Behavioral Ecology Vol. 14 No. 5: 679–686
DOI: 10.1093/beheco/arg045

# Selection for multiple mating in females due to mates that reduce female fitness

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If females are unable to discriminate among males before mating, remating by females that store sperm may have evolved as a hedge against having only "costly" mates (less preferred males that reduce her fitness). However, the benefit of remating is not guaranteed because she can also mate by chance with another costly male. We devised a model to explain the evolution of female remating by representing female fitness as a function of the proportion of costly mates. We examined the effect of a linear, a concave-up, and a concave-down fitness function and found that only the latter favors the evolution of female remating. With a concave-down function, females mating with 50% costly mates have nearly the same fitness as do females with none. A biological interpretation for a concave-down function is that sperm from good males are better at competing with sperm from costly males or are more preferred by females. A concave-up function implies the reverse, whereas a linear function will occur when sperm are equally competitive. We review specific situations in nature that might produce a concave-down function and find evidence that sterility and intragenomic conflict are two phenomena capable of driving the evolution of female remating by our model. *Key words:* bet hedging, female remating, intragenomic conflict, segregation distorter, sperm choice, sperm competition. *[Behav Ecol 14:679–686 (2003)]*

Diverse hypotheses have been proposed to explain why females with the capacity to store sperm often mate with multiple males (hereafter called remating; Halliday and Arnold, 1987; Harvey and May, 1989; Hosken and Blanckenhorn, 1999; Keller and Reeve, 1995; Knowlton and Greenwell, 1984; Loman et al., 1988; Sherman et al., 1988; Yasui, 1998). A subset of hypotheses involve females hedging their bets against mating with costly males that they cannot always detect and avoid (remating will not evolve in this context if females can avoid mating with costly males). For example, females may remate to reduce costs due to the possible sterility of their previous mates (see Olsson and Shine, 1997). A more recent hypothesis proposes that females remate as a hedge against fitness costs arising from intragenomic conflict when they mate with genetically incompatible males (Zeh and Zeh, 1996.) Intragenomic conflict, from the female's perspective, can refer to any genetically based trait in males that reduces her fitness, and it can be attributed to various causes ranging from endosymbionts and transposable elements to inbreeding, genomic imprinting, and segregation distorters (e.g., genes that cause deviation from a one-to-one sex ratio [sex-ratio distorters] Haig and Bergstrom, 1995, Zeh and Zeh, 1996).

Both male sterility and intragenomic conflict can provide an advantage to female remating because having sterile mates and having mates with sex-ratio distorters, for example, can reduce female fitness. When females remate, they gain by diluting the fitness costs of such mates (referred to hereafter as costly males). Male sterility, at one extreme of the range of costs to females, occurs at relatively high frequency in some natural populations (e.g., 4.5% in the sand lizard, *Lacerta agilis* [Olsson and Shine, 1997]; and 20% in two stalk-eyed fly species of the genus *Cyrtodiopsis* [Wilkinson et al., 1998a]). Sterility is thought to arise from parasite infections (Alvarez, 1993; Tagashira and Tanaka, 1998) and certain rearrangements of the sex chromosomes (McKee et al., 1998). There are obvious fitness costs for females who mate only with a sterile male. Several authors have proposed that females remate to avoid inviable offspring (but see Birkhead and Møller, 1982; Gibson and Jewell, 1982; Lifjeld, 1994; Wetton and Parkin, 1991). Olsson and Shine (1997) have shown that matings with sterile males can result in females laying eggs that do not develop. So there is some evidence that male sterility can negatively affect female fitness. As mentioned above, females can also incur less-severe fitness costs when mating with genetically incompatible mates such as males carrying sex-ratio distorter genes (Haig and Bergstrom, 1995; Zeh and Zeh, 1996) or males that are closely related to the female (Stockley et al., 1993; Zeh and Zeh, 1996; Tregenza and Wedell, 2002; for other examples, see Zeh and Zeh, 1996 and Tregenza and Wedell, 2000).

There have been three previous attempts to model the advantages of female remating for reducing fitness losses owing to mating with specific kinds of costly males; however, no general model exists. Haig and Bergstrom (1995) proposed a model based on remating to dilute the negative fitness effects of mating with males carrying sex-ratio distorters. This model derives the probability of choosing sperm carrying the distorter allele if a female mates once versus if she can choose from the sperm of all males in the population. Based on these two extremes, they conclude that female remating reduces the probability of choosing distorter sperm whenever distorter alleles pleiotropically reduce competitive ability of ejaculates in which they occur, leading to selection for increased female remating. Females will seldom, if ever, be able to choose sperm from among all males in a population. For this reason, the Haig and Bergstrom model is better at explaining the maintenance rather than the origin of female multiple mating, because it does not show an advantage to mating with two mates over a single mating. By using a graphical model based on variance discounting, Hosken and Blanckenhorn (1999) model the evolution of female remating to reduce inbreeding depression. These

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Received 11 April 2002; revised 9 November 2002; accepted 27 November 2002.

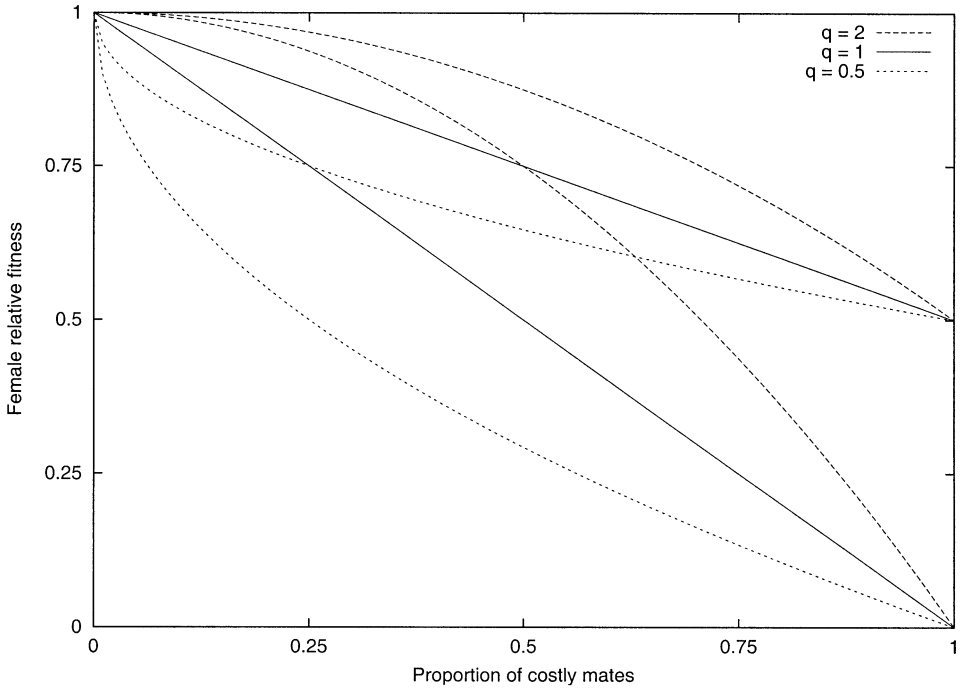


**Figure 1**
Female relative fitness as a function of the proportion of "costly" males ($n/m$) (graphical representation of Equation 1 for three values of $q$). The two sets of curves represent a minimum relative fitness ($a$) of 0.5 (top set) or zero (bottom set). Within each set of curves, there is a concave-down curve ($q = 2$), a linear curve ($q = 1$), and a concave-up curve ($q = 0.5$).

authors conclude that female remating will evolve if the relationship between female fitness and relatedness is increasing more than linearly (i.e., positive second derivative). Both of these models lack generality because they are based on specific types of costly males. A third model by Colgrave et al. (2002) examines genetic incompatibility more generally, comparing this force for the evolution of remating to selection for "good genes" choice. However, they limit their analysis to one mate versus two mates, missing advantages to remating after the second mating. The purpose of our article is to present a general model for the evolution of female remating in response to costly mates by modeling the way female fitness depends on the proportion of costly mates. This approach has been largely ignored in previous theoretical work on the *advantages* of female remating (but see Wu, 1983b).

The benefit of remating is not guaranteed because females can also mate by chance with another costly male (Haig and Bergstrom, 1995, Zeh and Zeh, 1997). With a simple model, we demonstrate this point by showing that female remating can evolve as a hedge against costly mates only under a restricted set of conditions: a female's relative fitness must be a concave-down function of the proportion of her mates that are costly. In other words, females mated to intermediate proportions of costly mates must have a fitness similar to females without such mates. We show how our model relates to three other models of the evolution of remating in response to costly males. We also discuss the effect on our results of both the postcopulatory assessment of male quality by females and subsequent selective sperm use (sperm choice, a mechanism of cryptic female choice; Eberhard, 1996), and of competition among sperm from a female's different mates (sperm competition). Finally, because there is recent interest in generic costs of mating that decrease fecundity by reducing survival probability (e.g., Chapman et al., 1995), we include a generalization of our model for this kind of cost.

## THE MODEL

We are interested in understanding whether female multiple mating can evolve as a way to reduce the effects of mating with what we have called costly males. To start, we need a model of female fitness in terms of the proportion of her mates that are costly (as opposed to good). The simplest model is a linear decrease in fitness (i.e., lifetime reproductive success) with increased proportions of costly mates. Alternatively, we can imagine that as the proportion of costly mates increases, female fitness decreases either more slowly or more quickly than the linear case. Once we have a female fitness function that includes these three possibilities, if we assume that females randomly encounter both costly and good males (in proportion to their frequency in the population), we can calculate the average fitness of females with various numbers of mates. Then we can compare the average fitness of females with $m$ mates to those with $m + 1$ mates (for a range of $m$) to see whether remating increases female fitness for a given kind of fitness function.

We can define the relative fitness of a female that mates with $m$ mates, of which $n$ are costly, as $f(n, m)$. For example, in the case of remating to avoid sterility, female fitness ranges from one when she mates with only fertile males to zero when she mates with only sterile males. To define the range of possible fitness with different proportions of costly mates, we can use the equation

$$f(n, m) = 1 - \left(\frac{n}{m}\right)^q (1 - a), \qquad (1)$$

where $q > 0$ (Figure 1; as in Charnov, 1979; Laguérie et al., 1993). The variable $q$ determines the shape of the female fitness function (i.e., how her fitness is affected by the proportion of costly mates she has [$n/m$]). It can be affected by sperm competition and sperm choice by females. When $q < 1$ the relationship is concave-up, when $q = 1$ the relationship is linear, and when $q > 1$ it is concave-down. The farther $q$ is from one, the more concave the function is and the more an intermediate proportion of sterile mates resembles either the all-fertile mate case for concave-down or the all-sterile male case for concave-up curves. The less-desirable mate produces some relative fecundity $0 \leq a < 1$, which sets the lower limit on female relative fitness ($a = 0$ for sterile mates).

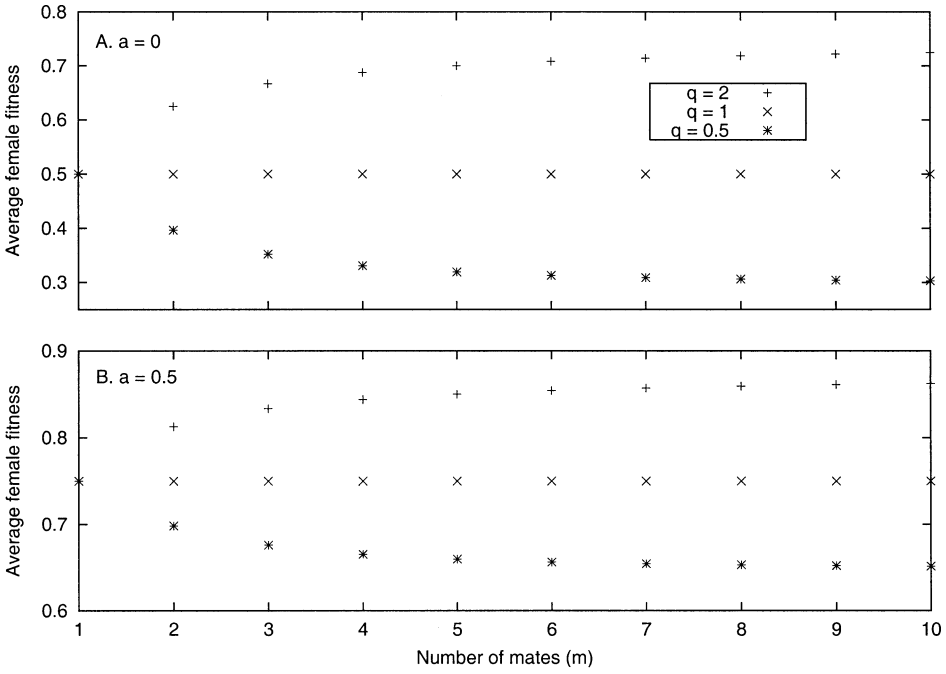


**Figure 2**
Average female relative fitness as a function of the number of mates ($m$) when the minimum relative fitness ($a$) is zero (A) or 0.5 (B). The proportion of costly males ($s$) is set at 0.5. In both A and B, the top set of points is for the case in which the exponent ($q$) of the female relative fitness function (see text) is two, the horizontal set is for $q = 1$, and the lower set of points is for $q = 0.5$.

If we assume that females randomly encounter males of both types, when the probability of a female mating with costly males is $s$ ($0 < s < 1$), the average fitness of females with $m$ mates is

$$\overline{W}_m = \sum_{n=0}^{m} f(n, m)g(n, m, s), \tag{2}$$

where $g$ is the binomial distribution $(m!/(n!(m-n)!))s^n(1-s)^{m-n}$. If females cannot discriminate between male types, the variable $s$ represents the proportion of costly males in the population. Alternatively, if females can assess whether potential mates are costly and reject them as mates, $s$ represents a function of the proportion of costly males and the probability of failing to properly assess male type (e.g., $s = [b(1-c)]/[b(1-c) + (1-b)d]$; where $b$ is the proportion of costly males, $c$ is the probability of recognizing and not mating with a costly male, and $d$ is the probability of recognizing and mating with a normal male). When $s$ equals either zero or one, there is no advantage to remating because all males have equal fitness.

We are interested in which types of relative fitness function give an advantage to remating. This amounts to finding what values of $q$ give a positive first derivative for Equation 2 with respect to $m$. Because we were unable to find an exact analytical solution to this problem, we derived an approximation for Equation 2 by using a Taylor series expansion. Numerical solutions of Equation 2 were used to verify that error from this approximation does not affect our conclusions.

## RESULTS

We were unable to obtain an exact analytical solution of Equation 2 to solve $\partial\overline{W}_m/\partial m > 0$ for $q$ when $m \geq 1$. An approximation of $\overline{W}_m$ is possible by using the first and third terms of the Taylor series expansion of $f$ evaluated at the mean number of costly mates ($\overline{n}$) for a given $m$ (the second term is zero when you evaluate the expansion at the mean because it contains $[n - \overline{n}]$; Hilborn and Mangel, 1997; 51) as follows:

$$\overline{W}_m \approx f(\overline{n}, m) + \frac{\mathrm{Var}(n)}{2} f''(\overline{n}, m), \tag{3}$$

where (because female mate types are assumed to be binomially distributed) $\overline{n} = ms$ and $\mathrm{Var}(n) = ms(1-s)$, and where $f''(\overline{n}, m) = (q(1-q)\overline{n}^{(q-2)}(1-a))/m^q$. This yields

$$\overline{W}_m \approx \overline{W}^*_m = 1 - s^q(1-a) + \frac{q(1-q)s^q(1-s)(1-a)}{2ms}, \tag{4}$$

where * denotes the approximation. If there is an advantage to remating, then the partial derivative of Equation 4 with respect to $m$ should be positive.

$$\frac{\partial\overline{W}^*_m}{\partial m} = \frac{(1-s)s^q(1-a)q(q-1)}{2m^2 s} \tag{5}$$

is positive when $q > 1$ and is negative when $0 < q < 1$. So for all $m \geq 1$, when $q > 1$, fitness increases with $m$ and remating is advantageous. In other words, it is only advantageous for females to remate when they have a concave-down fitness function.

In addition to the qualitative effect of $q$ just described, $q$ and $m$ have quantitative effects as well. The amount females gain by remating increases as $q$ increases above one (Equation 3 increases as $q$ increases above one). There are also diminishing returns from remating many times to avoid costly mates (seen by showing that $\partial\overline{W}_m/\partial m^2 < 0$ when $q > 1$; and shown numerically in Figure 2). This is because as $m$ increases, one extra mate brings a smaller possible change in the proportion of mates with the costly phenotype ($n/m$). When a female has mated once ($m = 1$), her proportion of costly mates is either zero or one, and an additional mate will either shift her to 0.5 or leave her where she started. When a female has six mates ($m = 6$), she can have seven possible $n/m$ ratios, ranging from zero to one. An extra mate can only shift her a fraction less than one-seventh up or down (as opposed to one-half for $m = 1$). So the maximum change in the $n/m$ ratio decreases with increasing $m$, and this translates into smaller changes in female relative fitness with increasing $m$. Finally, the magnitude—and interestingly the symmetry—of the fractional increase or

**Table 1**

**Asymmetric changes in *n/m* ratio and relative fitness owing to remating starting with either three out of six or two out of six costly mates**

| | Start | | | Start | | |
|---|---|---|---|---|---|---|
| | 3/7 | 3/6 | 4/7 | 2/7 | 2/6 | 3/7 |
| Change in $n/m$ ratio | −0.071 | | 0.071 | −0.048 | | 0.095 |
| Change in fitness with | | | | | | |
| $q = 0.5$ | 0.052 | −0.049 | | 0.043 | −0.077 | |
| $q = 1$ | 0.071 | −0.071 | | 0.048 | −0.095 | |
| $q = 2$ | 0.066 | −0.077 | | 0.029 | −0.073 | |

Fitness changes were calculated by using Equation 1 (see text). The two changes in fitness for a given $q$ must sum to one-seventh.

decrease in the $n/m$ ratio depends on how close to 0.5 a female is before remating. For example, if a female has three costly mates out of six, she will have either three or four out of seven after remating—a change of 0.071 (or one-half of one-seventh) either up or down. On the other hand, if she has two costly mates out of six before remating, she will end up with either two or three costly mates out of seven. Two out of seven represents a decrease of 0.048 in the proportion of costly mates, whereas three out of seven represents an increase of 0.095. This asymmetrical change in the $n/m$ ratio translates into asymmetry in fitness gains and losses (Table 1). As a result, there is a cost-benefit ratio asymmetry associated with remating for individual females that depends both on the ratio of $n/m$ and on $q$ (Table 1). This asymmetry could have important consequences for modeling female remating decisions. From the quantitative effects of $q$ and $m$, we turn to the effects of $s$.

For the case of sterile males, the largest increases in average relative fitness from remating come when the probability of mating with costly males ($s$) is nearly 100% (see upper curve [$a = 0$] in Figure 3). This means that when females cannot detect costly mates, the strength of selection on females increases with the frequency of sterile males in the population. If they can assess mate type before mating, the strength of selection on females increases with the product of the frequency of sterile males and the proportion of failed assessments a female is likely to make. Female remating is less likely to evolve when the costly male phenotype is rare or when female assessment abilities are good. However, when the probability of mating with a sterile males is 100% ($s = 1$; for whatever reason), there is no advantage to remating.

For the case of mates that are less costly than are sterile males ($0 < a < 1$; e.g., males with sex-ratio distorters), remating will still increase relative fitness only when fitness functions are concave-down. However, now remating increases relative fitness most when $s$ is intermediate (Figure 3). This means that female remating is less likely to evolve when costly males are either rare (or when these males are rare and assessment is good) or common (or when these males are common and assessment is poor). If $a > 0$, when $s$ is above a certain threshold (approximately 0.59 in lower curve of Figure 3), the fitness gains that females get from remating begin to decrease. The threshold is determined by the fitness of females who mate only with the least fit males ($a$) and by the asymmetry between the gains and losses in relative fitness resulting from remating (discussed above).

### Generic cost to mating

Here we consider a generic cost to mating that reduces the probability of survival by a fixed amount for each mating. Examples of this kind of cost include a constant risk of predation with each mating (Rowe, 1994) or a fixed reduction in female lifespan with each mate (Chapman et al., 1995) that reduce female lifetime reproductive success. Average female relative fitness for a given number of mates would then be

$$\overline{W}_m = h(m)\left(\sum_{n=0}^{m} f(n,m)g(n,m,s)\right), \qquad (6)$$

where $f(n, m)$ and $g(n, m, s)$ are as in Equation 2 and where $h(m)$ is either the probability of surviving $m$ matings or the proportion of an average unmated female's lifespan. We define $h(m) = 1 - (m/M_{\max})$, where $M_{\max}$ is some arbitrary maximum number of mates (so that $\overline{W}_m$ is still relative fitness; other definitions are possible).

To find the conditions for the evolution of female remating, we can substitute the approximation from Equation 4 for the sum in Equation 6 and find the partial derivative with respect to $m$. After rearrangement this yields

$$\frac{\partial \overline{W}^*_m}{\partial m} = \frac{(1-s)s^q(1-a)q(q-1)}{(2m^2 s)} + \frac{[s^q(1-a)-1]}{M_{\max}}. \qquad (7)$$

The left-hand term is identical to Equation 5. Because $0 < s < 1$ and $0 \le a < 1$, the right-hand term in Equation 7 is always negative. This term represents the additional constraint on the evolution of female remating imposed by the generic cost to mating. There is an advantage to remating whenever Equation 7 is positive, which can occur only if the left-hand side is greater than the right *and* if the left-hand side is positive. These conditions are met whenever $q > 1$ and

$$\frac{M_{\max}}{2m^2} > \frac{s}{(1-s)q(q-1)}\left(1 - \frac{1}{s^q(1-a)}\right). \qquad (8)$$

So even with the generic cost of mating, remating will still only increase female fitness when female fitness functions (with respect to $n/m$) are concave down. The additional constraint imposed by the generic cost to mating means that there is now an optimal number of mates

$$m_{opt} = \sqrt{\frac{M_{\max}(1-s)q(1-q)}{2s\left(1 - \frac{1}{s^q(1-a)}\right)}}. \qquad (9)$$

### Comparison to previous models

The models of Haig and Bergstrom (1995) and Colgrave et al. (2002) can be seen as special cases of our more general model. Haig and Bergstrom (1995) derived the probability of choosing sperm carrying a sex-ratio distorter for females who mate once ($p_1 = ks$, where $s$ is the proportion of males heterozygous for the distorter allele [homozygotes die] and $k$ is the fraction of sperm from these males with the distorter allele) and for the case in which a female could choose from the sperm of all the males in the population ($p_\infty = (ks[1-d])/(1-sd)$, where $[1-d]$ is the concentration of viable sperm in carrier male ejaculates relative to normal male ejaculates [d in $(-1, 1)$]). If you assume that female relative fitness is equal to one minus the probability of choosing a sperm carrying a driving allele, it is possible to derive an expression of female fitness for arbitrary numbers of mates:

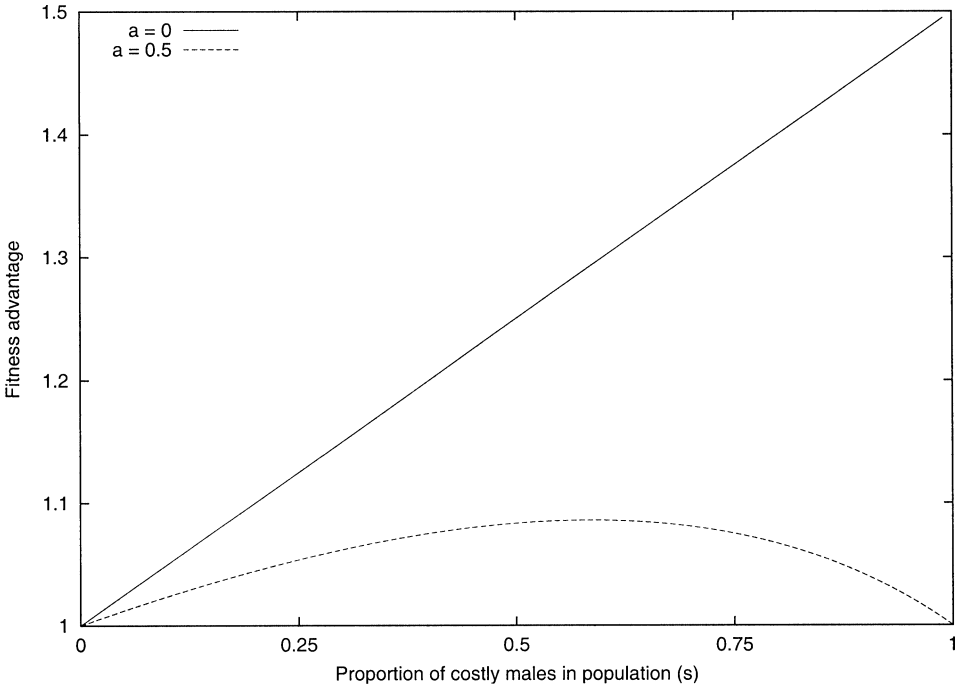


**Figure 3**
Proportional advantage to remating (fitness advantage, $\overline{W}_{m+1}/\overline{W}_m$) as a function of the proportion of costly males in the population for the case in which females mate twice relative to once ($m = 1$). For both curves, $q = 2$. The upper curve represents the minimum relative fitness ($a = 0$), and the lower curve is for $a = 0.5$.

$$\frac{kn(1-d)}{m\left(1-\frac{nd}{m}\right)}, \tag{10}$$

where $n$ and $m$ are as defined earlier. This equation turns out to be another way of generating concave-up and concave-down relative fitness functions. When $d > 0$, the function is concave-down, and when $d < 0$, the function is concave-up. In agreement with the results from our more general model, Haig and Bergstrom (1995) found that when $d > 0$, there will be selection for female remating. We are able to show that this is true for arbitrary numbers of mates, rather than just for the extreme case in which a female chooses sperm from among all males. The Haig and Bergstrom (1995) model is genetically explicit and includes an analysis of sex-ratio distorter gene frequency evolution.

Colegrave et al. (2002) compare the fitness of females that mate once to those who mate twice to see whether remating can reduce the cost from mating with genetically incompatible mates. They also consider the effects of female choice for overall genetic quality, but we ignore that part of their model here for simplicity. A general expression of female fitness for their model is possible, though complicated:

$$n = 0; \quad C^m, \tag{11a}$$

$$1 \le n \le m-1; \quad \frac{m!}{n!(m-n)!}(1-C)^n(C)^{m-n}(m-n)p + n(1-p)(1-I), \tag{11b}$$

$$n = m; \quad (1-I), \tag{11c}$$

where $C$ is the probability of a mate being compatible, $p$ is the proportion of a female's eggs fertilized by compatible males (degree of postcopulatory choice), $I$ is the reduction in offspring relative fitness from incompatible male sperm, and $n$ and $m$ are as in our model. Their formulation will yield something between a linear and a concave-down relationship, so that remating will evolve only if females can exert some postcopulatory choice ($0 < p \le 1$; numerical results not shown). This agrees with the results from our more general model.

Our model is designed for binary situations in which mates are either costly or not. Hosken and Blanckenhorn (1999) consider a variable range of costliness of mates—a range of relatedness with a corresponding range of inbreeding depression. Rather than consider the situation in which there are two classes of males, they allow males to be variably related to a focal female. They show that the shape of the relationship between relatedness and fitness will determine whether female remating increases average female fitness. They conclude that female remating will evolve only if there is a relationship between fitness and increased relatedness that decreases toward an asymptote. However, their conclusion hinges on the hidden assumption that the distribution of relatedness of potential mates is uniform or normal. In other words, males of all levels of relatedness are assumed equally abundant or normally distributed about some mean. They present no data to support this assumption. To devise a model like ours for the case of a range of costly males, it would be necessary to know (or make assumptions about) the distribution of relatedness of potential mates. This would allow the derivation of an expression for average female fitness in a way that is analogous to our Equation 2. We leave this for a separate article.

## DISCUSSION

For female remating to evolve as a hedge against costly mates, females with intermediate proportions of costly mates must have relative fitness similar to that of females with only good mates. In other words, the function relating female relative fitness to the proportion of costly mates (Figure 1) must be concave-down. A linear or concave-up relationship will not result in an advantage to multiple mating. This result agrees with the results of Haig and Bergstrom (1995) and Colegrave et al. (2002). The result holds true even when there is a generic cost to female fitness for mating owing to increased predation risk or reduced lifespan (agreeing with Colegrave et al., 2002). The generality of this result makes it interesting to speculate about what situations in nature would result in females having a concave-down fitness function. It turns out that such a function is likely whenever costly male sperm are

either less competitive at fertilizing eggs or are less preferred by females regardless of whether female fitness costs come from sterility or less costly genetic incompatibility. First, we examine two categories of mechanisms for producing male sterility and ask whether they are likely to produce concave-down female fitness functions. Next, we consider mates that carry smaller fitness costs. Finally, we focus on the evolution of female postcopulatory assessment of mate quality and consider some examples from nature.

### Fitness gains with sterile mates

Little is known about what produces male sterility (even hybrid sterility in matings between related species; Wu et al., 1996). Here, we distinguish two categories of mechanisms that are likely to have different consequences for female fitness: (1) males with no sperm or sperm that do not function properly, and (2) males with sperm that fertilize eggs that then fail to develop. Type 1 males do not reduce the number of eggs available to the sperm of a female's other mates, whereas type 2 males essentially "kill" eggs, removing them from the pool of available eggs. The first type of male sterility may result from parasites that prevent normal sperm formation (parasitic castration; Alvarez, 1993; Tagashira and Tanaka, 1998), the depletion of sperm stores (Walker, 1980), or the presence of mutations that affect either sperm motility (e.g., immobile or sticky sperm) or the ability of sperm to penetrate the outer membranes of the egg (McKee et al., 1998). Type 2 sterility may result from certain kinds of chromosome rearrangements that can interfere with meiosis, leading to nondisjunction and interrupted development (McKee et al., 1998). It may also result from cytoplasmic incompatibility induced by mutually incompatible strains of *Wolbachia* bacteria in the male and female (Werren, 1997). The well-known phenomenon of sterility in the offspring produced by hybrid matings may fall under either type 1 or type 2 sterility. We consider separately the likelihood of each type of sterility producing concave-down fitness functions.

If a female mates with one sterile and one normal male (in no particular order) is her fitness function likely to be concave-down? With type 1 sterility, the answer is very likely to be yes. The fertile mate should provide a female with all (or nearly all) the sperm she needs to fertilize her eggs, so her fitness should be close to that of a female with only one normal mate. The sperm of males with type 1 sterility simply do not compete for fertilizations, provided these males do not displace 50% or more of the normal mate's sperm. This much displacement is unlikely when castrated or otherwise depleted males must use their own reduced supplies of sperm and seminal fluid to force out older ejaculates. Even when males use other mechanisms for sperm displacement (e.g., the modified penis of many odonates; Waage, 1984), it seems unlikely that sterile males will consistently displace most of the normal male's sperm. Type 1 sterility is therefore very likely to cause a concave-down fitness function and to select for the evolution of female remating.

With type 2 sterility, a concave-down fitness function seems less likely. For type 2 sterile-male sperm to be less successful at fertilization, the genes underlying postfertilization developmental failure would have to have negative pleiotropic affects on sperm competitive ability (or be less preferred by females). Otherwise, a female that mates once with each kind of mate will have, on average, a relative fitness that is halfway between that of females who mate with either normal or sterile mates only, resulting in a linear fitness function. Something as simple as type 2 sterile males producing fewer sperm would be enough to allow a concave-down fitness function. If type 2 sterile-male sperm are not less plentiful (or less preferred), then type 2 sterility is unlikely to select for female remating.

### Fitness gains with less costly mates

Thus far, we have only discussed the effects on female fitness of having sterile mates. What about situations in which females get some low level of fitness from the lower quality mates (e.g., sex-ratio distorters, inbreeding or other forms of intragenomic conflict)? In these cases, a concave-down fitness function is again likely only when the sperm of costly mates have lower competitive ability (or are less preferred by females). Consider once more a female who mates with one normal and one costly mate in no particular order. If she does not prefer one male's sperm and there is no sperm competition, on average, her relative fitness will be halfway between the fitness of females who mate with either a costly mate only and a normal mate only, resulting in a linear fitness function: $0.5(a + 1)$. On the other hand, if costly males are not as capable of displacing the sperm of previous mates, giving them lower fertilization success, a concave-down female fitness function is expected. In *Drosophila pseudoobscura* (Beckenbach, 1978; Wu, 1983a) and in the stalk-eyed fly, *Cyrtodiopsis whitei* (Presgraves et al., 1997), the sperm of males with sex-ratio distorters fertilize fewer offspring than do nondistorter males (as little as half as many). Sex-ratio distorters and other segregation distorters that operate by reducing sperm numbers will therefore generally be expected to result in concave-down fitness functions and to select for female remating (the same conclusion reached by Haig and Bergstrom, 1995). Other sorts of costly males such as males with sexually transmitted parasites or males of related species whose sperm or genitalia interfere with conspecific fertilization would be expected to produce concave-up fitness functions and not to select for female remating. Recent empirical evidence supports the evolution of female remating in response to genetic incompatibility generally (Newcomer et al., 1999) and inbreeding depression specifically (Tregenza and Wedell, 2002).

### Postcopulatory assessment of mates by females

Our model does not consider precopulatory assessment because if females can assess costly males and avoid mating with them, remating is not expected to evolve. Assessing a mate's genetic compatability may be easier after mating than before mating because pleiotropic effects of alleles that cause genetic incompatibility may be easier to detect in the ejaculate or on the sperm inside the female reproductive tract. If mating carries a generic cost, females could remate only when their current mates are assessed to be costly. Once a good mate is found, females could selectively use or remove the sperm of certain mates. There is growing evidence that females control sperm displacement (several chapters in Birkhead and Møller, 1998; Smith, 1984). Females may use anatomical or physiological sperm-precedence adaptations to prefer the sperm of certain mates, or they may more actively use the sperm of particular mates for fertilizing eggs (sperm choice; Arthur et al., 1998; Ward, 1993; Werren, 1997). Either of these modes of preference can produce a concave-down fitness relationship.

Based on the potential strength of selection, postcopulatory assessment and discrimination by females seems most likely to evolve to detect type 2 sterility, in which costly male sperm are "killing" eggs; next most likely for less costly types of mates (such as sex-ratio distorters), in which fitness effects should be less drastic; and least likely for type 1 sterility, in which, unless females mate only with sterile males, fitness effects are expected to be small. We therefore predict that when assess-

ment occurs, it will most commonly involve female assessment of mates (or their sperm) that will result in the developmental death of eggs. Almost no data exist to test this prediction; however, we will discuss evidence (in a stalk-eyed fly) of assessment that may involve the detection of sex-ratio distorter mates using a morphological correlate (Wilkinson et al., 1998b).

### Evidence from nature

Two species of Malaysian stalk-eyed flies provide a useful pair of examples to consider the relevance of what we have discussed so far. In two species (*Cyrtodiopsis dalmanni* and *C. whitei*), females will mate multiple times in the laboratory (Lorch et al., 1993, Wilkinson et al., 1998a) and in the field (up to 20 times in 10 days; Wilkinson et al., 1998a). Sex-ratio distorters in both species cause female-biased sex-ratios (Presgraves et al., 1997), and both species suffer high levels of male sterility (Wilkinson et al., 1998a). At least some of the instances of male sterility could be owing to a lack of sperm transfer (31% of 83 laboratory-reared *C. whitei* males tested did not transfer sperm to a virgin female; Lorch et al., 1993), and male *C. dalmanni* with the sex-ratio distorter produce fewer sperm (maybe as little as half; Presgraves et al., 1997). Finally, Wilkinson et al. (1998b) have suggested that females may be using male eye-span to assess the presence of modifier genes that will ameliorate the effects of X-linked sex-ratio distorter genes.

There is support in these species for the evolution of remating as a hedge against mating with costly males. As mentioned earlier, when considering normal and sterile males, female fitness functions for mates that fail to transfer sperm (type 1 sterility) are likely to be concave-down, favoring the explanations we have been discussing. Males in these two species transfer sperm in a spermatophore (Kotrba, 1990), and these structures may make it difficult for females to detect the absence of sperm at least initially. If a female's normal mates transfer larger numbers of sperm, we would expect the female fitness functions to be concave-down. Female *C. whitei* can expel spermatophores after a variable amount of time (Kotrba, 1991), which would give them a mechanism for discriminating against particular mates by not absorbing their sperm, though there is no evidence currently that they use this mechanism to prefer certain mates. The fitness function for normal males and males with sex-ratio distorters will also likely be concave-down because distorter males will have half the sperm, reducing their ability to compete for fertilizations. Taken together, both of these types of costly mates are likely to result in a fitness function for females that is concave-down. We also note that, to the extent that multiple mating reduces the deleterious effects of sex-ratio distorters, it can be implicated in explaining the equilibrium levels of sex-ratio distorters in several species in which it is found in the field (Presgraves et al., 1997).

The evolution of multiple mating in stalk-eyed flies is probably only partly explained by the benefits of reducing the effects of either sterile mates or mates carrying sex-ratio distorters. At least for *C. whitei*, female sperm storage organs do not seem to fill up in as many as four matings (Lorch et al., 1993). Females may therefore be remating, at least in part, to ensure that they have adequate numbers of stored sperm. Both *C. whitei* and *C. dalmanni* have higher remating rates and smaller spermatophores than does a similar sized congener, *C. quinqueguttata*, supporting the hypothesis that remating may be intended, in part, to increase sperm stores (Kotrba, 1996). However, both *C. whitei* and *C. dalmanni* mate up to 20 times in 10 days in the field (Wilkinson et al., 1998a)—a seemingly large number of matings just to fill sperm storage organs or keep them full.

Are there other animals in which we might expect to see concave-down fitness functions? The sand lizard, *Lacerta agilis*, seems a likely candidate. As mentioned earlier, male sterility in the wild can be relatively high (4.5%). This example seems to fit into what we have called type 2 sterility because there is evidence that inviable eggs are the result of mating with sterile males (Olsson and Shine, 1997). If sterile male sand lizards transfer fewer sperm to females, if these sperm are less competitive or preferred, or if these males are less effective at sperm displacement, we would expect a concave-down fitness function for females. Olsson and Shine (1997) conclude that although multiple mating to avoid sterile males may have been involved in the origin of female remating, it is less likely to maintain remating than sperm choice through competition. We believe that sterile male avoidance could be involved in both the origin and maintenance of female remating in these lizards, but not unless sterile male sperm are at a competitive disadvantage. Without this sort of disadvantage, female fitness functions are not likely to be concave-down.

Support for the evolution of remating in response to genetic incompatibility can be found in several recent empirical papers. Two recent articles comparing the fitness of females with one mate versus two mates (in pseudoscorpions and field crickets respectively; Newcomer et al., 1999; Tregenza and Wedell, 2002) show that females with two mates do better than do females mated twice to the same male, indicating a concave down fitness function. There is also evidence that the sperm of sex-ratio distorter males will experience a competitive disadvantage, allowing the negative effects of these kinds of mates on female fitness to drive the evolution of female remating. Sex-ratio distorter genes act by interfering with the production of Y-bearing sperm, leading to reductions in the numbers of sperm transferred by distorter males (for review, see Haig and Bergstrom, 1995; Presgraves et al., 1997). This reduction in sperm numbers has the effect of reducing sperm displacement (Wu, 1983a) and reducing the ability of distorter males to win in numerical competitions for fertilizations. Consequently, we expect concave-down female fitness functions to be commonly associated with segregation distorters. It remains to be seen whether other forms of intragenomic conflict are likely to produce concave-down fitness functions, and of course, the generality of our model depends on whether or not this is true.

We would like to thank Gerald Borgia for suggesting that females might remate to avoid having single-sex broods. Thanks are also owing to Darryl Gwynne, Luc Bussière, Locke Rowe, Nick Collins, Gerald Wilkinson, John Jaenike, Steve Arnold, Sarah Otto, David Westneat, and several reviewers for commenting on drafts of this paper and for discussion of details of the model. P.D.L. was supported by a grant from the Natural Sciences and Engineering Research Council of Canada to D. Gwynne.

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