without cannibalism) brings about one unit of fitness gain; one unit thus equals the expected siring success from a copulation uninterrupted by cannibalism, averaged over all female fecundities. Additionally, after $p_2$ the male can carry on searching, with an expected future gain that again equals $W$ (note that we are using a recursive modelling technique where the expected future fitness gain of a searching male is the same whether it is his first search bout or whether he already gained fitness in the past, see e.g. Houston & McNamara 1999; Kokko et al. 2003; Schmeller et al. 2005). After $p_3$ (male rejects female) the male, similarly, can carry on searching, but $p_3$ obviously does not give the male any current fitness gains. As a whole, the expression for male fitness becomes

$$W = \frac{\alpha f}{\alpha f + \mu_m}[\beta p_1 + (1 + W)p_2 + W p_3] \tag{3}$$

Solving for $W$, we get

$$W = \frac{\alpha f(\beta p_1 + p_2)}{\mu_m + \alpha f p_1} = \frac{\alpha f(PR - 1 + C_0(1 - P)(1 - \beta) + C_1 P(1 - R)(1 - \beta))}{\alpha f(C_0(1 - P) + C_1(1 - R)P) - \mu_m} \tag{4}$$

The selection gradient for rejecting females (increasing $R$) equals

$$\partial W/\partial R = \frac{\alpha f P(\alpha f(1 - P)(C_1 - C_0) - \mu_m(1 - C_1(1 - \beta)))}{(\mu_m + \alpha f(C_0(1 - P) + (1 - R)C_1 P))^2} \tag{5}$$

The population-level (average) rejection behaviour of males, $R$, will determine the number of females, $f$, that appears in this equation. Thus when equation (5) is evaluated with the value $f$ given in equation (2b), we obtain $\partial W/\partial R > 0$ when selection favours increased rejection of risky females, $\partial W/\partial R < 0$ when selection favours less rejection, and $\partial W/\partial R = 0$ when there is no selection (an equilibrium).

Now $\partial W/\partial R$ is positive (there is selection towards stronger rejection of low-profit, or risky, females) if and only if

$$\frac{\alpha f}{\mu_m}(1 - P)(C_1 - C_0) > 1 - C_1(1 - \beta). \tag{6}$$

This is our central result, and it leads to straightforward predictions.

## RESULTS

### *Variation Among Females Matters*

Starting from the rightmost term in inequality (6), low-profit (or risky) females are most likely to be rejected if $1 - C_1(1 - \beta)$ is a small number (close to 0). Note that $1 - C_1(1 - \beta)$ equals the expected reproductive success when attempting to mate with a front-facing female, compared with 1 which is the gain from a successful copulation without cannibalism. If $1 - C_1(1 - \beta)$ is close to 1, in other words if $C_1(1 - \beta)$ is close to 0, then fitness can be gained with risky females too: either because the risk of cannibalism as a whole is low (low $C_1$ means that no female cannibalizes males very often), or because significant paternity occurs in cannibalistic matings too (high $\beta$). In *P. albofimbriata*, sexual cannibalism occurs in about 40% of interactions (Barry et al. 2009) and half of those result in significant paternity for the consumed male (Barry et al. 2008).

The above result, in isolation, makes sense: male mate choice pays only when females vary sufficiently in what they offer. The next term to the left, $C_1 - C_0$, in inequality (6) re-emphasizes this: the greater this difference in cannibalism risk posed by females facing the male or not, the more easily inequality (6) is fulfilled and male mate choice evolves. As a special case, if cannibalism is removed from this model ($C_0 = C_1 = 0$), male mate choice cannot evolve since inequality (6) becomes impossible to satisfy: $0 > \mu_m$. In this case there is no variation among females in the costs and benefits they offer, and males evolve to take advantage of any opportunity.

### *Variation Among Females is not the Only Thing that Matters*

There are also other terms that influence the result. Inequality (6) is easier to satisfy if $P$ is small (a small proportion of females turn to face males). If, for example, females are always aware of all male approaches ($P = 1$), then inequality (6) can never be satisfied and males should not reject a front-facing female as there will never be a safer option available. In this sense, the requirement $P < 1$ shows the importance of differences between females for male mate choice to evolve (Fig. 1). In mating trials involving *P. albofimbriata*, 13 of 21 females turned around after rear approach and 12 males approached from the front (Barry et al. 2009). Thus while $P$ is high (as a rough estimate $P = (13 + 12)/(21 + 12) = 0.76$), this species does not exhibit $P = 1$, and thus the 'no safe option available' argument alone does not explain lack of male mate choice in this species.

While $P < 1$ is a prerequisite for male choice to evolve because it indicates that females must vary, the term $1 - P$ in inequality (6) simultaneously shows that the best prospects for male mate choice do not coincide with the peak of variation in fitness prospects offered by females. Females vary most when $P = 1/2$, yet males are most likely to reject risky females when these form a small proportion of the population ($P << 1/2$). This is reflected in Fig. 1, where the 'choice' areas are always widest at low values of $P$. To put it loosely, the reason why small $P$ favours rejection is that it is not worth killing yourself in a rare dangerous mating if almost all other mating opportunities will be safer. Note, however, that while selection may in principle favour rejecting rare, risky females, their proportion must be large enough for sufficiently strong selection to elicit an evolutionary response (which is a different question from whether selection is positive in principle). This is reflected in equation 5 where selection for choice is positive for a large range of parameter values, but simultaneously very weak if $P$ is close to zero.

Finally, to proceed to the leftmost term in inequality (6), rejection evolves most easily if $\alpha f/\mu_m$ is high. The quantity $\alpha f/\mu_m$ has a biological interpretation: it is the expected number of receptive females encountered by a male in his lifetime if a population of males spend all their time mate searching but males do not do anything risky in mate encounters. The value of $\alpha f/\mu_m$ increases with male mobility and other traits that impact his mate location efficiency ($\alpha$), but it also depends on population dynamics: terms included are mortality of males, $\mu_m$, and that of females via the solution of $f$ in equation (2b), as well as how males and females are removed from the mating pool after mating, equation (2). Prospects for male mate choice become enhanced if males locate alternative mates easily, and this can happen for a number of reasons: high mobility that increases $\alpha$, high number of females $f$ and a long expected remaining lifetime of the searching male as indicated by low $\mu_m$ all favour the evolution of male mate choice.

To sum up, inequality (6) leads to many 'all else being equal' type predictions: for example, more variation between females enhances prospects for male mate choice (low $C_0$ combined with a high $C_1$, Fig. 1a, b). Still, a full prediction cannot be made by considering each factor in isolation, since it is their joint net effect that matters. This is illustrated in Fig. 1, where male mate choice is only expected to evolve in the shaded areas. It may appear surprising, for example, that low male mortality and low female mortality have similar effects (Fig. 1c, d) even though reduced female mortality improves mate availability for males while reduced male mortality has the opposite effect of stronger competition among males. Still, reduced male mortality can select for more male choice simply because a longer lived male has more time left to look for new females if he rejects the current one. Finding new unfertilized females will simultaneously be harder because there are other males living long enough to fertilize them, but while this might be argued to cancel the benefit, it does not fully do so because it is only the dangerous search phase that has become less risky when $\mu_m$ is low while risks of mating are unchanged, and these also kill off competitor males.

## DISCUSSION

Our study is a reminder that male mate choice does not self-evidently evolve even when females vary in their quality and matings are extremely costly. Quality variation, in fecundity or for example in the form of varying risk of sexual cannibalism, is an obvious prerequisite for its evolution (Owens & Thompson 1994; Pruitt & Riechert 2009). Importantly, however, it is a necessary but not sufficient condition for male mate choice to evolve. Recent theoretical (Kokko & Ots 2006) as well as empirical (e.g. Schäfer & Uhl 2005; Shackleton et al. 2005; Werner & Lotem 2006; Ivy & Sakaluk 2007; Uetz & Norton 2007) findings emphasize that mate choice follows different rules depending on whether potential mates are encountered simultaneously or sequentially. In a simultaneous choice scenario, and assuming they can only mate with one of the potential mates present, individuals are essentially forced to choose and thus small differences in the profitability of each mating opportunity can form a sufficient reason for selection to favour choice. The situation is different for sequential choice: choosing must involve rejecting some reproductive opportunities before it is known whether a new opportunity will ever arise. This uncertainty plays a large role only under conditions of low mate availability. Low mate availability for a given sex may be a permanent feature of the mating system (i.e. an outcome of sex-specific mortality patterns and time out's caused by sex-specific parental investment, e.g. Kokko & Jennions 2008), or it may occur only during part of a season: while we assumed female and male densities ($f$ and $m$) are at an equilibrium, in reality they may experience seasonal fluctuations (e.g. Forsgren et al. 2004; Kasumovic et al. 2008). Either way, low mate availability increases selection for making the most of any current mating attempt. This can take the

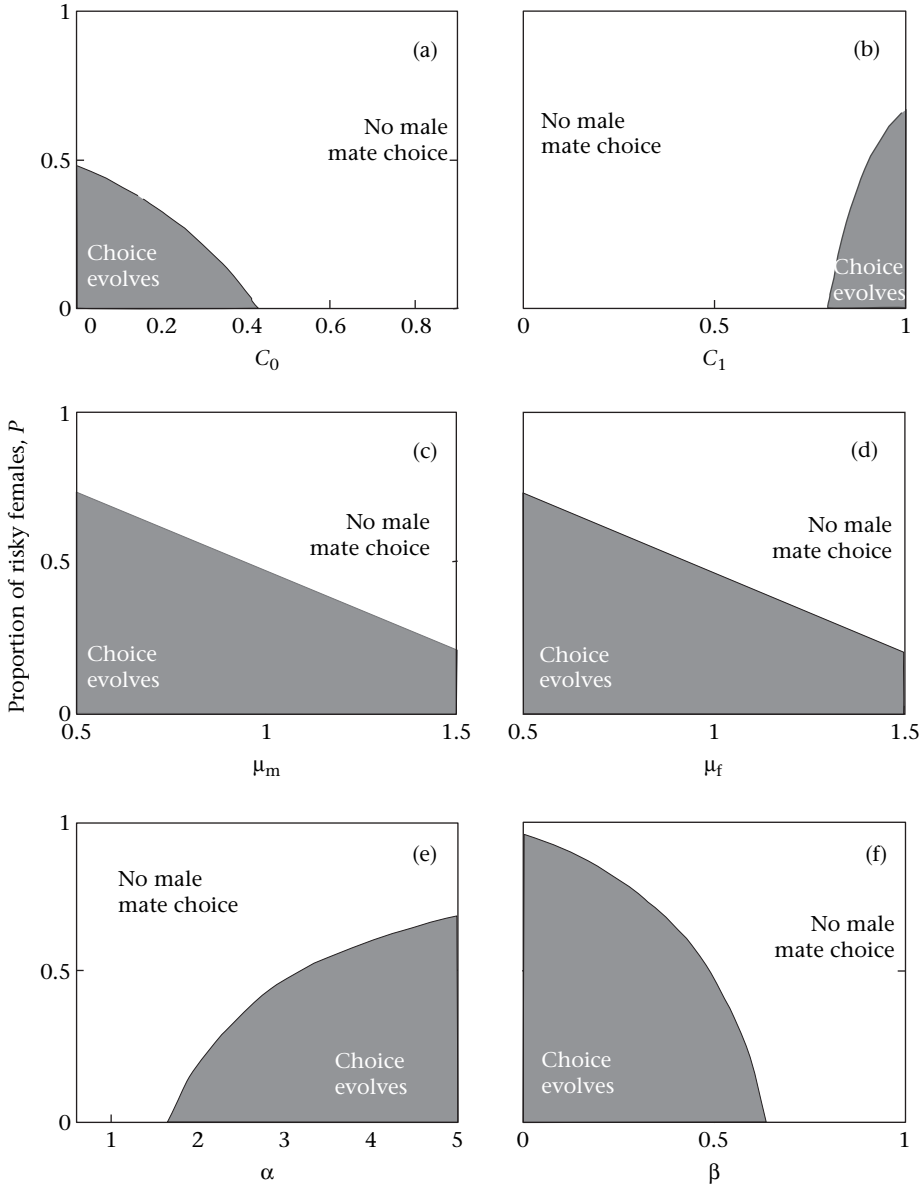


**Figure 1.** Parameter regions where male mate choice evolves (shaded) and does not evolve (white). Parameter values are $C_0 = 0.01$, $C_1 = 0.9$, $\mu_m = \mu_f = 1$, $\alpha = 3$ and $\beta = 0.5$ where not explicitly varied along the *X* axis. (a–b) Choice evolves only when away-facing females cannibalize rarely (low $C_0$) and front-facing females cannibalize frequently (high $C_1$), i.e. when fitness prospects offered by females vary greatly among females. However, this large variation is not sufficient for mate choice to evolve. In (c–f) $C_0 = 0.01$ and $C_1 = 0.9$, yet it is easy to find no-choice areas by changing other parameter values, e.g. if most females are front facing, (high *P* in c–f), if male and/or female mortality is high (c–d), if males do not find females efficiently (e), or if a cannibalistic mating yields significant fitness benefits to the cannibalized male (f). Note that in a continuous-time model mortalities are expressed as relative risks per time unit and can thus take any positive value, with expected life span = 1/mortality.

form of high mating effort (e.g. male-driven monogamy, Segoli et al. 2006; Fromhage et al. 2008) as well as not rejecting low-profit opportunities (Shelly & Bailey 1992; Kokko & Monaghan 2001; Kasumovic et al. 2007; Reading & Backwell 2007; Jennions & Kokko, in press). Our study shows that low mate availability can override all other conditions that favour choice (variation in female profitability, high mating costs) and this can extend to males accepting very dangerous encounters.

Although not every parameter of the model can be precisely measured in the wild, our results give a reasonably robust explanation for why males of the mantid *P. albofimbriata* do not reject females even if some mating opportunities are predictably and significantly more dangerous than others. The task is to evaluate whether *P. albofimbriata* falls into the white or the shaded area in Fig. 1. This figure has a baseline set of parameters with $C_0 = 0.01$ and $C_1 = 0.9$, indicating an extremely large difference in risk posed by away-facing and front-facing females. Either an increase in $C_0$ or a decrease in $C_1$ will destroy prospects for male mate choice (Fig. 1a, b), and the latter appears true for *P. albofimbriata* since the risk of being cannibalized by front-facing females has been estimated as 44% (Barry et al. 2009). This ($C_1 = 0.44$) clearly predicts no evolution of male choice in Fig. 1b. Additionally, in this species the value for β (offspring production by a male that is cannibalized, relative to matings not involving cannibalism) is very likely to be higher than the baseline value 0.5 used in Fig. 1. A shift towards higher β systematically selects for lack of male choice (Fig. 1f).

Of the remaining parameters, mate encounter rates are obviously hard to measure precisely. Still, data from large field enclosures indicate that male mortality is relatively high (20% and 25% disappearance of males over 3 days in 2008 and 2009, respectively),

and in the field only 20% of males were recaptured after 3 days (Barry, in press). This mortality rate is likely to be high enough to interfere with mate finding because the time to locate a female averaged 13 and 25 h in 2008 and 2009, respectively, in enclosures that mimic natural densities (these are minimum estimates as they were measured for males that did locate a female, and data from outside enclosures suggest even longer times; Barry, in press). Finally, the proportion *P* of front-facing females is fairly high for this species: 25 of 33 mating encounters in a previous study involved front-facing females (Barry et al. 2009), and this again selects against male choice (Fig. 1). To sum up, these parameters all imply that a male that is 'weighing' a current risky mating opportunity against his future prospects cannot rely on finding safer options if he rejects the current one.

We are not alone in emphasizing that male mate choice does not self-evidently evolve when females vary in quality (see e.g. Pelabon et al. 2003; Servedio 2007). Our study differs, however, from most other current studies of male mate choice in which males have a budget for courtship effort, sperm or time, and they can allocate their budget preferentially to high-quality females or spend it more evenly on a broader set of females (Itzkowitz & Haley 1999; Engqvist & Sauer 2001, 2002; Reinhold et al. 2002; Preston et al. 2003; Dukas et al. 2006; Servedio & Lande 2006; Servedio 2007; Härdling et al. 2008; Candolin & Salesto 2009; Wong & Svensson 2009). In such studies male choice is a priori selected against because it places males in direct, intensified competition with each other for the attention of the heavily targeted females (Servedio 2007). This selects against male choice, but the same principle (that it is beneficial to avoid competition) can have the opposite effect of favouring choice if males 'specialize' in targeting different sets of females depending on their own competitiveness or other traits (Fawcett & Johnstone 2003; Härdling & Kokko 2005; Bel-Venner et al. 2008; Härdling et al. 2008; Rowell & Servedio 2009). In this case male preferences do not have to exist despite heightened competition; instead they are driven by avoidance of competitive pressure from other males, and this makes maintaining preferences much easier (although simultaneously this option requires plasticity to enable specialization).

Compared with the above results, our case of sexual cannibalism is an unusually striking example of a failure of mate choice to evolve because it involves no direct interaction between competing males, and because the fitness prospects offered by different females vary greatly. A male has to choose between likely death (with some current chance of siring success) and searching for safer options. In this case, there is also no set of 'target' females towards which competition could intensify, because the same females can present front-facing (dangerous) as well as away-facing (safe) mating opportunities for any male. One might also predict that male mate choice is particularly likely because the females that offer least benefit are also the ones with which matings are most costly. Even under these conditions, limited mating opportunities can mean that the prospects of future success may be meagre enough for males that they should take full advantage of every encounter. This highlights that, in general, it is important to remember that mate choice is not satisfactorily analysed merely by focusing on the fact that some opportunities are better than others; more fundamentally it also always involves the question 'why refuse to take advantage of every opportunity?' (Jennions & Kokko, in press). This will force us to consider more rigorously whether choice should evolve at all. The same requirement of rigour can be extended to empirical tests of mate choice of either sex: if individuals of a given sex normally encounter potential mates sequentially rather than simultaneously, then tests of mate choice will mislead unless they use appropriate methodology (e.g. no-choice tests, Shackleton et al. 2005; Werner & Lotem 2006; Ivy & Sakaluk 2007; Barry et al. 2010).

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