

SEXUAL SELECTION WHEN FERTILIZATION IS NOT GUARANTEED

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Abstract.—Much of the theory of sexual selection assumes that females do not generally experience difficulties getting their eggs fertilized, yet sperm limitation is occasionally documented. How often does male limitation form a selection for female traits that improve their mating rate? The question is difficult to test, because if such traits evolve to be efficient, sperm limitation will no longer appear to be a problem to females. Here, we suggest that changes in choosiness between populations, and in particular between virgin and mated females, offer an efficient way to test this hypothesis. We model the “wallflower effect,” that is, changes in female preferences due to time and mortality costs of remaining unmated (for at least some time). We show that these costs cause adaptive reductions of female choice, even if mate encounter rates appear high and females only rarely end their lives unfertilized. We also consider the population consequences of plastic or fixed mate preferences at different mate encounter rates. If mate choice is plastic, we confirm earlier verbal models that virgins should mate relatively indiscriminately, but plastic increase of choosiness in later matings can compensate and intensify sexual selection on the male trait, particularly if there is last male sperm precedence. Plastic populations will cope well with unusual conditions: eagerness of virgins leads to high reproductive output and a relaxation of sexual selection at low population densities. If females lack such plasticity, however, population-wide reproductive output may be severely reduced, whereas sexual selection on male traits remains strong.

Key words.—Female choice, multiple mating, phenotypic plasticity, population consequences of sexual selection, sequential mate choice, sexual selection, sperm limitation, virgins.

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More than 10 years ago, de Jong and Sabelis (1991) modeled the evolutionary consequences of a process where choosy females experience a lack of males that satisfy their preferences. If a female with strong preferences runs a slight risk of remaining unmated, the possibilities of finding “run-away” evolution of sexual ornaments are greatly lowered (de Jong and Sabelis 1991). They term this the wallflower effect, although it should be kept in mind that the lack of suitable males results from the female’s own strict preferences, rather than male mate choice as the term might suggest.

The wallflower effect has not become a standard feature of sexual selection models, perhaps because it is “too obviously” maladaptive for a female to have such a strong preference that she refuses to mate at all. Put in a wider context, however, the work of de Jong and Sabelis (1991) poses an interesting question. In the case of conventional (not reversed) sex roles, it is generally assumed that females do not face difficulties in finding mates. This is because females are the sex that limits male reproductive success, therefore there should be a surplus of potential mates available for females at any time (Bateman 1948; Trivers 1972; Clutton-Brock and Parker 1992; Andersson 1994). Can evolution of female mating strategies nevertheless be influenced by the risk of remaining unmated either permanently or for an evolutionarily significant amount of time? The difficulties of mate location could arise through many mechanisms: examples include low mobility (e.g., Levitan 1998, 2004), low population density (e.g., McCarthy 1997; Møller 2003; Levitan 2004), biased operational sex ratios (Jiggins et al. 2000), and reproductive asynchrony where individuals are reproductively active for only a portion of the population-level breeding period (Calabrese and Fagan 2004). We suggest including any such mechanism—not just “too strong” fe-

male preferences (de Jong and Sabelis 1991)—in the term “wallflower effect,” by which we thus mean any influence that mate-locating difficulties have on female mating strategies.

It is obviously important for a female to have her eggs fertilized. Consequently, any risk of failure should select for female mating adaptations that ensure that sperm is available for fertilization whenever needed. Finding potential examples of such adaptations is easy: prolonged sperm storage capabilities (Parker 1970; Ridley 1988), female pheromones that help males find a female (Greenfield 1981), and multiple mating (Sheldon 1994; Preston et al. 2005). However, examining whether a lack of mates was responsible for the observed adaptation is challenging. This is because if such adaptations evolve to be efficient, one should no longer find many females whose eggs remain unfertilized. Even so, the explanation of such adaptations requires one to consider the original difficulty of finding a mate. A much clearer case is found when at least some eggs do remain unfertilized. But these cases should be rare precisely because selection to have one’s eggs fertilized should be strong, which makes it hard to find support for the wallflower effect exactly in the case that it is strong.

Here, we propose that a way to investigate this challenging problem is to focus on a particular adaptation of females: the adjustment of levels of choosiness when encountering males. It is often costly for a female to wait before reproduction can start, and it has been suggested that an optimally behaving female should first mate unselectively, and then improve in mate quality in later matings (“trade-up,” Jennions and Petrie 2000). But how serious should the risk of remaining unmated be before one expects an effect on choosiness? Formalizing this argument is necessary to answer the question phrased by

Peretti and Carrera (2005), ‘‘Why would unseminated females not also be interested in choosing the best male?’’ Here, we model optimal levels of choosiness and investigate how these depend on mate encounter rates and the mating status of a female (i.e., how many times she has mated).

We then proceed to asking how optimal adjustments of choosiness will be reflected in the intensity of sexual selection, both in cases where populations exist at their usual densities experienced during evolutionary history, and in cases where the environment has changed. Mate encounter rates in a particular population may differ from usual ones experienced during the evolutionary history of a population for a variety of reasons. Some of them arise naturally: populations may mainly respond to selective pressures in core areas of their range, leaving species at the edges of their distribution maladapted (Kawecki 1995; Holt et al. 2004). Populations may also undergo drastic changes in density due to anthropogenic influences, and these may influence mate encounter rates (Møller and Legendre 2001; Milner-Gulland et al. 2003; Rowe and Hutchins 2003). In either case, it is interesting to ask if changes in mate encounter rates alter the process of sexual selection, as it is increasingly recognized that sexual selection can have population consequences (e.g., accelerated levels of adaptation, Proulx 1999; Lorch et al. 2003; but also possibly heightened risk of extinction, Doherty et al. 2003; Kokko and Brooks 2003). But sexual selection by itself may operate differently at different densities (for a review see Kokko and Rankin 2005). Here, we shall show that population consequences of sexual selection will strongly depend on whether females can adaptively alter their choosiness based on their current mating status, and also whether they can assess current mate encounter rates independently of their mating status.

THE MODEL

We assume that females, upon becoming receptive, encounter potential mates at a rate M until they die. The death rate of a female is constant over time, μ , which results in an average of M/μ potential males encountered during the life span of a female. Note that μ merely scales the time unit, and thus it is sufficient to vary M to investigate the various values of M/μ .

Males vary in their value as mates, that is, their ‘‘quality.’’ Male quality, q , is defined as the benefit that the female gains by using sperm of this particular male, and it may arise through various direct or indirect mechanisms (Kokko et al. 2003) such as improved attractiveness or viability or offspring, the probability that the sperm is fertile, or resources such as nuptial gifts. We assume that the quality of encountered males follows a normal distribution with mean Q and variance σ^2 , and, for simplicity, that the distribution does not vary over time. These assumptions mean that we avoid the complication that changes in mate preferences could arise from changes in the quality distribution of available mates (such as in, e.g., Johnstone 1997); the only change over time is the female’s own state.

A female begins laying eggs when she has mated once, and continues laying eggs at a constant rate until she dies. We consider two scenarios for female choice. In the first

scenario of *fixed mating behavior*, the female has a fixed acceptance threshold, a , throughout her life; she rejects any male whose quality falls below this threshold. (Whether she only mates once, or mates multiply if she encounters several males that exceed the fixed threshold, does not change the analysis: in either case the mean fitness of sires is the average of all qualities above her acceptance threshold.) In the second scenario of *plastic mating behavior*, the female strategy is specified by her acceptance thresholds a_1, a_2, a_3, \dots for her first, second, third (etc.) mating; any encountered males that fall below the threshold will be rejected. For simplicity, we assume that the threshold simply depends on the number of times the female has mated, not on the quality of the mates she has mated with.

To simplify calculations, we additionally make the biologically realistic assumption that after a sufficiently large number of matings, k , the female will use the same acceptance threshold for all further matings (i.e., $a_n = a_k$ for all $n > k$). In the following, we derive the equations for the more general case of plastic mating behavior, by which we mean that females are able to adjust their acceptance thresholds according to their own mating status, up to the k th mating. The fixed behavior model is then obtained simply by setting $k = 1$.

After her first mating, the female lays eggs fertilized by the first mate up to the point where she mates again. After the second mating, we need to express the paternity distribution. We assume that eggs that are laid after the n th mating ($n \geq 2$) will be fertilized by the n th male with probability p . For example, insects often show last male sperm precedence (Simmons and Siva-Jothy 1998), and we will then have $p > 1/2$ (although the model applies for values below $1/2$ as well). The eggs not fertilized by the last male will be fertilized according to the presence of sperm distribution prior to the last mating, which leads to the following paternity pattern for eggs laid after then n th mating (p_i denoting the paternity of the male who was the female’s i th mate):

$$\begin{aligned} p_n &= p \\ p_{n-1} &= (1 - p)p \\ &\vdots \\ p_2 &= (1 - p)^{n-2}p \\ p_1 &= (1 - p)^{n-1}. \end{aligned}$$

For example, if $p = 0.8$, an egg laid after the third mating ($n = 3$) will have been sired by the third male with probability $p_3 = 0.8$, by the second male with probability $p_{n-1} = p_2 = 0.2 \times 0.8 = 0.16$, and by the first male with the remaining probability 0.04.

We now need to derive the fitness of a female that uses acceptance thresholds $\{a_1, a_2, \dots, a_k\}$. We denote the expected quality (reproductive value) of sperm used by the female to fertilize her eggs after the i th mating by q_i . For the first mating this equals

$$q_1 = \frac{\int_{a_1}^{\infty} qf(q) dq}{\int_{a_1}^{\infty} f(q) dq} \quad (1a)$$

and for subsequent matings

$$q_{i+1} = p\tilde{q}_{i+1} + (1 - p)q_i, \text{ where}$$

$$\tilde{q}_{i+1} = \frac{\int_{a_{i+1}}^{\infty} qf(q) dq}{\int_{a_{i+1}}^{\infty} f(q) dq}. \tag{1b}$$

Here, $f(q)$ is the probability density function of the normal distribution with mean Q and variance σ^2 .

A female’s strategy should maximize her reproductive value (Houston and McNamara 1999). This is the expected value of all future offspring production, where “value” refers to the fact that offspring numbers may have to be weighted with offspring quality. In our case, reproductive value calculations should include expected offspring production weighted with the sire quality, q (here, high q may be interpreted as more offspring being produced due to direct fitness benefits—e.g., when males vary in how fertile their sperm is, or how big nuptial gifts they give—or alternatively, more valuable offspring, e.g., due to indirect genetic benefits).

Let us derive the female’s reproductive value after her i th mating. The female now gains fitness at a rate proportional to the current quality of sires of her offspring, equalling q_i . There are two ways to calculate the reproductive value, v_i , associated with this state. They both lead to the same conclusion, but it is instructive to follow both routes. The first method, outlined by Hårdling et al. (2003) and subsequently used, for example, by Schmeller et al. (2005) keeps track of all possible changes in state and the rates at which these changes occur. Reproductive values are expressed as a weighted sum of these rates, including reproduction. In our case, the female may switch to a different reproductive value by mating again (her $(i + 1)$ th mating); this will change her reproductive value from v_i to v_{i+1} . Remating happens at a rate Mh_{i+1} , where h_{i+1} is the fraction of males acceptable in the $(i + 1)$ th mating: $h_{i+1} = \int_{a_{i+1}}^{\infty} f(q) dq$. Thus, the possibility of remating increases a female’s reproductive value by $Mh_{i+1}(v_{i+1} - v_i)$. But she may also die (rate μ), and in this case she loses all current reproductive value, i.e. the possibility of dying causes reproductive values to change by $-\mu v_i$. In a continuous-time setting where rates of state changes remain constant over time, the reproductive value in a given state should not experience a net change over time (e.g., Hårdling et al. 2003; Schmeller et al. 2005). Therefore, we obtain

$$dv_i/dt = q_i + Mh_{i+1}(v_{i+1} - v_i) - \mu v_i = 0 \tag{2a}$$

Solving for v_i yields

$$v_i = \frac{q_i + Mh_{i+1}v_{i+1}}{\mu + Mh_{i+1}}. \tag{2b}$$

Another way to obtain eq. (2b) is to consider that a female’s reproductive value is the sum of all future fitness gains. Her current rate of fitness gain through offspring production is q_i , and she will carry on producing at this rate until she either dies or mates again; the expected duration before either event happens is $1/(\mu + Mh_{i+1})$. If she dies, no further offspring production is possible. But if she remates, which happens with probability $Mh_{i+1}/(\mu + Mh_{i+1})$, she will have an ex-

pected future reproductive output v_{i+1} ahead of her. Combining all these terms lead to eq. (2b).

Two values will have to be calculated separately: the reproductive value after the last mating (k th) at which the female can still change her acceptance threshold, and the value of virgin females. After the k th mating, the female has an expected lifespan $1/\mu$ ahead of her. Thus, after her k th mating her reproductive value (expected fitness) is proportional to $1/\mu$ and to q_k as calculated from eq. (1b):

$$v_k = q_k/\mu. \tag{3}$$

The reproductive values of virgin females (v_0) is calculated similarly as in (2b), but without any chance to produce current eggs,

$$v_0 = \frac{Mh_1v_1}{\mu + Mh_1}. \tag{4}$$

In other words, the expected reproductive output of a virgin is given by the probability of mating, $Mh_1/(\mu + Mh_1)$, times the expected reproductive output of a once-mated female.

Optimal female acceptance thresholds can now be calculated by numerically searching for the sequence $\{a_1, a_2, \dots, a_k\}$ that maximizes reproductive value at the beginning of the female’s mating history, v_0 . The numerical solution is based on the fact that any sequence $\{a_1, a_2, \dots, a_k\}$ leads to a unique value of v_0 . This is achieved by first calculating the sequence q_i (eq. 1b), after which v_k follows from (3), and then eq. (2b) can be used $k - 1$ times to obtain $v_{k-1}, v_{k-2}, \dots, v_k$. Finally, v_0 follows from (4). The remaining task is to find the sequence $\{a_1, a_2, \dots, a_k\}$ which yields the highest possible value for v_0 values; Matlab’s (MathWorks, Inc., Natick, MA) solver “fmins” was used for this, after the crude location of the solution was first found using a grid of four different values for each a_i , approximately spanning the range of male qualities. Several choices for starting values for the “fmins” solver always yielded the same optimum.

Three other quantities of interest are the mean quality of genetic sires, the proportion of all mate encounters that lead to rejection (a measure of choosiness at the behavioral level), and the proportion of females who die as virgins. The expressions for these are given in the Appendix.

RESULTS

Female Choosiness

Unsurprisingly, limiting the expected lifetime number of mates inspected (M/μ , Fig. 1) reduces female choosiness considerably. Let us first consider the scenario of fixed mating behavior (Fig. 1, horizontal lines with squares). In figures 1a–d, the mean number of males encountered drops from 1000 (Fig. 1a) to an average of one (Fig. 1d), and the proportion of males rejected falls from 0.96 to zero. This is an example where the wallflower effect influences female choice. It is, of course, not surprising that a female who on average only ever encounters one male is not choosy. It is more surprising that the wallflower effect influences female behavior already in the range of 100 to 1000 males encountered in a lifetime. Comparing Figure 1a and b, there is a clear reduction in female choosiness in the latter, even

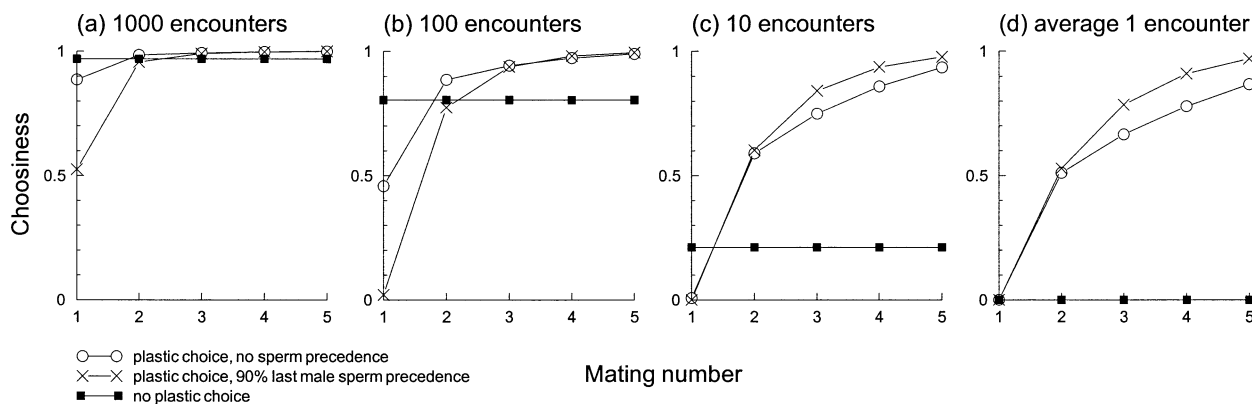


FIG. 1. Optimal strategies of females in their first five matings under different scenarios. “Choosiness” is defined as the proportion of males rejected in any encounter. Optimal strategies are calculated assuming that mating behavior is not plastic (squares), that it is plastic and there is no last male sperm precedence (open circles), or that it is plastic and the last male has 90% precedence (crosses). Other parameters: $Q = 10$, $\sigma^2 = 1$, $\mu = 1$. The mean number of lifetime mate encounters, M/μ , decreases from 1000 in the leftmost figure part to 1 in the rightmost part, which progressively reduces choosiness (due to the wallflower effect). However, if females can adaptively adjust their mating behavior, strong preferences are maintained by females who have already mated multiply (rightmost markers within each figure).

though, in Figure 1b, an average female still meets 100 males in her lifetime.

The situation changes somewhat if we assume that mating behavior is plastic, so that females may display different degrees of choosiness in different matings. Whether we assume last male sperm precedence or not, virgins are much less choosy than in the case of fixed behavior, whereas nonvirgins become typically much choosier (Fig. 1). The model predicts that choosiness should increase further with the number of matings a polyandrous female has experienced.

The difference between virgin and nonvirgin behavior is most striking when there is strong last male sperm precedence. Assuming 90% last male sperm precedence, the wallflower effect makes females much less selective in their first mating than later ones, even if females meet on average 1000 males in a lifetime. Virgins in this case reject only about 50% of males, compared to 90% in later matings (Fig. 1a). With no last male sperm precedence, virgin females accept close to 80% of males. If males are less readily available (Fig. 1b–d), the difference between virgin and nonvirgin behavior becomes even more striking.

The optimal strategy clearly reflects a solution to the trade-off between mate quality and quick commencement of reproduction. Virgins appear to use the first mating simply to be able to start laying eggs, and the purpose of later matings is then to improve mate quality. If there is strong last male sperm precedence, females can quickly commence reproduction and still not pay a high cost in terms of mate quality, by accepting any male as a virgin and being more choosy later. Most offspring will be sired by the males in these later matings, hence a large difference between virgin and nonvirgin behavior is expected. This also explains why strong choosiness can evolve in multiply mating females even if the average number of males encountered is extremely low (Fig. 1d; note that a mean number of lifetime encounters, $M/\mu = 1$, means that a female is at any time equally likely to die as she is to encounter another male). If a female finds several males, she is expected to be very choosy in the additional matings.

Consequences for Sexual Selection on Males: Constant Environment

How does female mate choice behavior translate into sexual selection on the male trait? Based on Figure 1, it is not straightforward to predict which case (fixed or plastic behavior, sperm precedence or not) leads to most intense selection. On the one hand, plastic behavior renders virgins much less indiscriminating in their mate choice, but on the other hand, plasticity also leads to stronger preference expression in nonvirgins. Given that virgins must necessarily be common in the mating pool (every female is once a virgin, while not everyone mates several times), one might think that the behavior of virgins dominates the mating system.

However, calculating the strength of selection on the male trait leads to the opposite conclusion (Fig. 2). Overall, sexual selection intensifies in populations where mate encounter rates are high, but at each mate encounter rate, the cases where virgins are least discriminating (plastic behavior and strong last sperm precedence) lead to strongest selection on the male trait (Fig. 2a). Last male sperm precedence is predicted to have little effect on observed probabilities of mate rejection (Fig. 2b), yet selection on male genotypes strengthens with last male sperm precedence, because last males who mate with nonvirgins experience much tougher screening effort by females. Plastic preferences by females allow them to reject more males (Fig. 2b) and enhance the operation of sexual selection (Fig. 2a), while at the same time reducing the time spent as a virgin and thus the risk of dying before any reproduction has commenced (Fig. 2c).

Consequences for Sexual Selection on Males: Altered Environment

In Figure 2, we assumed that plastic females respond to their own mating status and have evolutionary knowledge of the mate encounter and mortality rates, as the population has evolved in the environment where females are currently residing. An alternative assumption leading to the same outcome is that females may reside in environments that differ

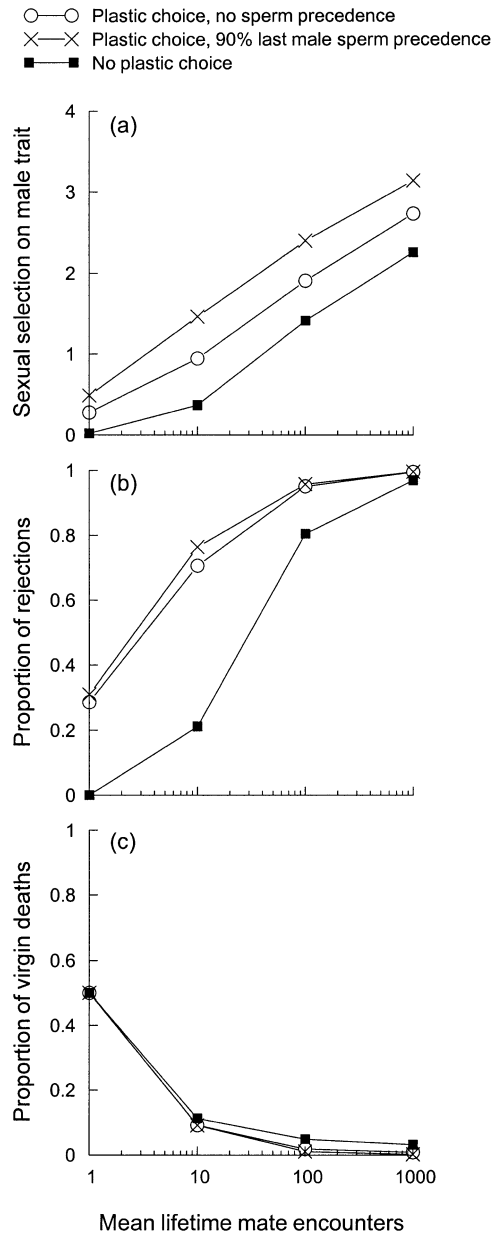


FIG. 2. Mate encounter rates M influence (a) the intensity of sexual selection, calculated as the difference between the mean quality of sires of all eggs produced and the mean quality of all potential males (and expressed in standard deviations of the male quality distribution), (b) behavioral choosiness: the proportion of mate encounters that lead to rejection by the female, and (c) virgin deaths: the proportion of females who die before they first mate. Females are assumed to follow the optimal strategy for each mate encounter rate M , given the plasticity and sperm precedence scenarios outlined in Figure 1 (squares, open circles, crosses). Other parameters as in Figure 1.

in mate encounter and mortality rates, but that they have evolved more advanced reaction norms than the simple response to one's own mating status, which was the limit of plasticity allowed by our model. More sophisticated adaptations could allow females not only to measure their own mating status, but also the relevant parameters of the environment: expected mate encounter and mortality rates. In

theory, one could then expect highly sophisticated reaction norms that respond both to a female's own mating status and, independently, to the expected mate encounter rate in the environment (and mortality), which will reproduce the results of Figure 2 (correct optimal behavior in each environment).

However, in many cases it may be doubtful whether reaction norms get to this high level of sophistication. For many systems, perhaps a more realistic assumption is that females either do or do not possess simple reaction norms that respond to their own mating status, and that they do not, in either case, possess reaction norms that track environmental changes in mate encounter rates. These two alternatives correspond to the fixed versus plastic behavior as defined in our model. The outcomes are described in Figure 3, where a species that has experienced an average lifetime encounter rate of $M/\mu = 100$ during the course of its evolution, currently finds itself in a situation where encounter rates are lower or higher. Compared with the optimal responses to low mate encounter rates (Fig. 2c), we find that many more females now die as virgins at reduced mate encounter rates, particularly so if there is no plasticity in choosiness (Fig. 3c). The preferences thus can be too strong, reducing female fitness and also population-level reproductive output, if females are maladapted in their current environment (e.g., edge of species range, novel environment, or lowered population density due to human influences).

But if female preferences are plastic such that they respond to their own mating status, an interesting response occurs at lowered mate encounter rate. Even if the evolutionary pressure for the plasticity was provided through individual random variation in mate encounters, rather than population-wide changes in mate encounter rates, plasticity produces an automatic response to lower mate encounter rates: the proportion of females dying as virgins (Fig. 3c) is not much larger than under optimal behavior (Fig. 2c). Instead of more females failing to reproduce, the consequence of lowered mate encounter rates is now a relaxation of sexual selection (Fig. 3a), as more females will only ever encounter few males, and they are relatively unselective in these first matings.

DISCUSSION

The Wallflower Effect as a Cause of Female Adaptations

Our model is the first one to quantitatively predict adaptive changes in choosiness in different situations of male availability and the female's own mating status. Our results show that a reduction in choosiness can be considered an adaptation, when its underlying reason is limited mate availability. The challenge is to realize that an adaptive change may have taken place when there is superficially nothing very striking in female behavior. In the case of no plastic choice of Figure 1b, females encounter potential mates frequently, and they are choosy, rejecting 80% of all males encountered. Nevertheless, their choosiness is much lower than it would be under "ideal" conditions (Fig. 1a) where potential males are still more frequently encountered, and this lowering is a sign that the wallflower effect is operating.

Interestingly enough, even fairly small risks of remaining unmated can significantly reduce female choosiness. If females encounter on average 100 males before dying ($M/\mu =$

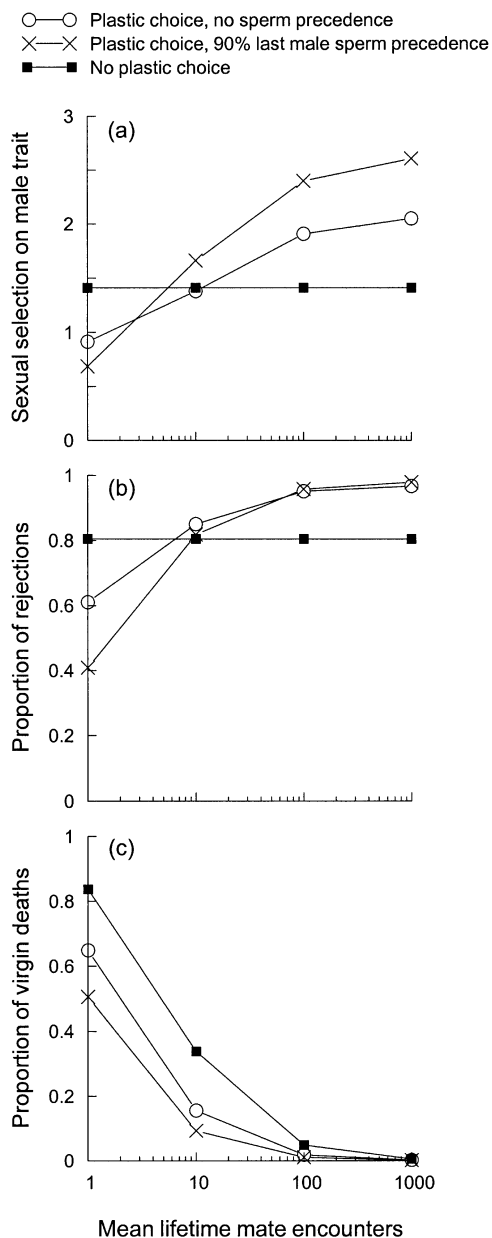


FIG. 3. Current mate encounter rates influence (a) the intensity of sexual selection, (b) behavioral choosiness, and (c) virgin deaths, all calculated as in Figure 2, but now assuming that females use strategies that have evolved at a different mate encounter rate ($M = 100$) than they currently experience ($M < 100$ or $M > 100$, as indicated on the x-axis). Other parameters as in Figure 1.

100), females run less than 1% risk of dying before encountering any male. In our example of plastic mate choice (Fig. 1b), this small risk is sufficient to make more than half of all females accept the male they first encounter, and if there is last male sperm precedence, all virgin females should accept every male. There are examples in which much larger fractions than 1% of females do remain unmated. Insects often feature high mating investment of males in the form of time or energy (Bonduriansky 2001), and there is evidence from other taxa as well that females can become sperm limited (Wedell et al. 2002; Preston et al. 2005). Several studies

document that sperm availability can then limit female reproductive success. In flightless and short-lived female bagworms, *Metisa plana*, the proportion of females that remained unfertilized varied from year to year between 6% and 18% (Rhainds et al. 1999); males of this species have limited fertilization capacity. Similarly, in the Glanville fritillary *Melitaea cinxia*, a substantial fraction of females are found unmated in small local populations (Kuussaari et al. 1998). In the moth *Epiphyas postvittana*, controlled laboratory conditions resulted in 13% of females remaining unmated, and 1:1 adult sex ratios were not sufficient to produce the highest possible fertilization rate (Danthanarayana and Gu 1991).

Under conditions of low densities or low mobility, females may be selected to actively improve mate encounter rates (Wickman and Rutowski 1999; Levitan 2004). Perhaps the most striking, albeit indirect, evidence for male limitation is the production of sex pheromones by female moths to attract males (Cardé and Bell 1995; Svensson 1996; Alexander et al. 1997). If females have immediate and unlimited access to males, it is very difficult to explain the evolution of potentially costly and dangerous pheromone production by females. Moths are generally short-lived, female mobility is often poor (Tammaru and Haukioja 1996; Rhainds et al. 1999), and the number of matings a male can perform can be limited by costs of sperm production or through trade-offs with male survival (Callahan and Cascio 1963; Svensson 1996). Among Lepidoptera (e.g., in families Psychidae, Geometridae, Lymantridae, Tortricidae, Pyralidae, Oecophoridae) and in many other insects, such as Thynnid wasps, females can be entirely wingless and thus are fully dependent on male searching activity. It therefore seems highly unlikely that females always have a choice among several males, even if males perform the majority of mate-location tasks (the asymmetric tracking hypothesis; Phelan 1992, 1997). It should also be noted that our model predicts changes in female behavior even if the risk of finding no mate at all is small: any delay in reproduction is costly if the life span is short. Moreover, we have not included factors such as declining offspring value with time, which can be important in some systems (mostly studied in birds; Rowe et al. 1994) and would hence intensify the hurry of females. In altered environments, the potential for sperm limitation appears stronger still, and may threaten population persistence: in saiga antelope *Saiga tatarica* harems, trophy hunting of males causes severe sperm limitation and reproductive collapse (Milner-Gulland et al. 2003).

Clearly, the wallflower effect has the potential to strongly limit the strength of female preferences. Thus, when Peretti and Carrera (2005) phrased the question why unseminated females should not be interested in finding the best male, the answer may be simple: the time and mortality costs of not being able to commence reproduction are powerful selective forces (see also Wickman and Rutowski 1999), and this can easily explain why first matings in particular should be indiscriminate. This is particularly true if there is last male sperm precedence, which makes it easy for females to later “trade up” in terms of sire quality (Jennions and Petrie 2000)—in which case the strength of selection on males may also become restored (see Consequences for Sexual Selection, below).

Despite the inherent difficulties involved in how to detect a possible wallflower effect that the evolutionary process may have already solved, we believe that with future work it should become possible to estimate it in nature. Our model makes several testable predictions. First, the reduction in choosiness with declining mate encounter rates (Fig. 1a–d) should be evident in between-population as well as between-species comparisons (see also Real 1990; Kokko and Johnstone 2002). There is some evidence that females are less choosy in low-density conditions than when they can compare plenty of males (for reviews, see Jennions and Petrie 1997; Kokko and Rankin 2005). In the Glanville fritillary, females do not discriminate against mating with brothers despite severe costs of inbreeding (Haikola et al. 2004). Haikola et al. (2004) interpreted this as an indication that a female in a small, isolated subpopulation may only have related males to mate with, and she may fail to mate at all if she rejects them. It would be extremely interesting to see if females that originate from high or low density populations respond in a different way to variations in current encounter rates.

Another prediction is that females should become increasingly choosy as they have mated more often: virgins should mate fairly indiscriminately to commence breeding, and later matings serve to improve offspring quality. There is data that females are less selective as virgins than later (e.g., Jennions and Petrie 2000; Lynch et al. 2005; Peretti and Carrera 2005), but the interpretation of such evidence is challenging, as alternative explanations such as increased experience of older females or accumulating mating costs need to be excluded. For example, Bateman et al. (2001) showed that female crickets, *Gryllus bimaculatus*, were less discriminating in their first mating than later, but the authors interpreted this in the context of experience: virgin females are also naive and have thus limited information on male size or quality. Future work should clearly compare the relative importance of information acquisition with the life-history effects of waiting for reproduction to commence (see also Sullivan 1994). Therefore, a more specific prediction from our model may be more useful: in species with strong last male sperm precedence, the difference between virgin and nonvirgin behavior should be enhanced. Unfortunately, suitable data is often lacking (e.g., Peretti and Carrera 2005).

Overall, we encourage researchers to take into serious consideration that female choosiness can respond adaptively to mating status, and in particular to ask if a difference in choosiness between virgin and nonvirgin females can be quantified to be optimal. Currently, there is a regrettable tendency to either exclude virgins from experiments because their indiscriminate behavior is considered to cloud the “real” preference (Houde 1997, p. 167), or to standardize mating history in the opposite way by using virgins only (critique provided by Peretti and Carrera 2005). Such practices can make us blind to a fundamentally important process determining the strength of sexual selection. Empirical tests should also shed light on the exact cues according to which females adjust their choosiness. Our model assumed that females only “remember” the number of times they have mated (together with the knowledge of acceptance thresholds used). In reality, it is not impossible that they keep track of the actual rather

than expected qualities of sires. Whether this alternative leads to stronger sexual selection than that outlined by our model remains to be investigated.

Our model does not consider costs of multiple mating, or of resisting male mating attempts. Instead, a female was assumed to remate if, and only if, it leads to a distribution of paternity that enhanced the quality of offspring produced. In nature, resistance (and choosiness) may combine with some effort by females to enhance mate encounter rates: Virgin female biting midges, *Culicoides nubeculosus*, produce pheromones but are also choosy, whereas nonvirgins resist male copulation attempts and have a reduced output of the pheromone (Mair and Blackwell 1998). These results are much in line with our theoretical predictions: If we interpret enhanced resistance as a stronger (more discriminating) preference (see Cordero and Eberhard 2003; Kokko 2005), and at least one mating is required for the female to have any fitness, it is clear that a virgin should be more eager to mate than an already mated female. If direct costs of mating play a strong role, we would expect stronger differences between virgins and nonvirgins, because only the former experience a net benefit through mating. If, on the other hand, mating brings about direct benefits, differences in choosiness might be weaker, although an exact study of this question would require modeling the fitness benefits of accumulating direct resources.

It is notable that most of the experiments on female choice have been conducted in a situation in which females have simultaneous choice over several males. In nature, however, sequential choice is often a much more realistic scenario, making the problem of female choice substantially more complex (Dombrovsky and Perrin 1994; Mazalov et al. 1996). Experimental work addressing this issue appears surprisingly scarce at present. Our results indicate that female preferences might be substantially weaker under sequential choice than under artificially induced direct comparisons between two or more potential mates. Moving towards more realistic studies of female choice should clearly take natural mate encounter rates into account (Peretti and Carrera 2005; Schäfer and Uhl 2005; Shackleton et al. 2005).

Consequences for Sexual Selection

The influence that the “wallflower effect” has on the strength of sexual selection is not straightforward. As such, an adaptive reduction in choosiness implies relaxed sexual selection. Because the reduction is predicted to be stronger when mate encounter rates are low, we predict that choosiness and the consequent selection on male traits should, overall, become much weaker in species that face difficulties finding mates and/or in which waiting for reproduction to commence is particularly costly. These conditions could arise through a variety of mechanisms, including low mobility, low population density, or short adult life span that makes females “hurried.”

However, it is also possible that mate-location difficulties select for plasticity in choosiness, which allows nonvirgins to maintain strongly expressed preferences. The result is that the behavior of nonvirgins largely determines selection on male traits, even if virgins mate very indiscriminately. It has

been long recognized that observed mating behavior does not necessarily accurately reflect sexual selection at the genetic level (Eberhard 1996; Birkhead and Møller 1998; Evans et al. 2003). Restoring sexual selection through multiple mating works particularly well if there is last male sperm precedence: it is then particularly easy for females to “have the cake” (mate indiscriminately to commence reproduction) and “eat it too” (most of the offspring will be fathered by later, more carefully chosen males, provided that the female is able to find another mate). For any given level of mate availability, the net effect is that plastic mate preferences leads to stronger sexual selection on male traits than nonplastic preferences, particularly if there is last male sperm precedence.

The picture changes again, however, if mate availability varies in a way that is not “anticipated” by the evolved responses by females. If populations suddenly experience new conditions but still use outdated reaction norms, sexual selection may now remain strongest if there is no plasticity. If female behavior remains fixed, they will “assume” much higher mate encounter rates than occur in reality, and many end up dying before mating. This obviously reduces population-wide reproductive output, while also maintaining strong sexual selection. Under phenotypic plasticity, their reaction is completely different: At low mate availability females mate much more indiscriminately because they encounter fewer males and thus end up less often using the highly selective rules of multiply mated females. As a consequence, sexual selection can become very weak, whereas rates of reproduction remain high. Plastic rules can thus perform well in novel environmental conditions; the above scenario did not require any new adaptation to take place (for a similar result in the context of optimal habitat choice, see Kokko and Sutherland 2001). Thus, the details of how female choice rules respond to novel environmental scenarios can strongly influence population persistence. Our lack of systematic knowledge of plasticity is regrettable, because there is a real possibility that mating behavior influences extinction risk, particularly if environmental conditions change (Møller and Legendre 2001; Bessa-Gomes et al. 2003).

Finally, we should note that our results on sexual selection on the male trait apply to traits used by females to screen males. If the wallflower effect is strong, we have shown that the emphasis of selection will move away from such “conventional” displays, but this may be replaced by selection for mate-location and “passive attraction” traits (Parker 1983). The possibility should always be kept in mind that males are selected to produce conspicuous signals simply to make it easy for time-limited females to find them quickly (Alatalo et al. 1998). The emphasis in current textbooks on female assessment of male displays could therefore be exaggerated for many species that do not meet the requirements for sensory capabilities and high mobility, that are necessary to perform efficient mate choice. Importantly, we have shown here that female choice for male quality is nevertheless not excluded: All that is required is multiple mating and simple plastic behavioral rules of females that do not require estimating current population density. Obviously, this provides one possible explanation for the evolution of multiple mating per se (Jennions and Petrie 2000).

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APPENDIX

A female dies as a virgin if death (rate μ) happens sooner than the first mating (rate Mh_1), thus the proportion of virgin deaths is $d_1 = \mu/(\mu + Mh_1)$. For $i \geq 2$, the probability that a female dies sooner than mates the i th time is

$$d_i = d_{i-1} + (1 - d_{i-1}) \frac{\mu}{\mu + Mh_i}.$$

The average time that a female spends between matings i and $i + 1$ is $t_i = (1 - d_i)/(\mu + Mh_{i+1})$. Note that this is smaller for later matings even if equally many males are accepted in later matings, because of a smaller probability that the female is alive and can

spend time in this state. In a random sample of individuals, the number of females who will accept a proportion h_i of males is proportional to t_i , therefore the overall proportion of rejected males is

$$P(\text{male rejected}) = 1 - \frac{\sum_{i=0}^{\infty} t_i h_{i+1}}{\sum_{i=0}^{\infty} t_i}.$$

A female who is between matings i and $i + 1$ ($i \geq 1$) uses sperm with expected sire quality q_i , thus the mean quality of sires is

$$\bar{q} = 1 - \frac{\sum_{i=1}^{\infty} t_i q_i}{\sum_{i=1}^{\infty} t_i}.$$