Evolution of female choosiness and mating frequency: effects of mating cost, density and sex ratio

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The evolution of female mating preferences is mainly driven by two types of nonexclusive benefits: the effect of mate quality on offspring viability and the Fisherian advantage of ornamented sons (Fisher 1930; Andersson 1986). As choosy females gain greater benefits, female choosiness and the related male traits coevolve. However, this process is constrained by the cost of choice (Lande 1981; Gavrilets et al. 2001) and by the cost of condition-dependent sexually selected traits (Andersson 1982, 1986; Gavrilets et al. 2001). Female mate choice is strongly influenced by the variance in the costs of breeding (Kokko & Monaghan 2001) and in mate quality, because choosiness is expected to increase with differences between males (Johnstone et al. 1996). As an additional constraint, highly choosy females run the risk of remaining unmated, since there may be no males that satisfy their preferences (De Jong & Sabelis 1991). Choosiness should thus evolve towards a value that counterbalances the benefits of obtaining high-quality males, the costs of mating and the risk of remaining unmated. This, however, should not prevent females having preferences, as long as the variation in male traits is maintained (Cameron et al. 2003; Kokko et al. 2006).

The number of mates is another key element of female mating behaviour. This question has often been considered at the population level, to investigate the reasons why a mating system should evolve towards a single strategy, for instance monandry or polyandry. Although useful, such a view can be simplistic as females may vary in the number of mates they have within populations. In particular, monandrous and polyandrous females often coexist, even in promiscuous mating systems (Laloi et al. 2004; Chapple & Keogh 2005; DiBattista et al. 2008). Multiple mating can be costly simply because it multiplies the cost of one mating by the number of mates (Daly 1978; While et al. 2009). However, it may also provide direct and/or indirect benefits (Newcomer et al. 1999; Jennions & Petrie 2000; Simmons 2005).

Choice for mate quality and number of mates are key components of female mating strategies. We investigated how selection on female choosiness also influences number of matings in various ecological conditions. In our individual-based model, females choose their first mate according to an evolving acceptance threshold and then mate with males of increasing quality (trade-up choice). We simulated evolution of this threshold under various conditions of density, sex ratio and mating cost. Thresholds rapidly evolve towards a small set of values that depend on the tested parameters. Consistent with intuitive predictions, choosier females are selected when either number of encounters with males or mating cost is high. Selection results in most females sharing the same threshold. Variation in female mating patterns remains because some variation in thresholds is maintained, at least by mutations, and because of random events affecting number of matings. Our model indicates that mating cost strongly affects evolution of female choosiness and mating frequency. Moreover, it influences the relative importance of other factors: when mating cost is low, selection on acceptance thresholds is weak and relatively more females use thresholds that differ from the norm. In that context, mate quality is therefore the most important factor affecting female reproductive success. When mating cost is high, females evolve thresholds such that both the cost of multiple mating and the risk of remaining unmated become as important as mate quality. High mating cost, by selecting for high choosiness, also leads to females mating with fewer males. 

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balance is complex: short-term benefits, for example increased fecundity, may be associated with delayed costs, for example reduced survival (Arnnqvist & Nilsson 2000). The analysis is further complicated by many intergenerational effects through the influence of female mating strategies on offspring quality and behaviour (e.g. Hosken et al. 2003; Klemme et al. 2008; Laloi et al. 2009; Kekäläinen et al. 2010). Recent studies have emphasized that individual variation in the number of mates may be maintained, in particular, because the costs and benefits of a given strategy differ between individuals. For instance, even when polyandry is on average beneficial, the benefits may vary according to female—male combinations (Kekäläinen et al. 2010) or female condition (Richard et al. 2005; Eizaguirre et al. 2007).

Both components of female mating strategies, that is, the choice for mate quality and the number of mates, can be linked. High selectivity in mate choice should increase the risk of remaining unmated, while low selectivity should increase the probability that a female mates multiply since a large number of males will satisfy the preference criteria. In this study, we addressed specifically the question of the evolution of female choosiness and mating frequency when these two components are interrelated. For this purpose, we modelled the evolution of choosiness in a promiscuous context and examined the consequent changes in mating patterns. We chose to investigate the variation in female mating patterns in a system with no predetermined mating strategies, assuming that the variation in the number of mates is a by-product of female choice. In our model, females choose their first mate according to a given threshold and then copulate only with males of increasing quality (trade-up choice: Halliday 1983). Such a pattern of choice has been observed in a wide range of taxa: fish (Bakker & Milinski 1991; Pitcher et al. 2003), amphibians (Gabor & Halliday 1997), birds (Kempenaers et al. 1992) and insects (Bateman et al. 2001). We first verified whether these rules generate the coexistence of monandrous and polyandrous females. We then focused on the stability of this pattern and on the evolution of the acceptance threshold under various ecological conditions: (1) population density and sex ratio, since these parameters affect the mate encounter rate and have been suggested to correlate positively with the degree of polyandry (Rowe et al. 1994; Rowe & Arnnqvist 2002; Uller & Olsson 2008), and (2) mating costs (Gavrilets et al. 2001; Uller & Olsson 2008). Finally, we investigated how the resulting female choosiness influences both the quality and the number of mates.

**MODEL DESCRIPTION**

Our individual-based model is spatially explicit. The surface is a two-dimensional grid of 50 × 50 cells and is a torus (there are no margins). Each cell is connected to its eight neighbouring cells. At each time step, females and males can move a fixed distance of one cell. Sequentially, each individual chooses a random direction and moves to this new cell, if possible. The individual does not move towards cells in which there is an individual of the same sex. When two individuals of opposite sexes meet on a cell they can copulate, according to the female's decision. If two individuals are already mating, they do not move until it has ended. When unmated, a female accepts a male if his quality is superior to her threshold of acceptance. When already mated, she mates only with males of higher quality than the previous one. Thus females will mate with males of increasing quality (trade-up choice). There is no direct cost for female preference, but she can remain unmated, as the search for mates is time consuming. Mating is also costly in time: each mating lasts 10 time steps and is followed by a refractive period (eight time steps) during which both the male and the female refuse to copulate (these parameters were chosen after preliminary tests to obtain a realistic number of matings from a small-vertebrate perspective). Moreover, multiple mating is potentially harmful for the females (direct mating cost, K). The reproductive success of each female i is determined by its fitness $W_i$ computed as follows:

$$W_i = Q_i (1 - K)^{a_i - 1}$$

$W_i$ is a quantity that increases with the mean quality of all mates ($Q_i$), but that may decrease with the number of copulations ($a_i$) according to their direct cost, $K = [0, 0.05, 0.1, 0.2, 0.4]$. In this model, sperm competition is assumed to be a fair raffle, without any sort of precedence. We assumed also that generations do not overlap and that populations are at a demographic equilibrium (same density and sex ratio across generations, so the encounter rate was stable). A female's relative fitness determines the proportion of her offspring in the next generation. Males do not evolve and their quality follows a normal distribution ($\mu = 3$, $\sigma^2 = 1$, truncated at 0 and 6; the distribution is shifted from 0 to avoid negative values of quality). Since mating depends on the relative quality of successive mates, the values of male quality are not important per se, but the distribution of these values is. The threshold of acceptance is transmitted vertically to female offspring, potentially with mutations (probability of occurrence = 1%; the new value is picked in a normal distribution: $\mu = \text{ancestral value}, \sigma^2 = 0.5$).

Thresholds are uniformly distributed among the females at the start of a simulation. The length of a mating season is fixed (300 time steps) and the females produce their offspring synchronously at its end (one clutch per breeding season). Simulations were stopped after 200 generations (time at which the thresholds have converged and the system tends to equilibrium) and were run 200 times across a range of combinations of sex ratios, densities and mating costs ($K$). Sex ratio is defined as the percentage of males in the population. We tested sex ratios between 20 and 80. To change the sex ratio we modified the proportion of each sex, not the total number of individuals (which was modified with changes in densities). We tested three densities: a low density (250 individuals), an intermediate density (500 individuals) and a high density (1000 individuals).

**RESULTS**

**Evolution of Choosiness**

Acceptance thresholds converge towards a single value after a few dozen generations (after 15–80 generations depending on the conditions). At the end of a simulation, most of the females in a population share the same acceptance threshold, while some variability is always maintained. The value of the ‘most common’ selected threshold is generally above the mean quality of males and is very sensitive to changes in the parameters tested: as one can expect, females are choosier when either the number of encounters with males or the mating cost is high (Fig. 1). Selection on acceptance thresholds appears stronger when the mating cost is high since the proportion of females using alternative thresholds is lower (Fig. 2).

The evolution of the acceptance threshold can be influenced by (1) the benefits of obtaining high-quality mates, (2) the risk of remaining unmated at the end of the season and (3) the cost of multiple mating. We quantified, at the end of the simulations, how and why females using alternative thresholds to the population norm (most common selected threshold) have a lower fitness. On average, females with a lower threshold than the norm have a lower fitness both because they obtain mates of lower quality and because they suffer higher costs from multiple matings (Fig. 3); females with a higher threshold have a higher fitness as soon as they succeed in...
mating but they experience a higher risk of remaining unmated (Fig. 3). The three effects 1, 2 and 3 act together, but the relative importance of each effect varies with the mating cost $K$. Consequences of suboptimal (either higher or lower) thresholds for mate quality remain roughly constant for all $K$ (Fig. 3). Conversely, suboptimal thresholds have an increasing influence on both the cost of multiple mating and the risk of remaining unmated when $K$ increases (Fig. 3).

**Variation in the Number of Mates**

In all the tested conditions, a high variance is maintained in the number of mates a female has; in particular, monandrous and polyandrous females always coexist even in extremely male-biased populations (Fig. 4). Noticeably, variations in density affect the number of mates less than variations in sex ratio do (Fig. 5), and mating cost has the strongest effect on the mating pattern (Fig. 4 and data not shown). As the mating cost increases, the influence of demographic parameters decreases (Fig. 4 for sex ratio, data not shown for density). In particular, the proportions of females that mate only once and females that remain unmated increase with increasing mating cost (Fig. 4).

**DISCUSSION**

We modelled female mating decisions in a promiscuous population, assuming that mate choice includes an evolving threshold of mate acceptance (choosiness) and trade-up choice for multiple mates. This study shows five major results. First, acceptance thresholds converge rapidly, indicating that most females use the same threshold in a given set of conditions. Second, mating cost has a strong influence on the evolution of choosiness, selection on choosiness being stronger at high mating cost, which leads to less variation in acceptance thresholds. Third, variation in female mating patterns is maintained. Two nonexclusive reasons can explain this variation: (1) the maintenance of some variation in thresholds, owing to the strength of selection on choosiness and to mutations occurring during the threshold transmission, and (2) random events that can lead to different numbers of matings even when females share the same acceptance threshold. For instance, a female that meets by chance a first male of very high quality will not be prone to remate. Owing to random events, the degree of female choosiness does not entirely dictate mating frequency, and there is no need for determined (genetically for instance) strategies to allow the coexistence of various mating patterns. Fourth, the distribution of the number of mates is drastically affected by the variation in mating cost and is almost unaffected by the demographic parameters. Finally, in a given situation (fixed density, sex ratio and mating cost), choosier females indeed mate with males of higher quality, although this leads to an increase in the proportion of females that mate only once or remain unmated.

In our model, acceptance thresholds evolved towards a small set of values, with most females using the same threshold. The value of the threshold is related to mating cost and demographic conditions. For a given set of parameters, very high levels of selectivity (higher threshold) lead to a high risk of remaining unmated, whereas low levels of selectivity (lower threshold) lead to inferior males being accepted and a higher probability of multiple matings. These two risks stabilize the evolution of the threshold to an optimal value. As
demographic conditions change, the risk of remaining unmated and the probability of mating multiply also change and select for different acceptance thresholds. An interesting consequence of threshold evolution is thus that mating frequency remains relatively unchanged. This suggests a small effect of mate encounter rate (influenced by population density and sex ratio, as well as by mobility of individuals) on the distribution of the number of mates, at least under nonextreme conditions. Consistent with this result, the model proposed by Härßling & Kaitala (2005) showed that the female remating rate was not affected by changes in density since females encountered more males but refused copulations more often in a high-density environment. These findings are also supported by results from natural populations, such as those of common lizards, Zootoca vivipara, in which the proportions of monandrous/polyandrous females are very similar between populations with different densities (Laloi et al. 2004) and sex ratios (Fitze et al. 2005). The generality of such a pattern can still be questioned. Although models suggest that demographic factors do not determine mating patterns in a wide range of conditions, their effect may be important in very small populations (e.g. Jensen et al. 2006) or in socially structured systems (Westneat & Sherman 1997). Finally, in the present study, we have explored the effects of constant demographic conditions on the evolution of female choice. However, we expect unusual situations to have different consequences for female choice than the evolved stabilized situations. For example, when individuals colonize a new habitat, they face extremely low densities to which they are not adapted. If the female mating response is not plastic, this demographic change is expected to have a strong effect on the number of mates (e.g. Kokko & Mappes 2005; Contarini et al. 2009). Experiments on natural populations would be useful to assess whether a mating system is actually influenced by strong demographic changes.

Mating cost influences both choosiness and the distribution of the number of mates, and this more strongly than demographic parameters. Threshold evolution results from a complex equilibrium between the risk linked to demographic parameters, as explained above, and the cost of multiple matings. When the cost of one mating increases, avoidance of the cost of multiple matings becomes more important than the risk of remaining unmated, leading to a decrease in mating frequency. Thus, we expect the selection of different thresholds, resulting in different mating frequencies. This was confirmed by our model, in which increasing mating cost resulted in a decrease in the number of mates. This reinforces the idea that mating cost is a major determinant in the evolution of mating systems (Kokko & Monaghan 2001). Moreover, mating cost also influences the strength of selection on choosiness (shown by variation in thresholds) and the relative importance of the other selective factors: when mating cost is low, females evolve thresholds such that the quality of the mate is the most important factor affecting their reproductive success. When mating cost is high, the cost of multiple mating and the risk of remaining unmated are equally important in the evolution of acceptance thresholds.

As an assumption of our model, we have considered females that do not change their choosiness within a season. However, since the duration of a season is fixed, the threshold selected across generations should allow most females to mate before the end of the season. In natural situations, we may expect an interaction between female choice and the time of season: females would be less choosy when the reproductive season is almost over (Lynch et al. 2005). We have also considered that male quality was at equilibrium, not being affected by the evolution of female acceptance thresholds. This would mirror the case of some noninherited male qualities that can be important to a female, such as increased feeding by a male in good condition (Hoelzer 1989). Otherwise, if sons inherit their father’s attractiveness, selection would presumably favour even choosier females (Kokko et al. 2006). Although the numeric value of the threshold will increase with the mean quality of males (shift in the distribution of male quality), this should not affect the relative choosiness of females. But inheritance could be a double-edge sword: while it does favour choosier females, evolving choosiness could deplete male variation, consequently decreasing the benefit of female choice, as in the lek paradox (Kirkpatrick & Ryan 1991; Kokko et al. 2006). Finally, our model

Figure 3. Differences between females using alternative thresholds and females using the most common selected threshold in (a) the mean quality of mates they obtain, (b) the cost related to the number of matings and (c) the proportion of mated females. ■ females using the acceptance threshold selected as the population norm; – females using a higher threshold than the norm (i.e. choosier females); — females using a lower threshold than the norm (i.e. less choosy females).
assumed that the first-mating and the remating decisions are coupled, given a strict trade-up rule. Empirical evidence of trade-up choice supports this assumption (e.g. Bateman et al. 2001). Moreover, coupled first-mating and remating decisions can constitute an evolutionary response to the risk of diluting the genes of a good male in a promiscuous context. Nevertheless, it is not the only plausible rule; both decisions may be decoupled, allowing each of them to evolve independently. This alternative assumption is likely to bring complementary insights on the possibility for a female to adjust mate number and mate quality independently.

Figure 4. Percentage of the different females after 200 generations for each sex ratio tested in the two extreme mating cost conditions (a) $K = 0$ and (b) $K = 0.4$ (mean ± SD, 200 replicates) and a fixed population density (intermediate density = 500 individuals). ●: monandrous females; ○: females mated twice; △: females mated three times; □: females mated four or more times; *: unmated females.

Figure 5. Percentage of the different females after 200 generations for each sex ratio tested in the two extreme population density conditions (a) low density (250 individuals) and (b) high density (1000 individuals; mean ± SD, 200 replicates) and a fixed mating cost ($K = 0.1$). ●: monandrous females; ○: females mated twice; △: females mated three times; □: females mated four or more times; *: unmated females.
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