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.

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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 pop-ulation-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 nutri-tional 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 varia-tion 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 profit-ability of each mating. Males should be able to detect clear differ-ences 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 canni-balize 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 μ_m which excludes death by canni-balism (which we deal with separately, below). Females waiting to be mated have a mortality rate μ_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 αmf 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 α 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 αf per male) or die (rate μ_m). It follows that a searching male encounters a female before dying with probability $\alpha f/(\alpha f + \mu_m)$, and dies before