

Multiple mating by females is a natural outcome of a null model of mate encounters

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Abstract

Why do females of so many species mate multiply? The question makes use of an implicit null model that females by default should be monandrous and that polyandry requires an explanation. Here, we make the simple point that females encounter mates over their lifetime in a stochastic manner, and as they should accept at least one male, acceptance of all males may be a better null model than the more advanced strategy of accepting the first satisfactory one and rejecting all others. The advantage of this view is that it makes it explicit that females must accept and reject mates without precise knowledge of future mate encounters. In insects, for example, limitations of cognitive and sensory capabilities make it hard for females to compare many potential mates simultaneously. It is then not always possible for a female to be very choosy (i.e., to reject a large proportion of encounters) without simultaneously increasing the expected time spent as a virgin and decreasing the overall expected number of mates she accrues during her lifetime. We show that this fact easily leads to a pattern where choosiness is reduced and most females mate with more males than their optimal mate number. Our results suggest that monandry and polyandry may be less distinct strategies than they first appear as they may, to a large extent, reflect chance events influencing mate encounters. Polyandry can arise as a side effect of avoiding the risk of encountering too few acceptable mates – a viewpoint that is easily missed if females that have remained unmated are not included in datasets.

Introduction

Females and males often differ in their mating rate optima. Typically, the mate-limited sex benefits more from each additional mating (it has a steeper Bateman gradient, defined as the slope of the relationship between mating success and reproductive success). This has led to female multiple mating being a harder question to answer than the corresponding male behaviour. There are diverse solutions and suggestions; a non-exhaustive list includes ensuring a sufficient sperm supply (Baker et al., 2001; Evans & Marshall, 2005; Hasson & Stone, 2009), direct

benefits from multiple mating [Gowaty et al., 2010; although often these decline after an optimal mate number has been reached (Arnqvist & Nilsson, 2000); see also Rubenstein, 2007; Larsdotter Mellström & Wiklund, 2010], females minimizing costs of harassment by accepting matings by coercive males (convenience polyandry; Lee & Hays, 2004), preventing infanticide (Agrell et al., 1998), sexual antagonism (Mokkonen et al., 2012), and various types of indirect effects (e.g., Jennions & Petrie, 2000; Bernasconi & Keller, 2001; Ivy & Sakaluk, 2005; Simmons, 2005; Fisher et al., 2006; Evans & Simmons, 2008; Fossey et al., 2008; Rodríguez-Muñoz et al., 2008; Pryke et al., 2010).

In all the work quoted above, the quest is to understand how a female benefits (directly or indirectly) from multiple mating. Implicit in this quest is the assumption that if there are no such benefits, all females should mate just once. It is, however, unclear if this really is an appropriate

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null prediction. If the Bateman gradient is totally flat (zero) beyond one mating such that no benefits of multiple mating exist (nor is multiple mating costly), it will make no difference to a female whether she mates once or several times. This makes it difficult to understand why a null model should posit females to have evolved separate rules for their behaviour when encountering mates as a virgin and when encountering them later.

The switch from asking ‘why should a female mate multiply?’ to asking ‘why should a female not mate in all mate encounters?’ is subtle: it is a way to phrase the same question in a different way. As we will show here, this subtle shift in viewpoint is important because it will make it easier to appreciate that the inherent unpredictability of mate encounters (Bleu et al., 2012) may lead to a pattern where most females appear to behave maladaptively – they mate too often and pay significant costs for doing so – yet selection does not reduce mating rates of females further towards monandry. Such cases may be particularly common in insects, which perhaps more often than vertebrates encounter potential mates in a sequential fashion (Barry & Kokko, 2010), making simultaneous comparison of potential mates difficult. This has been shown to select against mate choice (Barry & Kokko, 2010), thereby increasing mating rates.

Insect studies often compare monandrous and polyandrous females as if these were distinct categories. This diverts attention away from the fact that ‘mate number’ might be an unrealistic trait for selection to work on directly. Instead, a female is likely to possess behavioural rules that dictate how she behaves at each mate encounter. The total number of mates in her lifetime emerges as a result of these behaviours and the number (and behaviour) of males that she encounters (Bleu et al., 2012), as well as the timing of her death. Here, we show that this simple fact has the potential to change the way we should ask questions about populations that consist of a mix of monandrous and polyandrous females.

The rationale

Our model is based on the insight that accepting and rejecting individual mates (mate choice) is intrinsically linked with changing the number of mates a female is likely to mate with. If female A is choosier than female B, this can be stated in two ways: A uses a more stringent acceptance threshold in her mate encounters than female B, or female A rejects a higher proportion of mates than B does (example in Figure 1 where A rejects 80% of males, B only 50%). Therefore, all else being equal, A will have a lower mating rate than B. For example, if females encounter 10 potential mates per time unit and their traits evalu-

ated by females are normally distributed (Figure 1), A’s mating rate in Figure 1 is lower than that of B (two acceptable mates per unit time compared with five). On average, a female following the threshold B will have $5/2 = 2.5\times$ as many mates in her life than A. Specifically, if both females suffer a mortality rate of 0.1 per time unit, then A has a 4.76% risk of dying without ever mating, whereas for female B this is only 1.96% [computed as $0.1/(0.1 + 5)$; for a generalization of these calculations, and the exact distribution of the number of mates, see the Equations below].

Although the scenario depicted in Figure 1 is useful for making the point that choosiness thresholds have an impact on mating rates and consequently the numbers of mates, it should be kept in mind that females can also achieve differences in their mating rate by accepting a random, rather than a specific, subset of males. For example, if female A accepts only 20% of mate encounters and female B accepts 50% of them, and acceptance is random with respect to any male traits, the impact on A and B’s mating rates and numbers of mates is identical to the calculations above. Selection can act on acceptance in these cases too, as the number of mates can have a strong impact on female fitness.

We use these insights to model females that can adjust their mating rate upwards or downwards by rejecting a higher or lower proportion of males that they encounter. The accepted subset of males may be random, in which case rejections have no impact on the quality of mates (and rejecting some males simply serves the purpose of adjusting the mating rate), or alternatively, the female may be accepting only males whose traits exceed some thresh-

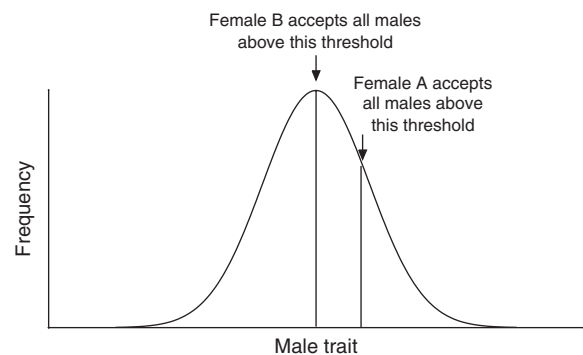


Figure 1 A hypothetical scenario where female A accepts a lower proportion of mates (20% of encounters lead to a mating) than female B that accepts the upper half of male trait values. Our argument is based on the necessary relationship between the proportion of mates accepted and the mating rate that follows; if A and B are approached by males equally often, B will mate on average $2.5\times$ as often as A.

old (as in Figure 1). The fitness consequences for the female are simpler in the first case (random acceptance with respect to male traits) than in the latter. In the first case, the proportion of mates accepted only impacts the likely number of times she mates, including the probability of mating zero times, i.e., virgin death. In the latter case where mate identity matters, i.e., acceptance requires that a male has a trait value above a female's acceptance threshold, female fitness is, as before, strongly influenced by the distribution of the number of times she mates, but now one must also consider that the quality of partners she mates with is impacted by the threshold she employs.

We have previously (Kokko & Mappes, 2005) considered optimal female choosiness in cases where they can trade-up. Trading up refers to cases where females become more choosy (use more stringent acceptance thresholds) as they have mated more often (Moya-Laraño & Fox, 2006; Bleu et al., 2012). In this study, we do not allow for trade-up to happen, and instead we investigate what happens when females accept the same proportion of males accepted (denoted by x) in all her mate encounters.

We are interested in this constrained life history scenario for two reasons. First, a null model should use simple, rather than complex, adaptations, and identical behaviour in all mate encounters is by far the simplest alternative. Second, it is by now an outdated view that individuals behave ideally in every possible situation (McNamara & Houston, 2009). At the extreme, female receptivity to matings is known to be influenced by correlated selection on male mating rates (Forstmeier et al., 2011), or by selection to improve feeding rates (leading to sexual cannibalism; Arnqvist & Henriksson, 1997). There is growing recognition that selection on behavioural traits may have to act on behavioural syndromes (Sih et al., 2004) or 'personalities' (Dall et al., 2004; Bergmüller, 2010) rather than more finely defined traits. There is also much data showing that females may suffer negative fitness consequences when mating 'too little' as well as 'too much' (Arnqvist & Nilsson, 2000). Against this background, it is surprising that no model, with the recent exception of Bleu et al., (2012), has explored how females balance the risks of mating 'too little' and 'too much' when mate encounters are inherently unpredictable, and it may be hard for selection to adjust female receptivity in each mate encounter independently of other contexts (e.g., receptivity when a virgin vs. receptivity later in life).

Throughout, we will contrast our results with a female's ideal life history. Here, we make the opposite assumption to the null model: now a female never mates after reaching her optimal number of mates. Although some females may still die before reaching their optimal mate number, the ideal life history will lead to higher fitness than the con-

strained life history in cases where multiple mating is costly. If a female is completely able to stop mating as soon as the optimal mate number (which can be as low as one) has been reached, females will avoid all negative fitness consequences of mating too often.

Our contrast of two extremes allows us to explore the extent to which multiple mating can evolve as a response to being constrained to behave similarly in different mate encounters. For example, consider the case where the optimal mate number is 1 (monandry). An ideal life history might be to mate with the first ever male encountered and stop being receptive ever after. If this strong a response is not possible, females will have to balance risks of remaining mateless with those of mating too much. Because mate encounters are stochastic, it is often not possible to always end life as a once-mated female, even if monandry as such would produce the highest fitness. If selection acts on a general trait of female receptivity in mate encounters (such that we assume it does not fine tune responses to all details of mating history), receptivity may evolve to be relatively high, as this avoids spending too much time in the virgin state. The receptivity of virgins then carries on to later stages in life as well, meaning that optimally behaving females will not be very choosy and they will, on average, mate more often than the ideal (which remains at one mate).

The model

We model a female's life as a continuous-time process where she begins her mature life as a virgin at $t = 0$. Throughout her life she encounters potential mates at a rate M , of which she accepts a subset (either random or a specific subset) such that she mates with a proportion x of all males (where $0 \leq x \leq 1$). Her mating rate consequently becomes $m = xM$. In the example of Figure 1, female A's mating rate is $m = 0.2 \times 10 = 2$, whereas for female B this is $0.5 \times 10 = 5$. In our alternative model formulations below we give several interpretations for the acceptance proportion x . Selection to increase or decrease x can relate to mate identity, in which case a female expresses a preference for certain males over others. Alternatively, mate identity can be irrelevant, and rejecting some matings is then simply a way to adjust the mating rate m towards the fitness-maximizing rate for a female. All our model results can be expressed either in terms of x or in terms of m , via the relation $m = xM$.

We incorporate stochasticity by assuming that M is the parameter of a Poisson process, which is appropriate when the precise timing of each encounter is independent of what other males in the population are doing. Note that m is then a parameter of a similar Poisson process: M describes the mean number of males encountered per time

unit in a Poisson process of mate encounters, whereas m is the Poisson process describing the accumulation of accepted matings. Obviously, the latter process depends on the proportion of mates accepted by the female ($m = xM$).

The female also experiences a continuous risk of death. In some versions of our model, this risk is dependent on the female's mating status: for example, in *Drosophila melanogaster* Meigen (Priest et al., 2008), and in windmill butterflies, *Atrophaneura alcinous* (Klug) (Kawagoe et al., 2001), multiple mating increases female mortality. However, for simplicity we assume that each mating takes a negligible amount of time, and thus excludes immediate costs of being in copula (say, impoverished escape ability in butterflies during mating; Almbro & Kullberg, 2009). Note that in our continuous-time formulation we will make use of rates as well as probabilities. Rates can exceed unity (e.g., mortality rate = 10 means an exponentially distributed lifespan where individuals on average live for 1/10 units of time). Rates will be used to form probabilities (these cannot exceed 1) when calculating eventual fates, such as 'probability that a twice-mated female dies before she mates with her third male'. If a twice-mated female has a mortality rate of 10 and a mating rate of 5, the probability that she mates at least once more before she dies is $5/(5 + 10) = 1/3$ and the probability of dying before mating is conversely $10/(10 + 5) = 2/3$. Similar formulations apply to the calculations of dying before ever mating (see the 'Rationale' section, above).

After the female has mated once (if she did not already die as a virgin), reproduction can commence. Our model is inspired by a typical life history of insects, thus we equate reproduction with egg laying, which is assumed to yield a continuous fitness gain at an instantaneous rate F_1 . The model is, however, equally appropriate for any system in which reproductive activities commence once at first fertilization and thereafter continue steadily until death. The rate of fitness gain F_1 is the product of number of eggs laid per time unit and the reproductive value of each egg. This continues until she mates another time or dies. A doubly mated female will gain fitness at a rate F_2 , which again continues until she mates another time (or dies), and so on until death. In some versions of the model, we allow the fitness gains F_i to depend on her mate's quality. This can be interpreted as either a direct or an indirect fitness benefit as the product of offspring number and value can be increased by improving either fitness component.

The task is to calculate a female's lifetime fitness, i.e., production of offspring optionally weighted with offspring reproductive value ('optionally' refers to our open

interpretation of the meaning of female fitness gain F_i). We consider various scenarios, and in each case compare the distribution of female mating status at the time of death with the theoretically ideal life history, i.e., how many times a female should ideally mate if she were able to choose this precisely.

Multiple mating when mate identity does not matter

In the scenarios of this section we assume that male identity has no impact on a female's fitness gain. This means that choosy females, who reject some males ($x < 1$) and thus lower their mating rate m ($m = xM$) downwards from the maximum $m = M$, cannot improve their F_i . However, we assume that the F_i can be unequal: for example, direct benefits may make F_i increase with the number of mates i , or costs may make it decrease. Thus, females will evolve according to potentially opposing selection pressures: they are selected to keep their mating rate m high enough so that the risk of dying before accepting any mate is low, but increasing m may mean that females more often end up mating too much even if monandry would have been optimal for them. We also assume that the mortality rate of a female may depend on her mating status: it equals μ_i for females mated i times. Thus, for example, toxic seminal fluids will make μ_i increase with i .

In the case where F_i increases with i and mortality does not depend on i , a model is not needed to produce the prediction that females should mate with every male encountered: a high m is then favoured both for allowing reproduction to commence, as well as to increase the rate of fitness gain later in life. We thus concentrate first on the case where F_i decreases with i . Females in other words would be better off if they mated fewer times (but not $0 \times$).

A female's lifetime options are depicted in Figure 2. A female may leave each state by mating (rate m) or by dying (rate μ_i). The probability that the female dies as a virgin is

$$P_0 = \frac{\mu_0}{m + \mu_0}. \quad (1)$$

This is calculated as the probability that death (occurring at rate μ_0) occurs before mating (at rate m).

The probability that the female ends her life as a once-mated female is conditional on the first mating occurring before death, and after this has happened, death must occur before an additional mating:

$$P_1 = \frac{m}{m + \mu_0} \frac{\mu_1}{m + \mu_1}. \quad (2)$$

The time that a newly matured female can expect to stay in the once-mated stage is

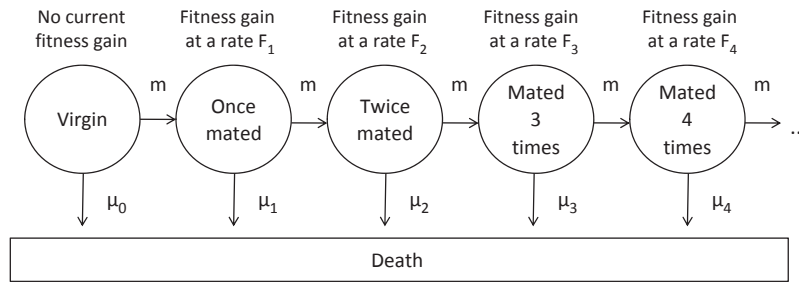


Figure 2 A schematic illustration of the constrained life history of females. The death rate μ_i and the current rate of fitness gain F_i depend on female mating status as depicted. Females can differ in their mating rate m depending on the proportion, x , of mates they accept, as $m = xM$. Increasing m makes reproduction commence sooner – thus avoiding the risk of virgin death – but a higher m also makes the female move faster through each state towards higher numbers of matings (and possibly also towards higher death rates if μ_i increases with i).

$$T_1 = \frac{m}{m + \mu_0} \frac{1}{m + \mu_1}. \quad (3)$$

This expression is obtained by multiplying the probability that she ever mates (the first term) with the expected duration of staying once-mated. This time is exponentially distributed with mean $1/(m + \mu_1)$ because she leaves the once-mated state at a rate that combines the rate of mating again (m) with the rate of dying when in that state (μ_1).

Similarly, for the i -th mating, the expressions are

$$P_i = \frac{m}{m + \mu_0} \frac{m}{m + \mu_1} \dots \frac{m}{m + \mu_{i-1}} \frac{\mu_i}{m + \mu_i}, \text{ and} \quad (4a)$$

$$T_i = \frac{m}{m + \mu_0} \frac{m}{m + \mu_1} \dots \frac{m}{m + \mu_{i-1}} \frac{\mu_i}{m + \mu_i}. \quad (4b)$$

During the time spent once-mated, twice-mated, and in general i -mated, females gain fitness at a rate F_1, F_2, \dots, F_i . Female fitness is obtained by weighing these gains by the expected time that a newly mated female will spend in each state:

$$W = \sum_{i=1}^{\infty} T_i F_i. \quad (5)$$

The simplest scenario: multiple mating evolves to minimize the risk of virgin death

In the special case where all F_i are identical ($F_i = F$ for all i , i.e., fecundity and offspring value do not depend on mother's mating status beyond the first mating), and mortality does not depend on mating status but is $\mu_i = \mu$ for all i , female fitness can be simplified by noting that

$$T_i = \frac{m^i}{(m + \mu)^{i+1}}. \quad (6)$$

Thus, female fitness becomes

$$W = \sum_{i=1}^{\infty} T_i F = \frac{mF}{\mu(m + \mu)}. \quad (7)$$

This expression always increases with mating rate m and hence with the proportion of accepted mates x (remembering $m = xM$). Thus, if the only state that deviates from the others by having a lower instantaneous fitness gain is the virgin state, then females are selected to be very eager to mate: this shortens the time spent as a virgin during which no fitness can be gained. Females who do not reject any matings ($x = 1$) will mate at a rate $m = M$. The ideal life history is any mate number from 1 upwards, but the constrained life history differs from this because a certain proportion of females, $\mu/(\mu + M)$, will die before they encounter anyone. Note, however, that this proportion is very low if mortality, μ , is low compared to the mate encounter rate, M . The average female lifespan is $1/\mu$, and an average female mates M/μ times. Thus, in this situation, the constrained life history of females evolves to be close to the ideal life history, unless the availability of mates is severely limited (relative to the time that a female on average has available to find mates).

When monandry is optimal, most females may still mate multiply

The situation becomes far more interesting if the rate of fitness gain F_i declines with each mating, i . For example, consider the case where $F_1 = 1$ is the relative fitness gain of a once-mated female, and every subsequent mating reduces fecundity from that mating onwards by a cost

factor c . In other words, $1 - c$ specifies how much of a female's instantaneous fitness gain is left after she has mated one more time, relative to immediately previously; if $c = 0$ there is no cost. Thus, $F_i = (1 - c)^{i-1}$, and with $c > 0$ (and mortality μ_i constant across all i) the ideal life history is monandry. However, under a constrained life history a female cannot directly choose monandry, but she can adjust her mating rate upwards or downwards. What is the mating rate favoured by selection? Equivalently expressed, what proportion of the mate encounters should the female accept?

The expected time that a female spends in each state is the same expression for T_i that we already had above (Equation 6). Thus, we obtain

$$W = \sum_{i=1}^{\infty} T_i F = \sum_{i=1}^{\infty} \frac{m^i}{(m + \mu)^{i+1}} (1 - c)^{i-1} \quad (8)$$

$$= \frac{m}{(m + \mu)(mc + \mu)}.$$

The value of m that maximizes female fitness is obtained by setting the derivative of Equation (8) to zero, and we find the best female mating rate

$$m^* = \frac{\mu}{\sqrt{c}}. \quad (9)$$

If this value is higher than the mate-encounter rate, M , then females never reject any males and optimal mate acceptance consequently equals $x^* = 1$.

Equation (9) predicts that high female mortality and a low cost of multiple mating increase the mating rate that is in the best interest of females. This is not surprising. It is more interesting to derive the proportion of females who mate a specific number of times over their lifetime (assuming mate availability does not limit their mating rate, i.e., $M \geq m^*$). We obtain the results: proportion of females dying as virgins:

$$P_0 = \frac{\mu}{m^* + \mu} = \frac{\sqrt{c}}{1 + \sqrt{c}}, \quad (10a)$$

proportion who ever mate only once:

$$P_1 = \frac{m^*}{m^* + \mu} \frac{\mu}{m^* + \mu} = \frac{\sqrt{c}}{(1 + \sqrt{c})^2}, \quad (10b)$$

proportion of females who mate multiply:

$$P_{2+} = 1 - P_0 - P_1 = \frac{1}{(1 + \sqrt{c})^2}, \text{ and} \quad (10c)$$

average number of mates a female has mated with by the time she dies:

$$N = m^*/\mu = \frac{1}{\sqrt{c}}. \quad (10d)$$

It is interesting to note that all these quantities P_0 , P_1 , P_{2+} , and N are independent of mortality μ even though they all depend on m^* which again depends on mortality. For example, for P_0 (probability of virgin death), the explanation is as follows. All else being equal, the risk of dying before mating increases with mortality, but simultaneously all else is not predicted to be equal: the optimal mating rate m^* also increases linearly with mortality which decreases the time that individuals will spend in the virgin state before mating. These effects cancel each other out, and in general females are expected to evolve to keep the risk of virgin death at the same level across all mortality scenarios (assuming that other parameters, such as c , remain constant). Similar arguments apply for why P_1 , P_{2+} , and N evolve to become independent of mortality μ .

Thus, we can concentrate on the more interesting effect of the mating cost. Consider, for example, $c = 0.1$, meaning that a female pays a 10% cost for each subsequent mating. Thus, a female has 90% of her reproductive rate intact after two matings, and after three matings this has dropped to $0.9 \times 0.9 = 81\%$. Despite this dramatic reduction, females that mate optimally (with the constraint that they have to use the same level of selectivity in each mate encounter) mate on average with more than three males: $N = \frac{1}{\sqrt{0.1}} = 3.16$. It is interesting to look at how this average comes about. The proportion of females dying before ever mating is $P_0 = 0.24$ (from Equation 10a), the proportion of monandrous females is $P_1 = 0.18$ (from Equation 10b), and the majority of females, $P_{2+} = 0.58$, mate multiply, some of them very many times (from Equation 10c). Thus, if one categorizes females as 'never mating', 'monandrous', and 'polyandrous', then the ideally performing females form the smallest group (18%) of all observed female life histories. If one were to collect data on mated females only, then again monandrous females would form the minority: $P_1/(P_1 + P_{2+}) = 24\%$.

The general prediction from this model with constant mortality and a reproductive cost of multiple mating is that the mean number of mates declines with costs of mating c , but still, the average number of matings for a female will exceed 1. Moreover, for all other costs than the highest possible cost $c = 1$, polyandrous females will be more common than monandrous ones (Figure 3A). High costs decrease the mating frequency and this increases the relative proportion of monandrous females, but simultaneously the proportion of virgin deaths increases too (Figure 3A). Note that this result of multiple mating is derived assuming no direct costs of resisting male mating attempts (no convenience polyandry; see Discussion).

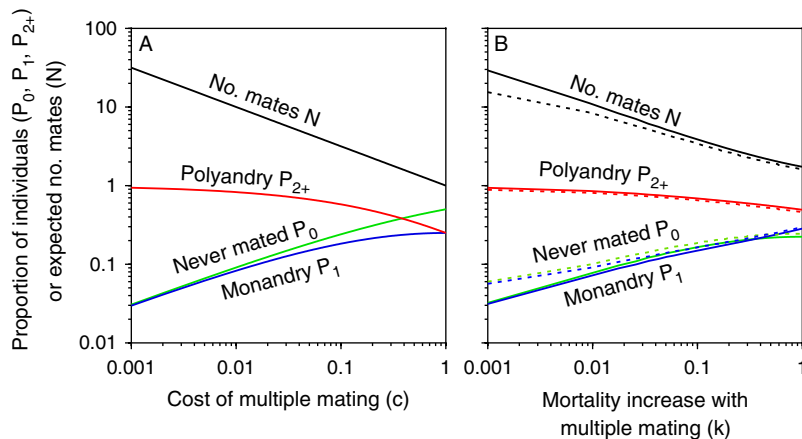


Figure 3 Model predictions: the average number of mates (black), as well as the proportion of females who end their life in the virgin state (green), singly mated (blue), or after multiple matings (red), as predicted from (A) the model with constant mortality and a reproductive cost c of multiple mating, and (B) the model where multiple mating increases mortality. In (B), solid lines refer to the scenario where females adjust mating rates, but do not target any particular subset of males, whereas the dotted lines give predictions for the scenario where females choose males who yield superior fitness benefits. Choosiness decreases the overall number of mates (N) and the proportion of polyandrous females compared with simple adjustments of mating rate, but does not change the overall result that most females mate multiply.

Most females may also mate multiply when multiple mating increases mortality

Now let us assume that the instantaneous rate of fitness gain is independent of the number of matings (beyond one), but female mortality increases with each subsequent mating. Again, the ideal life history is monandry (it leads to the longest time spent in the reproductively active state of once-mated). However, under a constrained life history the result is different.

The expected time that a female spends in each state is no longer expressible as (Equation 6) because the death rate μ_i increases with i . Consider, for example, $\mu_i = \mu_0 + ki$ and $k > 0$, meaning that each mating brings about a linear increase in the instantaneous mortality risk that the female experiences afterwards. Inserting $\mu_i = \mu_0 + ki$ into Equation (4b) leads to an expression of female fitness that is unwieldy enough so that it does not yield an analytical solution for an optimal mating rate m^* . This can, however, be easily found numerically. The consequences for P_0 , P_1 , P_2 , and N of females are likewise easy to derive numerically after the optimal m^* (together with the optimal acceptance proportion $x^* = m^*/M$) has been found. The solutions show that once again females are very likely to mate multiply (Figure 3B, solid lines) – indeed, once again, the population exists as a mix where polyandrous females are the most common type, even if mortality increases sharply with multiple mating. Although harder to prove analytically than in the previous section, numerical results indicate that as above, the results on P_0 ,

P_1 , P_2 , and N are independent of baseline mortality μ_0 (not shown).

Multiple mating when mate identity matters

Up to now we have assumed that females can evolve to adjust their mating rate m by altering their acceptance threshold x upwards or downwards, but acceptance is random with respect to male phenotype. We now turn our attention to a scenario where we ask explicitly which males females are accepting, as we now consider that male identity has an effect on female fitness gain F . Choosiness makes females accept a subset of males, and if they behave adaptively then they will select a subset such that it includes males with the best effects on F . Simultaneously, because some males must be rejected, increasing choosiness lowers the mating rate m . Very choosy females will only accept the very best males and they can expect a high fitness gain F after each mating, but their mating rate m is simultaneously very low.

We assume no direct costs of mate sampling: mate encounters still happen at a rate M , and females simply accept or reject each encounter. The most fundamental cost of choice in such a scenario is that too strong a choice can lead to death occurring before any mate has been accepted. This cost has been extensively dealt with by Kokko & Mappes (2005). This earlier work, however, concentrated on the plastic case where females keep benefitting if they mate multiply in a ‘trade-up’ fashion (Halliday, 1983; Pitcher et al., 2003; Fedina & Lewis, 2007), and it did not

include any mechanism that might make female fitness decline if they mate suboptimally often. Thus, we now add the assumption that female mortality increases with each consecutive mating. In other words, we use the same assumption $\mu_i = \mu_0 + ki$ as in the above section, but now in a context where choosiness can have a beneficial effect on mate quality.

For simplicity, we assume that female fitness gain F_i is a function of the (so far) last mate's quality, thus in a sequence of mates with qualities q_1, q_2, \dots, q_i the i -th male is the only one whose quality matters for all eggs produced between matings $i-1$ and i . We assume that the q_i are normally distributed with mean 1 and standard deviation σ , with the probability density function denoted $f(q)$. We also assume $F_i = q_i$, thus a male's quality is effectively measured as his effect on the female's instantaneous fitness gain. Mate quality is not assumed to have an impact on the mortality increase that follows mating.

A randomly mating female's mating rate equals the population-wide mate-encounter rate, M . A female who rejects all males with $q < 1$ will mate at a rate $M/2$, and in general a female who rejects all males whose quality falls below a threshold Q will have mating rate $M \int_Q^\infty f(q) dq$, i.e., the rate of meeting acceptable mates whose quality exceeds her threshold. The expected fitness gain F_i of a female does not depend on how many times she has mated, i , in this scenario. We thus have

$$F_i(Q) = \frac{\int_Q^\infty qf(q) dq}{\int_Q^\infty f(q) dq} \quad (11)$$

for all i . It follows that the ideal life history is once again monandry, although in this case the number of matings is better described as a neutral trait: multiple mating leads to no improvement on average on mate quality compared with what the female already obtained by using the same threshold Q in her previous matings.

Given that improving F can be achieved by rejecting a subset of potential mates, it is not surprising that introducing mate choice for F reduces the average number of mates and the proportion of polyandrous females, as well as increasing the proportion of monandrous females (Figure 3B: compare the height of the dotted lines with the solid lines). It also increases the proportion of females who experience virgin death (Figure 3B). However, the qualitative pattern is similar to our earlier model that had no mate quality variation: females do not easily stop mating multiply even though the cost of multiple mating increases dramatically from left to right in Figure 3B.

Note that our model is a null model in the sense that it does not include any effects of choosiness that usually have

been associated with multiple mating: there is no option to 'trade up' (become more choosy in successive matings). Thus, mate qualities do not vary systematically across matings. Also, we assume no post-copulatory choice because the (thus far) last male was simply assumed to father all the young. These assumptions mean that choosiness always decreases mating rates in our model, yet these remain high enough to make a large fraction of females mate multiply under all scenarios. If females cannot independently adjust choosiness and mating rates, and a sufficient mating rate is required to avoid the unfortunate blunder where no male was found acceptable until the female dies, then optimally choosy females will develop choice rules that also make them accept males beyond their first mating.

A hypothetical experiment

The following point could be made with any version of our model, but for simplicity we turn back to our first scenario where mate identity plays no role and females do not vary in their instantaneous fitness gain or mortality beyond their first mating. Assume that an experimenter wants to create two selection lines, selecting for monandry in one and for polyandry in the other. As her material, she is using a population of 1 000 females (and a sufficient number of males). This population of females exhibits a normally distributed mating rate with mean 0.5 and standard deviation 0.1 (truncated at zero mating rate; Figure 4). She selects the same number of offspring from each female who mated one single time before dying (in the monandry line) or more than once before dying (in the polyandry line) and discards all other eggs. The precise number of offspring/female chosen is the integer that forces the new generation to consist of as close to 1 000 females as possible. Also, to consider the best of possible worlds for this experimenter, we assume that the mating rate trait is passed on from mother to daughter without error – thus, one could expect maximally high heritability for monandry or polyandry.

However, heritability is compromised because offspring of monandrous females are not always monandrous themselves. The inherited trait is a mating rate rather than the behavioural categorization of monandry/polyandry/virgin death. This has interesting consequences. The mating rate distribution shifts clearly towards smaller values in the monandry line, whereas the shift towards high mating rates is less strong in the polyandry line: because most females are polyandrous to begin with, actual selection on mating rates is relatively relaxed in this scenario. More interestingly, however, both selection lines will show a high proportion of polyandrous females after any number of generations. The main difference is that the monandry line

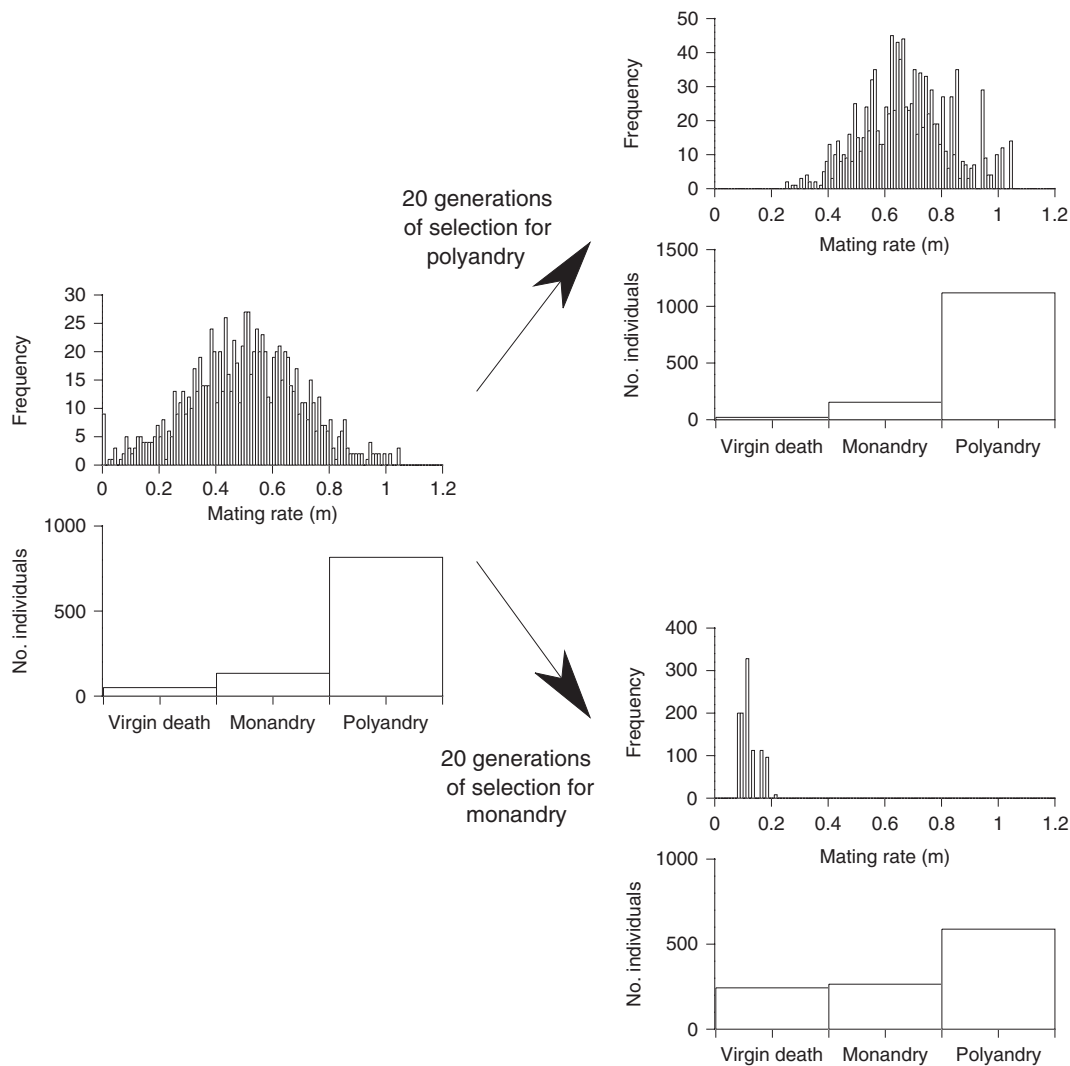


Figure 4 A hypothetical experiment that begins with an initial distribution of mating rates and a consequent number of females who mate with 0, 1, or at least 2 males (left); and the same quantities measured after 20 generations of selection when the experiment has created lines of high (top right) and low (bottom right) mating rates.

evolves to exhibit a much higher proportion of females who never mate (Figure 4). As never mating is predicted by a low mating rate, and females who never mate do not contribute to new generations (in selection lines or in nature), the monandry line does not select for the lowest possible mating rates. Instead it keeps a high enough mating rate such that most females remain, in fact, polyandrous.

Discussion

Much of the literature on polyandry asks why females mate multiply. This way of phrasing the issue reveals a curious tendency to think of monandry as a ‘null

model’ such that deviations from it require us to search for a reason. The opposite way to think about the situation is to ask, under what conditions should an individual reject a mating opportunity (Jennions & Kokko, 2010)? Our approach does not invalidate any of the studies that indeed have found that females enjoy benefits of multiple mating (Arnqvist & Nilsson, 2000), but it reminds us that multiple mating can be the expected outcome whether or not such benefits exist. An appropriate null model is not monandry, but a distribution of lifetime matings that results from mating at every encounter. Deviations from this distribution are then the pattern that necessitates explanation.

Regarding ‘always mate’ as the null makes it easy to see, for example, why higher mating costs select for more vigorous rejections of superfluous matings if there are insufficient compensatory benefits. If monandry combined with the absence of benefits was the null expectation, it would be hard to see why mating costs would have any impact on female behaviour (for a non-insect example see Albrecht et al., 2006).

In our model we have explicitly derived the distribution of the number of matings based on a set of simple assumptions: females are assumed to behave adaptively in that the proportion of mates accepted is an appropriate response to typical mate-encounter rates in the population, and selection is influenced by fitness consequences of mating ‘too little’ as well as ‘too much’. To keep the model as close to a ‘null’ as possible, we assumed no plastic behaviour based on mating history or their own past frequency of mate encounters. This assumption may require some defending, given that there is ample evidence that females can become unreceptive after a mating (e.g., Teuschl & Blanckenhorn, 2007), or adjust their choosiness depending on their age (Moore & Moore, 2001; Maklakov et al., 2006) or mating history (e.g., Pitcher et al., 2003; Fitze et al., 2010; for theory see Kokko & Mappes, 2005; Bleu et al., 2012). Null models, however, are not useful for the reason that real behaviour never deviates from them, but for providing a baseline expectation, which enables us to examine reasons why a real system deviates from the null. For the reason explained above (monandry assumes that a female’s behaviour when encountering mates changes from virgin to mated state, even when the Bateman gradient is flat such that there is no selection to change the behaviour), similar receptivity across all mate encounters can be considered a simpler null than monandry. Deviations from this pattern then point at adaptive processes of added complexity.

The choice of a null expectation has a strong influence on research traditions. As outlined in our ‘Rationale’ section above, evidence is accumulating to favour the interpretation that it is unreasonable to expect selection to mould behaviour to reach perfect optimality for each potential scenario encountered (e.g., in an idealized way for each past mating sequence of a female). Researchers should not ignore the possibility that rejecting superfluous matings might be hard to achieve without compromising mating success in those stages of life when a female should accept mates. The number of mates encountered is a stochastic variable in nature (Jennions et al., 2012), hence examples where monandrous and polyandrous females coexist (Eizaguirre et al., 2007) do not necessarily need an explanation any more compli-

cated than it being the expected null pattern when females use a rule of thumb to accept or reject matings, and not all females encounter the same number of males due to chance events (see also Bleu et al., 2012).

Our finding that polyandry is often the prevailing pattern even when it is costly to females is a reminder how strongly it can matter that some females never produce any offspring (del Castillo & Núñez-Farfán, 2002; Rhainds, 2010; Rodríguez-Muñoz et al., 2010). Fecundity or mortality costs (or direct benefits) of multiple mating, or the fitness consequences of female choice, are much more popular study topics than the risk of never mating (but see de Jong & Sabelis, 1991; Bode & Marshall, 2007; Calabrese et al., 2008; Rhainds, 2010; Elzinga et al., 2011). Interestingly, even in studies that document significant reluctance to mate, there is a tendency to exclude non-mated females when making statements about fitness. In some cases, such practises are followed up to the point of excluding two thirds of all data (Pai et al., 2007). Because there is often a much larger fitness difference between never mating and mating, than between the different fates of already reproductive females, the risk of virgin death does not have to be large for it to have a very strong effect on selection (Kokko & Mappes, 2005). Here, we have shown its power to override costs that are paid later in life, such that most females may end up mating in excess of their optimal mate number.

We suspect that our findings would remain similarly relevant if other aspects often found in real mating systems – from male harassment to cryptic female choice – were included. In our model, the stage when females should mate more is the state of being a virgin (for an empirical example see Larsdotter Mellström and Wiklund, 2010; Larsdotter Mellström et al., 2010), but one could easily extend the model to cover other situations. For example, if an intermediate number of mates is the best outcome for a female (Arnqvist & Nilsson, 2000), females behaving adaptively might appear ‘too reluctant’ to mate when they are below this number and keep on mating ‘too much’ when they are above. All it takes for this to happen is that selection works on a general trait of receptivity (or ‘choosiness’) instead of making very precise adjustments to receptivity after each mating.

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